THE FACILITATION OF EXPLORATORY BEHAVIOUR AND OTHER BEHAVIOURAL CHANGES BY THE PRESENTATION OF NOVEL OBJECTS TO RATS (*Rattus norvegicus*), CHIMPANZEES (*Pan troglodytes*) AND CARACALS (*Felis caracal*)

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the Degree of
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~ Psychology Department, University of Adelaide ~

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★ ***I dedicate this thesis to my incredible daughter,*** ★
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who is allowing me to re-experience
the beauty and wonder of nature
and the animal kingdom anew,
through the eyes of a child!

SUMMARY

Studies of exploratory behaviour within psychology have been conducted for over a century, and typically take place within the laboratory with rats. Arguably, researchers have failed to choose stimulus configurations that are relevant to conditions likely to be encountered in natural environments. Yet, exploratory behaviour is vital to the survival of wild rodents, felids and primates. Wild rats are subject to predation, which can be avoided if they are familiar with their environment, and familiarity with the home range is maintained through regular patrolling. Wild felids also patrol and monitor their home ranges, and exploratory behaviour forms a part of successful hunting strategies. The many field studies of chimpanzees provide a rich source of material on exploratory behaviour: patrolling, object play, object manipulation and tool-use. However, evidence for reactions to novel objects is usually anecdotal in nature, and this is indeed the case for most species.

Since the 1980s, schedules of reinforcement have largely become tools used to investigate other phenomena. For example, researchers have used them to model general foraging strategies, but have not always manipulated the key variables in an ecologically relevant way. Researchers have also developed more naturalistic open-field style Skinner boxes, which allow more extensive investigations of behaviours (other than the operant response) that occur during schedules of reinforcement. Rats will engage in exploratory behaviour during schedules of intermittent food-reinforcement, if the opportunity is available. Certain schedules coupled with the appropriate environmental conditions increase the probability of adjunctive behaviours occurring. Importantly, the gap between psychological and ecological research is rapidly diminishing.

Exploratory behaviour and other non-instrumental responses have been found to occur in rats run in an open-field style Skinner box during ***fixed-ratio*** (FR30), ***continuous reinforcement*** (CRF) and ***extinction*** sessions. The first two experiments in the present study investigated exploratory (& other) behaviour in the laboratory rat during ***fixed-interval*** (FI60s), ***variable-interval*** (VI60s), ***variable-ratio*** (VR30), and ***differential reinforcement of low rates*** (DRL15-s) schedules of reinforcement (& subsequent ***extinction***).

The larger and more naturalistic open-field environment extended the repertoire of possible responses. Unexpectedly, extinction of ***bar pressing*** did not occur more rapidly in the ***fixed-interval*** groups, and a greater ***resistance to extinction*** in the ***variable-interval*** groups was not apparent (Experiment 1). As expected, extinction of ***bar pressing*** did indeed occur more rapidly in the ***DRL*** groups, with a ***greater resistance to extinction*** apparent for the ***variable-ratio*** groups

(Experiment 2). As expected, more stable post-reinforcement pauses (PRPs) occurred during the predictable ***fixed-interval*** and ***DRL*** sessions (high proportions of total frequency & duration measures occurred during PRPs). The unpredictable ***variable-interval*** and ***variable-ratio*** sessions lacked stable PRPs (low proportions of total frequency & duration measures occurred during PRPs).

Therefore, even in the larger and more naturalistic open-field environment, the predictions concerning PRP development (or lack of development) on these simple schedules were supported. Thus, some features of operant responding (or the stimuli present immediately after reinforcement) appear to be less affected by the size or complexity of the experimental environment. The findings of this study suggest that the development of PRPs on the predictable FI60-s and DRL15-s schedules appears to be a robust phenomenon (unlike ***resistance to extinction***, which appears to be less predictable outside the typical Skinner box). However, it should be pointed out, that a proportion of every behavioural measure did take place outside the PRPs, at other times of non-operant responding throughout the interval.

Experiment 3 investigated exploratory (& other) behaviours in an open-field Skinner box during a ***fixed-interval*** schedule (FI60s), with a concurrently available water source. It was predicted that the chance to explore novel objects might minimize (or even prevent) the occurrence of "aberrant" behaviours, such as polydipsia. The findings indicate that it is difficult to predict which behaviours will occur excessively in the larger and more complex open-field situation if a water source (& the actual bottle itself) is concurrently available. The FI60s schedule resulted in high levels of ***aggressive behaviour*** (directed at the stimulus objects & water bottle), but acceptable levels of ***drinking*** and ***escape-directed behaviour***.

Although it is only possible to speculate upon the existence of schedules of reinforcement in zoo or natural (“wild”) environments, it is possible that they exist, particularly in zoos where animals are fed at fixed times, or in natural environments where animals are provisioned with food. These human-imposed feeding strategies, may also lead to the development of aberrant behaviours. If zoo animals are housed in traditional barren enclosures and fed according to traditional methods (e.g., every 24-hours), then the 24-hour temporal pattern of stereotypic behaviour (e.g., pacing) observed is similar to the adjunctive behaviours (terminal & interim activities) seen in laboratory animals run on non-contingent, intermittent schedules of food-reinforcement. Zoo managers must be aware of the behavioural effects of such predictable non-contingent feeding schedules.

The final preliminary experiments were conducted at Adelaide Zoo (qualitative analysis only). A number of novel objects (food-related & non-food-related) were presented to a group of six chimpanzees, and a different set of objects was presented to a pair of caracals, in an attempt to facilitate exploratory behaviour and reduce aberrant behaviours. The food-related enrichment devices elicited the greatest levels of exploratory responses in both species- all three food "puzzles" for the chimpanzees, and the "flying-fox" style feeder for the caracals.

Not surprisingly, researchers today are opting for a more integrative approach (e.g., ***behaviour systems approach***) to the study of learning and behaviour, combining naturalistic ethological observations with experimental findings, and considering the ecological implications of their findings. Principles of exploratory behaviour can and should be applied to improving both captive environments (e.g., effective behavioural enrichment) and the management of protected areas (e.g., adequate size of the home range for all the populations within a protected areas & effective reintroduction programs). Laboratory studies have already provided valuable information about effects of rearing animals in impoverished or enriched environments. Zoo studies can provide information about behaviour in naturalistic enclosures. Field studies should determine which factors are the most ecologically relevant and which behavioural traits must be performed efficiently. This thesis concludes that a comparative and integrative approach to the study of exploratory (& other) behaviour across environments is both possible and desirable.

TABLE OF CONTENTS

CHAPTER 1 PSYCHOLOGICAL STUDIES OF EXPLORATORY BEHAVIOUR IN ANIMALS

CHAPTER 2 ADAPTIVE SIGNIFICANCE OF EXPLORATORY BEHAVIOUR IN ANIMALS

CHAPTER 2 (continued) **Page**

CHAPTER 3 SCHEDULES OF REINFORCEMENT, ADJUNCTIVE BEHAVIOURS AND EXPLORATORY BEHAVIOUR

CHAPTER 3 (continued) **Page**

CHAPTER 4 LINKING LABORATORY, ZOO AND FIELD RESEARCH: A COMPARATIVE AND INTEGRATIVE APPROACH

CHAPTER 5 PRACTICAL APPLICATIONS OF LABORATORY BASED RESEARCH ON EXPLORATORY BEHAVIOUR

CHAPTER 5 (continued) **Page**

CHAPTER 6 EXPLORATORY BEHAVIOUR IN THE LABORATORY RAT: EXPERIMENT 1: FI60 AND VI60 SCHEDULES OF INTERMITTENT FOOD REINFORCEMENT

CHAPTER 6 (continued) **Page**

CHAPTER 6 (continued) Page

CHAPTER 7 EXPLORATORY BEHAVIOUR IN THE LABORATORY RAT: EXPERIMENT 2: VR30 AND DRL15-s SCHEDULES OF INTERMITTENT FOOD REINFORCEMENT

CHAPTER 7 (continued) **Page**

CHAPTER 8 EXPLORATORY AND OTHER BEHAVIOURS IN THE LABORATORY RAT DURING FIVE SIMPLE SCHEDULES (FR, FI, VI, VR & DRL)

CHAPTER 8 (continued) **Page**

CHAPTER 9 POLYDIPSIA, AGGRESSION AND EXPLORATORY BEHAVIOUR IN THE LABORATORY RAT: EXPERIMENT 3

CHAPTER 9 (continued) **Page**

CHAPTER 9 (continued) **Page**

CHAPTER 10 FACILITATION OF EXPLORATORY BEHAVIOUR AND REDUCTION OF ABERRANT BEHAVIOURS IN CAPTIVE CHIMPANZEES (*Pan troglodytes*) AND CARACALS (*Felis caracal*): PRELIMINARY STUDIES AT ADELAIDE ZOO

CHAPTER 10 (continued) **Page**

CHAPTER 11 OVERVIEW AND CONCLUSIONS

LIST OF TABLES

LIST OF TABLES (continued)

LIST OF TABLES (continued)

LIST OF TABLES (continued)

LIST OF TABLES (continued)

LIST OF TABLES (continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

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LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

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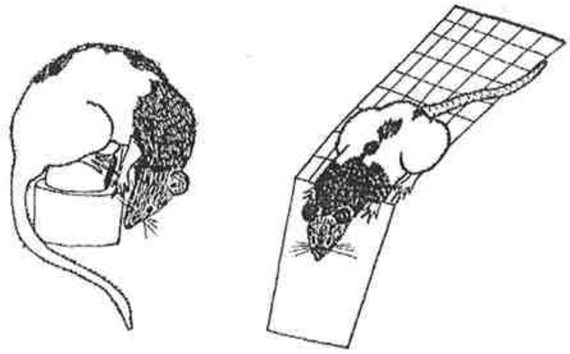
CHAPTER 1

PSYCHOLOGICAL STUDIES OF EXPLORATORY BEHAVIOUR IN ANIMALS



1.1 GENERAL OVERVIEW OF STUDIES

The earliest studies of exploratory behaviour within psychology can be traced back to Small's (1899) study of young white rats (Russell, 1983). Some research into "stimulation-searching" behaviour took place in the 1920s, when it was discovered that rats would move across electrified grids in an attempt to explore novel areas (Dashiell, 1925; Nissen, 1930). The systematic investigation of exploration, however, was largely ignored until the 1950s. For the first half of this century, Darwin's influential theory of evolution by natural selection, together with the rise of behaviourism, led psychologists to investigate the more obvious "survival behaviours". These included eating, drinking and reproductive behaviours, which were crucial to the survival of an animal. The biological and adaptive significance of these behaviours were recognised by psychologists during this early period.

The adaptive significance of exploration, on the other hand, was not realised until relatively recently. Previously, exploration was primarily viewed as a series of undirected meanderings, without a clear function or adaptive role. As a consequence, exploratory behaviour was considered to be of little importance, and set aside as unworthy of further research (Fowler, 1965).

A revival of interest in exploration and curiosity, within psychology, occurred in the 1950's, when: "the concept of an exploratory drive first tumbled into the psychological literature" (Fowler, 1965). Russell (1983) attributes this renewed concern with exploratory behaviour to the fact that accounting for this behaviour posed problems for the prevalent theories centered on drive motivation, and drive reduction.

Two main approaches to the study of exploration have developed concurrently since then, with little interchange between the two. These are the psychological theory-oriented approach; and the more naturalistic, ethological approach. Russell (1983) criticises the psychological approach for merely viewing animals as laboratory "preparations", which conveniently exhibit a: "theoretically interesting behavioural phenomenon" (p.22). He favours the ethological approaches, which stress the importance of studying exploration as an adaptive behaviour, within natural habitats. Such ethologically based studies are exemplified by the work of Australian researchers, such as Barnett (1958), Barnett and Cowan (1976), and Cowan (1983). Studies monitoring the exploratory behaviour of wild rodents were started by a group of zoologists primarily interested in rodent pest control. These eventually led to a series of systematic laboratory studies, contrasting the exploration (approach/avoidance patterns) of wild and laboratory rodents (Cowan, 1983).

Russell (1983) further criticises the psychological approach to exploration for its failure to expand the selection of species examined. The traditional few are adhered to: laboratory rats, some other rodents, birds and primates. In addition, the variety of different environments used are minimal, and the range of behavioural measures narrow. Yet, as early as 1924, Warden was attempting to develop an experimental method and apparatus that would allow psychologists to make cross-species comparisons in "incentive-drive indices", including the exploratory drive (Warden, 1931). By 1931, Warden and Nissen were planning to standardise this apparatus, so that it could be used on a number of species, including dogs, cats, raccoons and monkeys (p.48). This early work on exploratory behaviour will be discussed in the next section. It is worthy of note, since Warden (1931) and his coworker's aim to allow cross-species comparisons was quite far-sighted, and the experimental results show that rats will even cross electrified grids in order to engage in exploratory behaviour.

1.2 SMALL'S (1899) OBSERVATIONS OF EXPLORATORY BEHAVIOUR IN YOUNG WHITE RATS

Curiosity and play were two of the behaviours recorded by Small (1899) in his "psychic development" study of white rats. Five rats from the same litter were observed daily from birth to four weeks of age, with additional interesting observations of other rats included over a two-year period. Small's use of terminology and concepts, almost a century later, seem quaint, whimsical and quite "unscientific". He talks about the "psychic make-up (emotional and intellectual traits)" of rats, and of the aim to work towards a "*comparative embryology* of the soul" (p.80). Yet, in the same work, Small (1899) deals with very current issues, such as, the adaptive significance of behaviours in natural or "wild" conditions. He recognises that a biological function or "necessity" underlies the behaviours observed in a laboratory setting. He also suggests that the fundamental "traits" or behaviours are exhibited in both natural and artificial (laboratory) environments. These fundamental behaviours: "persist with undiminished vigor through the vicissitudes of an environment different in all its factors from that of the free wild life in which his psychic nexus was woven in the loom of necessity" (Small, 1899, p.100).

Small (1899) draws a distinction between "emotional" and "intellectual" traits in rats, and includes fear or timidity in the former category, and curiosity in the latter. He maintains that the precursor or "premonition" of curiosity, in the form of "restlessness", is seen by the time rats can move freely, and "by the time they are three weeks old it is inordinate and overbalances fear" (Small, 1899, p.99). He equates curiosity with "boldness" as described by natural history writers of the time. Small (1899) also suggests, that the "psychic life" of adult rats "oscillates" between the states of fear and curiosity (or perhaps neophobia & neophilia).

Small (1899) considers the adaptive significance of curiosity, and suggests that curiosity or exploratory behaviour may serve a dual purpose. "It may be supposed that a large part of their inquisitiveness is in the service of nutrition; but the biological necessity of safe surroundings is not less imperative. There is certainly a double root to this trait" (Small, 1899, p.100).

At about the same time that Small was investigating exploratory behaviour, another psychologist, Groos (1898) was studying play. He too was aware of the importance of taking the "biological significance" of the behaviour into account. Groos (1898) recognised that play was commonly perceived as an outlet for "surplus energy", when animals or humans were feeling: "particularly cheerful, healthy and strong" (p.xix). However, Groos (1898) points out that there is an important biological basis, since: "the play of young animals serves to fit them for the tasks of later life" (p.xix). He even goes so far as to suggest that: "perhaps *the very existence of youth is due in part to the necessity for play*; the animal does not play because he is young, he has a period of youth because he must play" (Groos, 1898, p.xx). With respect to curiosity (especially towards objects) in animals, Groos (1898) suggests that it is the "only purely intellectual form of playfulness...The necessity for mental exercise is the primary reason for this kind of playfulness, added to the increase in knowledge…it aids in the preservation of the species" (p.214). Like Small (1899), Groos (1898) uses some quaint terminology (love plays, coquetry of females), but he also focuses on the important themes of natural selection, biological significance and adaptation. Thus, it is somewhat surprising that today's psychologists are still suggesting that we must take the adaptive significance of behaviours such as exploration and play into account, as though it were a fairly new concept (Russell, 1983).

1.3 AN EARLY STUDY OF EXPLORATORY BEHAVIOUR: EXPLORATION BEFORE EATING IN FOOD-DEPRIVED RATS

In 1925, Dashiell chose exploratory behaviour as a means of quantitatively demonstrating an animal drive. He used white rats as subjects, because they could be easily controlled experimentally (compared to humans). He states, that: "an inner organic condition may serve as a drive to produce exploratory behavior of a fairly continuous sort that is terminated typically only when a particular stimulus appears to arouse an end-reaction" (p.205).

Dashiell chose hunger as the "incentive" or drive, and expected food-deprived rats to show greater amounts of exploratory behaviour than the satiated control group rats. It is important to note that he only measured exploratory behaviour as total locomotor activity (number of blocks of the maze entered). The apparatus was a modified maze, with a cork floor marked off into blocks, black galvanised iron walls, and a wire mesh top. Satiated and food-deprived rats were each given sixty seconds in the maze, and the number of blocks entered was recorded. As Dashiell (1925) points out, both groups explored the box, since it was a novel environment. However, more "restless activity" was observed in the food-deprived rats, with each rat on average entering 42.9 blocks, compared with an average of 26.7 blocks in the satiated group.

Whilst the findings of this study are interesting, it is one of Dashiell's (1925) concluding remarks that is most interesting:

> "One who has handled white rats knows well enough that when these animals are returned to a renovated nest box they pay little or no attention to food placed there even though unfed for twenty-four hours, but give themselves up for a while to explorations over and through their new bedding. Whatever the finally assigned status for the "instinct of curiosity", it is undeniable that novelty in the environment is pretty sure to awaken "curious" behavior" (Dashiell, 1925, p.208).

This is hardly surprising, since from an adaptive significance point of view, if changes have occurred in a rat's environment, these should be investigated so that potential danger can be avoided. A hungry rat would only be expected to eat if in a safe situation, or its very survival could be at risk.

1.4 AN EARLY STUDY OF EXPLORATORY BEHAVIOUR: CROSSING AN ELECTRIFIED GRID IN ORDER TO EXPLORE

Nissen (1930) states that the: “tremendous amount of activity expended by rats in "exploring" a novel situation or environment can hardly escape the notice of anyone working with these rodents in the laboratory” and that exploratory or “curious” behaviour of rats was a “factor not of the least importance in determining the widespread adoption of these animals for laboratory use, especially in studies of learning” (p.361). He points out that few studies specifically investigate or measure exploratory behaviour, despite the fact that rats had been observed to engage in this behaviour before eating (when food-deprived) and before copulation (when “sexually vigorous”). That is, rats will explore their environment before satisfying other primary needs, such as, hunger. “Apparently a novel situation - one which does not frighten the animal - provokes exploration, the expression of other drives...being temporarily deferred…exploration is more than a mere general activity drive which finds its outlet in the most common activities in the repertory of the animal, such as running, climbing, sniffing, and moving the vibrissae” (Nissen, 1930, p.362).

Nissen (1930) argues that if exploration is a drive, then rats could be expected repeatedly to “overcome a certain obstruction in order to explore” (p.362). That is, they would cross an electrified grid, in order to reach a novel and “interesting” situation. On the other hand, if exploratory behaviour is just general activity, Nissen (1930) maintains that it would be unlikely that a rat “would repeatedly overcome its negative reaction to such an obstacle or obstruction in order to reach an external situation which is especially favorable to exploration” (p.362). Nissen’s (1930) work on exploratory behaviour, was part of a series of animal motivation studies run by Professor Warden and student coworkers at Columbia University, with white (albino) rats serving as subjects. The exploratory “drive” was part of the series of drives investigated (along with hunger, thirst, sex & maternal drive), using the Columbia Obstruction Method.

The Obstruction Apparatus consisted of an entrance compartment, an adjoining electric grid compartment (the “obstruction”), a third “incentive reaction compartment” and then the compartment, which provided the incentive to explore. This “exploratory incentive compartment” was based on a design used by Dashiell (1925), which provided the rats with a number of pathways and corners, objects (blocks of wood, corks, & a small rubber mat), two walls made of wire mesh, and a section with wood shavings piled up to the top of the walls.

Nissen (1930) suggests that these items tend to "stimulate" exploratory behaviour in rats. The incentive compartment used to investigate the exploratory drive was larger and more complex than the one used for the other drives, to ensure that the incentive was great enough to elicit exploratory behaviour. Thus, the experimental method and apparatus presented the rats with a shock as the obstruction, and the exploration compartment as the incentive, in an attempt to: "determine the influence of each in the measurement of "exploratory" drive behavior" (Warden & Nissen, 1931, p.35).

The 20 albino rats used in Nissen's (1930) study were males that were group housed with females until approximately 150 days of age, before being removed 35 days before testing, and group housed with about six other males. In order to ensure that the rats were not deprived of the opportunity to exercise, they were housed in large cages (5900 cubic inches capacity). They also had access to food and water at all times. Thus, the hunger, thirst, and "activity" drives were considered "satisfied" by Nissen (1930). The experiments were usually run between 9 and 11 p.m.

Nissen (1930) found that during the twenty-minute test period (following preliminary runs), the 20 rats made a total of 120 crossings (an average of six crossings per rat, but ranging from 1-23) of the electrified grid to reach the "exploration" compartment, with 40% of these crossings occurring in the first five minutes. However, 16.7% of crossings were still taking place in the last five minutes. Nissen (1930) suggests that rats provided with the opportunity to engage in exploration, crossed the electrified grid more often than the control groups who were provided with incentives of low exploratory "value" (p.374). That is, they were given a food incentive (rats not food-deprived), a water incentive (rats not water-deprived), or an empty compartment (rats at a "period of maximum sexual vigour", p.369). He concludes that "exploration is a definite form of dynamic behavior similar to the hunger, thirst, sex, and maternal drives" (Nissen, 1930, p.372).

1.5 MAJOR THEORETICAL ACCOUNTS OF EXPLORATION

Psychological studies of exploration flourished in the 1950s and early 1960s. Many of these early studies (*e.g.*, Harlow, 1953; Montgomery, 1954) concentrated on "investigatory" or "manipulatory" behaviours, which were seen to be dependent upon a "non-homeostatic...exteroceptively aroused" exploratory drive (Fowler, 1965, p.20). These studies led to an extension of ***general drive theory***. That is, exploratory behaviour was held to have its own "drive", which would satiate some "need" state. A number of difficulties arose when exploration was included in the classical ***drive theory***. Fowler (1965) states that the concept of an exploratory drive was ill defined and, more importantly, the concept was described by experimental findings, which were then accounted for by the concept in a circular fashion. Such a criticism leveled at the drive theory of exploration, was framed by a contemporary drive theorist, Brown (1953), who stated:

> "...the presence of a drive to explore is sometimes inferred from, and at the same time used to explain, behavior of moving from one place to another, especially if there is no other apparent reason for the movement. The postulation of an exploratory drive in this way is quite circular, and therefore of questionable worth as a scientific explanation" (Fowler, 1965, p.21).

Hull's formalised ***drive reduction theory*** (1943, 1952), which recognised drive reduction as the mechanism of reinforcement, was very influential in the 1940s and 1950s. He postulated that any response occurring in close temporal contiguity to a reduced drive would become reinforced. Consequently, exploration was considered a drive that could be reduced and reinforced. Berlyne (1950) maintained that novel stimuli would elicit the "exteroceptively aroused" exploratory drive. This drive would be reduced by exploratory behaviour and prolonged contact with the stimuli, which would, in turn, reinforce these exploratory behaviours. This theory lacked strong empirical support, and could not account for findings, which showed that animals would learn an instrumental response with a simple stimulus change as the only reward (*e.g.*, Butler, 1953; Myers & Miller, 1954).

Another set of theories of exploration emerged in the 1950s. These were the ***boredom theories***, which suggested that exploration was elicited by a boredom drive. Myers and Miller (1954) postulate that the boredom drive could be: "reduced by sensory variety, freedom of action...and that such drive reduction is the reinforcement involved in learning for `exploratory', manipulatory and exercise rewards" (p.434). As with the other theories, it was found to be an inadequate account for the experimental findings. Inglis (1983) points out, that this theory does not incorporate a "curiosity" component, or explain the control exerted by a novel stimulus. It also cannot account for findings that show that extreme novelty is aversive, or that sensory impoverishment leads to reduced levels of stimulus seeking.

A major theory of exploration that was again formulated in the 1950s, but has remained popular until recently, is the ***optimal arousal theory***. Hebb (1955) found that a relationship exists between an animal's performance and its level of arousal. He suggested, that this relationship was best described by an "inverted U" curve, which illustrates the fact, that animals perform best at intermediate levels of arousal. If arousal is too low, the animal's performance suffers as a result of low alertness or interest. On the other hand, if arousal is too high, the performance is interrupted by anxiety or emotional disturbances. Leuba (1955) used this evidence to support the notion that, within learning theory, drive reduction is only one aspect of a more general principle of "optimal stimulation". Accordingly, animals tend to learn exploratory (or other) behaviours, which lead to an optimal level of stimulation.

The ***optimal arousal theory*** has been used to account for the effects of novelty, and for the habituation of exploration. A number of researchers have discussed habituation and novelty, including Dember, Earl and Paradise (1957), and Montgomery (1953). Without a doubt, the most prolific, extensive and influential coverage of novelty, habituation and exploration is the work of Berlyne (1950, 1955, & 1960). He found that exploration was most readily elicited by moderately complex and novel objects. Over time or repeated exposures, habituation occurs, which results in decreased exploration. That is, repeated contact or familiarisation with a novel stimulus leads to a decrease in the sensory stimulation impact of that stimulus. Once a stimulus loses its sensory impact, or ability to arouse the animal, less exploration is produced. If a stimulus is novel and too complex, it may be over-arousing, and consequently, avoided by the animal. Over time and repeated exposures, habituation would begin to take effect, the stimulus would decrease in arousal to an optimal level, and the animal would begin thoroughly to explore it. Berlyne (1960) emphasises the strong influence that novelty can exert upon an animal by stating that the tendency to explore often overcomes feeding in food-deprived animals if novel stimuli are present.

Berlyne (1960) and Welker (1961) maintain that a stimulus can regain novelty (not to the same degree as on the first exposure) and sensory impact, if the animal is separated from the stimulus for a period of time. As a result, an optimal level of arousal can again be reached. Baldwin and Baldwin (1977, 1978) provide a more recent formulation of the ***optimal arousal theory***. They use it to account for exploration in primates, restating that over-stimulation is aversive, whilst moderate stimulation is reinforcing.

Recently, the theoretical emphasis has shifted from the drive, drive-reduction and optimal arousal theories to a more cognitive stance (Morris, 1983). Psychologists have also realised the need for more "biologically-oriented" studies, which examine the adaptive significance of exploration in more "natural" environments:

> "Exploratory behaviour is all pervasive - because of its nature, the role of exploratory behaviour, its function, cannot be evaluated in isolation from other aspects of behaviour and ecology" (Cowan, 1983, p.169).

There is still no adequate generally agreed upon theory of exploration. Psychological studies of exploration have begun to follow different lines, suggesting an overall integrated theory of exploration is still some way off. Ecologically oriented studies, such as those carried out and discussed by Cowan (1983), are looking at exploration in rodents in the wild and in the laboratory. Others are physiologically oriented, employing lesion and drug studies to examine the importance of the hippocampus, which “is intimately involved in spatial memory” and “thereby plays a role in structuring normal exploration” (Morris, 1983, p.141). Yet another orientation is exemplified by Toates (1983). He interprets exploration in terms of theories of incentive and cognition, placing emphasis upon cognitive, or spatial maps (which can be traced back to Tolman, 1932). Toates (1983) favours an integration of the theoretical positions adopted by Tolman (1932) and Hull (1952), defining his orientation as “cognitive-behaviourism”, a combination of cybernetics and behaviourism.

1.6 DEFINING AND CLASSIFYING EXPLORATORY BEHAVIOUR

Berlyne (1960) identified most of the categories of exploratory behaviour. However, his early work largely ignored the adaptive significance of the various types of exploratory behaviour, which led Russell (1983) to reassess these categories by taking adaptive considerations into account.

1.6.1 EXTRINSIC AND INTRINSIC EXPLORATION

Birke and Archer (1983) suggest that ***intrinsic exploration*** is now usually referred to as “exploration”, and ***extrinsic exploration*** as “search”, and in many species (not laboratory rats) the two may be synonymous. ***Extrinsic exploration*** involves the organism “obtaining information about a conventional reinforcers or other biologically significant event”, for example, observing responses that provide information about food availability (Russell, 1983, p.25). ***Extrinsic exploration*** has typically been readily explained by primary drive theories of motivation, and as a result, Russell (1983) suggests that it has been of less interest to psychologists. ***Intrinsic exploration***, on the other hand, refers to: “exploration directed at stimuli of little apparent biological consequence” (Russell, 1983, p.25). Psychological studies of this category typically observe the exploratory responses of animals in a maze or arena, devoid of conventional reinforcers, and with the animal not under any obvious primary drive state (Russell, 1983).

Russell (1983) questions the validity of this distinction between ***extrinsic*** and ***intrinsic exploration***, from an ecological or adaptive point of view. In natural habitats, any change in the environment may be biologically significant. To any animal living in its natural habitat, information concerning cover, escape routes and sleeping sites (not primary reinforcers) is just as important for survival as information about food and water (primary reinforcers). That is, topographical information about the environment may not relate directly to conventional reinforcers, but is vital to an animal's survival (Russell, 1983).

1.6.2 INSPECTIVE AND INQUISITIVE EXPLORATION

Berlyne (1960) also distinguished between ***inspective*** and ***inquisitive exploration***. ***Inspective exploration*** involves an organism "responding *to* an environmental change", by "increased contact, through approach and proximal interaction, with changes in the organism's immediate stimulus field that are acting on its receptors" (Russell, 1983, p.26). By contrast, ***inquisitive exploration*** involves "responding *for* a change" by bringing "about contact with changes that are not already present in the immediate stimulus field and involves seeking out or producing changes" (Russell, 1983, p.26). Both types of exploration allow the animal to monitor and familiarise itself with its environment, which Russell (1983) points out is adaptive. If a rat bar-presses to turn on a light in a dark Skinner box, then it is responding *for* a change (*i.e.*, ***inquisitive exploration***), as well as, providing conditions that enhance its ability visually to explore the box. If a rat explores changes to its current environment, or an experimental box, where it has encountered changes before, then it is responding *to* changes (*i.e.*, ***inspective exploration***), just as a commensal rat might patrol its natural environment.

Russell (1983) stresses that the adaptive significance of ***inspective exploration*** is very clear. Changes in an animal's environment must be recognised and monitored, since these changes may enhance or threaten the animal's survival. However, by maintaining a familiar environment, through regular patrolling of the home range, the level of stimulation or stimulus change may be predictable, constant or low. Russell (1983) suggests that this in turn leads to the animal seeking out stimulus change or a higher level of stimulation. ***Inquisitive exploration***: "involves self-induced environmental changes" (Russell, 1983, p.26). Such behaviour is also adaptively significant, since it allows the animal to learn about and effectively master and deal with its environment. Thus, "exploration may actually facilitate the development of new, innovative behaviour patterns that permit exploitation of the environment in new ways" (Russell, 1983, p.27). With respect to primates in particular (& other animals), this is linked to tool-use, which allows the animals efficiently to exploit their environments. Selection pressures have resulted in increased sensorimotor skills, the development of new patterns of tool-use, and the "motivation to seek out and investigate new objects for their potential as tools" (Russell, 1983).

1.6.3 SPECIFIC AND DIVERSIVE EXPLORATION

A further distinction made by Berlyne (1960), is between ***specific*** and ***diversive exploration***. As its name suggests, ***specific exploration*** involves the animal gaining information about a ***specific*** change in an object or event. ***Diversive exploration***, on the other hand, involves the animal obtaining information or stimulus change from any (***not specific***) source in its environment (Russell, 1983). The two are considered "motivationally distinct", and have mainly been studied in humans. Based on Berlyne's (1960) work, Russell (1983, p.27) maintains that "curiosity" and ***specific exploration*** appear to be linked ("increased arousal generated by lack of information about a specific stimulus change"). Similarly, "boredom" and ***diversive exploration*** appear to be linked ("increased arousal stemming from a lack of stimulus change of any sort"). The underlying adaptive significance of both types of exploratory behaviour is similar to that discussed in the previous section. That is, ***specific exploration*** involves exploring changes and maintaining familiarity, whilst ***diversive exploration*** involves seeking out changes, which can lead to learning of skills and mastery of challenges provided by the environment (Russell, 1983).

1.7 EXPLORATORY BEHAVIOUR AND PLAY

Einon (1983) states that although a number of researchers (*e.g.*, Welker, 1961) have suggested that it is difficult to differentiate between exploration and play, such researchers: "are in fact asking if we can distinguish *exploratory manipulation* of objects from *playful manipulation* of objects" (p.221). She suggests, that play and exploration are certainly not equivalent behaviours, with non-primate mammal exploratory behaviour and "play" being very different, and most categories of primate play and exploration being quite distinct. Some categories of play that are not related to exploration include rough and tumble "fighting", play chasing, predatory and sexual play (in animals), and locomotor play (to name a few).

Clearly, the main confusion lies in the distinction between manipulative or object-play and exploration of objects. Einon (1983) points out, that exploration appears to precede play (ontogenetically & phylogenetically), and may appear more frequently in adults, when compared with frequency of play (p.222). With respect to defining behavioural categories, Einon (1983) suggests, that there are: "things we hate to classify, behaviour we see as all fuzz and no hard centre: play is one such behaviour, exploration is another" (p.210).

Having determined that object play and object exploration may be difficult to separate, Einon (1983) goes on to suggest, that true object play (or playful manipulation of objects) is really only observed in the great apes and humans. Zoo animals, such as rhinos and giant pandas have reportedly engaged in object play, but Einon (1983) stresses that such behaviour is not observed in their wild counterparts, and thus may be attributed to captive conditions (since there is more time & opportunity available). Captive and domesticated carnivores (especially young cats & dogs) demonstrate "predatory" object-play, such as, "predation" of ping-pong balls by kittens (Einon, 1983, p.226). Such object play is uncommon in other carnivores. Captive primates commonly engage in object manipulatory play, but with the exception of apes, it is rarely observed in wild primates (Einon, 1983).

Nunnally and Lemond (1973) suggest that when a novel object is first encountered by an organism, attention and exploratory behaviour are initially elicited, followed by play behaviour, and then further searching, in a continuous cycle (Hughes, 1983). A diagramatic representation of the exploration-play cycle is shown in Figure 1. Thus, with respect to novel objects, exploratory behaviour and play appear to be connected, with the former preceding the latter.

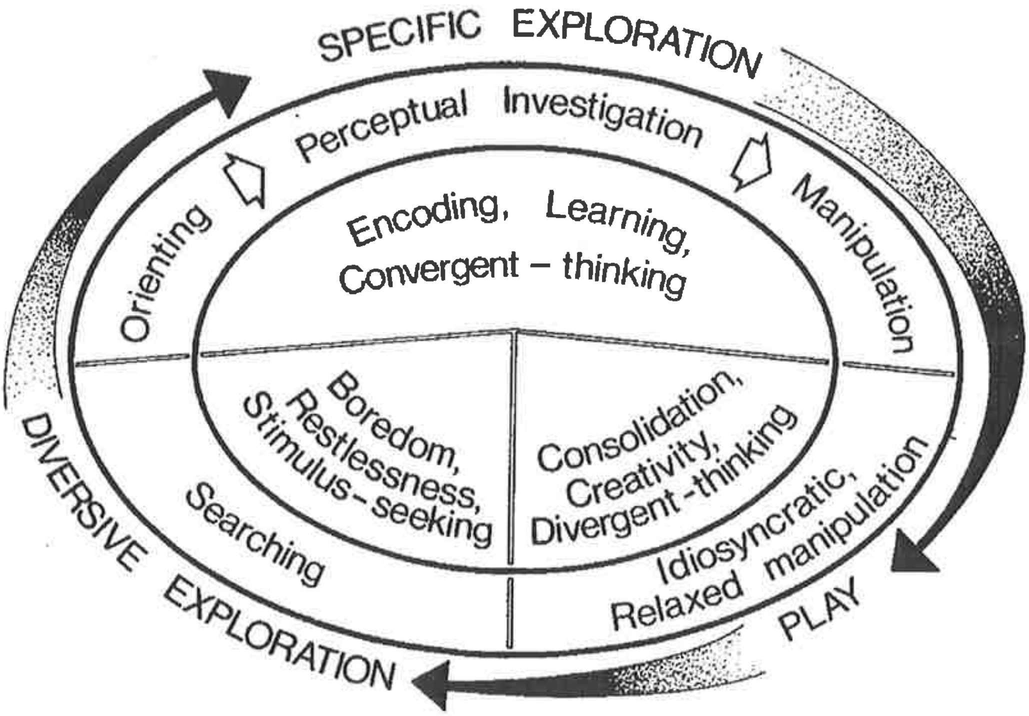


Figure 1.1. The exploration-play cycle, with the inner circle most relevant for humans and the Great Apes (Figure 10.1 in Hughes, 1983, p.231).

Aldis (1975) maintains that object play is usually quite distinct from object exploration and manipulation. "If an animal spends a great deal of time sniffing an object, he is obviously exploring it and not playing with it" (Aldis, 1975, pp.69-70). In primates there are typically three stages of object exploration. Firstly, the object is visually inspected at a distance. Secondly, the object is sniffed and cautiously patted or fingered. Finally, the object is mouthed and manipulated.

The initial approach to an object is one of the factors that Aldis (1975) proposes as a differentiating factor between object play and object exploration and manipulation. These factors are laid out in Table 1.1. He does, however, recognise that some object interactions combine exploration, manipulation and play. For example, if an animal encounters a novel object, it may initially explore the object, then manipulate it (some transitionary interactions may be difficult to label as exploration or play), and finally play vigorously with the object. Further, the gnawing of an object by a carnivore may be play (mouthing) or exploration (taste & texture). Similarly, the bending and twisting of an object by a primate may be play (wrestling) or exploration (manipulation). However, overall, Aldis (1975) stresses that the distinction between object play and exploration is very clear.

Hole and Einon (1984, p.96) maintain that most researchers have classified animal play into three categories:

- ***Object play***, which is "either of a manipulative-cum-investigative kind or by a young predator with prey surrogates"
- ***Locomotor play***, such as "running, frisking, and gambolling"
- ***Social play***, which usually involves "play-fighting and play-chasing".

These researchers quickly point out that most instances of ***object play*** in rodents are more likely to involve exploratory behaviours. Only the other two forms of play could "unequivocally" be considered to occur in rodents (Hole & Einon, 1984, p.96). For higher primates, on the other hand, object play "forms a significant part of the behavioural repertoire" (Smith & Simon, 1984, p.199). Smith and Simon (1984) maintain that it can aid in the development of tool-using skills, and may facilitate learning of new behaviours or "proto-cultural" traditions in chimpanzees.

According to Hole and Einon (1984), the labeling of juvenile behaviours, that serve no obvious function as "play" is "legitimate, but not informative" (p.113). They suggest that researchers tend to overuse the term "play" and lump different types of "playful" behaviour together, which only leads to further confusion. In fact, Hole and Einon (1984) posit that only rough-and-tumble play and play-chase fit the typical "play" criteria (*i.e.*, no immediate function, occur in an "amicable" context, & employ unique behaviour patterns). They conclude that it is unlikely that the term "play" can be adequately defined, but researchers should accurately describe behaviours considered to be "playful".

Table 1.1
The eight main distinguishing characteristics of solitary object play and object exploration as proposed by Aldis (1975).

DISTINGUISHING FACTORS	OBJECT PLAY	SERIOUS EXPLORATION AND MANIPULATION OF OBJECTS
(1) Function		
(a) Immediate	♦ Increases ***effector activity***	♦ Increases ***receptor activity*** or contact with different facets of object
(b) Long-term	♦ Helps develop strengths & skills useful in adult life	♦ Acquire information about the environment (learn about food sources & which stimuli are harmless or dangerous)
(2) Initial approach	♦ Usually approach object in a direct & relaxed manner	♦ If object is novel, it is approached slowly, or alternate between approach/retreat ♦ Body is tense & there are changes in the autonomic nervous system
(3) Most responses	♦ most are predator or play fighting responses (*i.e.*, little mouthing, more tugging & shaking, seizure & holding - some wrestling, throwing or pawing rolling object, stalking & pawing - charging if object moves, like play with captured prey)	♦ most are related to receptor contact (look, smell, feel, taste *etc*) ♦ several sensory modalities are used
(4) Response intensity	♦ relaxed muscle tone ♦ like play with species members ♦ object play is vigorous ♦ chasing occurs at speed ♦ seizing & wrestling is rapid & forceful	♦ more tense muscle tone ♦ not vigorous ♦ caution can lower intensity even further
(5) Temporal patterns		
(a) Duration and frequency	♦ Occurs in bouts ♦ Longer sessions made up of several bouts ♦ Return periodically to object after pauses between bouts	♦ Novel object explored continuously & then ignored if it has no function ♦ Not returned to periodically (may be passed over during periodic reconnaissance of a familiar area)
(b) Response sequence	♦ Usually variable ♦ Constantly changing pattern of interactions (stalk, charge, flee, seize, mouth)	♦ Tends to follow a fixed pattern
(c) Preceding or following events	♦ Often follows play with species members	♦ May occur during general reconnaissance of an area
(6) Play signals	♦ May accompany play (e.g. dog wagging tail & panting)	♦ Do not occur
(7) Eliciting stimuli	♦ Play is "controlled" by movement ♦ Novelty may play a secondary role	♦ Stimuli that lead to food ♦ Novel or potentially dangerous stimuli
(8) Learning	♦ Occurs by ***response differentiation*** ♦ Proprioceptive stimuli are differentiated on the basis of selective reinforcement	♦ In the form of ***stimulus-discrimination*** ♦ Certain exteroceptive stimuli in the environment lead to various reinforcers (*e.g.*, food or danger)

Burghardt (1984) presents five categories of play and investigative behaviour in decreasing order of "apparent topographic complexity" (p.6):

Social play
Object play
Locomotor play

Curiosity
Exploration

Current researchers interested in exploratory behaviour do not typically refer to the term "curiosity" any longer. However, Burghardt (1984) uses "curiosity" to refer to object-directed exploration, which he suggests is "structurally akin to object play" (p.7). He uses the term "exploration" to refer to locomotor exploration, which is "structurally akin" to locomotor play. Unlike Aldis (1975), Burghardt (1984) maintains that the distinction between play and exploration is not clear, especially early in ontogeny. Both involve learning and have delayed benefits, and are thus "functionally akin". However, whilst curiosity, exploration and investigation (as defined by Burghardt, 1984) occur in reptiles, mammals and birds, the play observed in reptiles is different to mammal play (& difficult to identify).

Hole and Einon (1984) point out that if rats are isolated prior to sexual maturity and thus deprived of rough-and-tumble play (e.g., between 20 & 45 days of age), they may be more active, slower to habituate, slower to extinguish, and slower to reverse previously learned discriminations. Thus, isolation-induced effects may impact on the behaviours observed in a laboratory situation.

1.8 STIMULUS DETERMINANTS OF EXPLORATORY BEHAVIOUR

Typically, the two most commonly used descriptions of stimuli or stimulus configurations are the terms "novelty" and "complexity" (Birke & Archer, 1983). Both are difficult to define and somewhat arbitrary in terms of the animal's own experiences and conditions likely to be faced in natural environments. That is, outside the laboratory, these terms may have little adaptive significance or relevance (Birke & Archer, 1983).

1.8.1 STIMULUS NOVELTY

Novelty "has to be defined with respect to the animal's own past experiences", which may be difficult, since the stimuli chosen as novel are based upon "expectations of the type of stimuli that the animal is likely to have encountered" (Birke & Archer, 1983, p.9). That is, the experimenter must make an informed guess as to what would or would not have been encountered or experienced to date. As Birke and Archer (1983) point out, this is not difficult under laboratory conditions, where the complete history of the animal is known, but it poses a major challenge if the subjects are wild or feral animals. They also assert that any distinctions made between stimuli in terms of "absolute" or "relative" novelty, or other terms used to imply that some stimuli are completely novel, is arbitrary, since "it is extremely unlikely that the mature organism ever meets *entirely* new stimuli" (Birke & Archer, 1983, p.10).

Birke and Archer (1983) stress that exploratory behaviour is not the only behaviour that is elicited by novel stimuli, and therefore "novelty" cannot be used to define "exploration". They suggest that it would be more accurate to state that animals appear to seek out "stimulus change" rather than "novelty". If "novelty" is to be defined, it must be in terms of "what the animal actually does" and this depends on the nature of the stimulus and context in which it occurs, as well as the animal's physiological and behavioural state at the time of encounter (Birke & Archer, 1983, p.10). With respect to responses to novelty, there are few comparative studies, despite the fact that different species are certain to react in different ways. The environmental context in which a "novel" stimulus is encountered (novel or familiar environment), and the presence or absence of conspecifics (*e.g.*, social facilitation may play a role) appear to be very important in determining an animal's response (Birke & Archer, 1983).

Sheldon (1969) investigated whether rats showed a preference for novel or familiar stimuli. Testing took place in an unfamiliar environment (a raised and modified Y-runway), with a choice of approaching a familiar object (ceramic figure) or a "comparable" novel object (metal locket, scrub cloth, plastic block, garden label, mousetrap, spoons, postcard, fish), suspended in the goal boxes. When the environment was unfamiliar (first trial or exposure), the rats preferred the familiar object. However, once the rats habituated to the environment (on average after a cumulative exposure of eight minutes), they preferred the novel stimuli. The novel objects were changed daily. Sheldon (1969) undertook a further study, which used eight different types of stimuli and five different environments, and found the same effect. That is, the familiarity (novel or familiar) of the environment has an effect upon a rat's preference for familiar or novel objects.

1.8.1.1 RESPONSES TO NOVEL ENVIRONMENTS

Studies of responses to novel environments often use locomotion as a measure of exploration. However, although an "active animal is likely to acquire information about its environment", locomotion around a novel environment may actually represent an attempt to escape (Birke & Archer, 1983, p.4). Furthermore, an animal that is rapidly moving around an enclosure may be paying less attention to environmental cues than a stationary animal that is systematically orienting towards features of the environment and sniffing the air. Activity levels are also affected by other factors, such as hormonal state, and food or water deprivation (Birke & Archer, 1983).

Birke and Archer (1983) point out that studies which sample a wider range of behaviours (*i.e.*, not just locomotion) are likely to incorporate other forms of exploratory behaviour. They suggests that rearing is one such exploratory response often found in rodents, which in the past has been used as a measure of "excitability level", since it also correlates positively with grooming, defensive and sexual reactions (but should not be viewed as synonymous with general drive). However, like activity levels (locomotion), responsiveness to stimuli (excitability) is also affected by other factors, such as hormonal state, food deprivation, and early experience (*i.e.*, whether animals are reared in enriched or impoverished environments).

Perhaps the biggest shortcoming of studies of novelty, is that most do not systematically investigate the different responses to stimuli in unfamiliar and familiar surroundings. That is, they often present novel stimuli in a novel apparatus, thus making it difficult to determine which cues the animal is responding to (a better alternative is to present novel stimuli in a relatively familiar environment). As Birke and Archer (1983) stress, animals may respond differently to the same stimuli if presented in a novel situation, when compared to a familiar situation. Commensal rats (*Rattus rattus*) have been found to avoid novel objects if they were introduced into the home cage, but actively investigated objects that were already present when the rats were first introduced (Cowan, 1976). In natural environments, animals would be expected to initially avoid new objects appearing in their familiar home range (may be traps or dangerous), whereas new objects in a new environment would just be one of the features that would need to be systematically investigated.

1.8.1.2 RESPONSES TO NOVEL STIMULI

Not all animals respond to novel or conspicuous stimuli in the same way, but may exhibit orienting responses, or freeze, flee, attack, scent-mark, sniff at or even pick up an object (Birke & Archer, 1983). A number of factors may influence the response- species of animal, prior experience with similar objects, and type of stimulus. Birke and Archer (1983) posit that orienting and direct investigation are the most common exploratory behaviours directed towards novel objects.

Berlyne (1960) refers to orienting responses as "passive exploration". Birke and Archer (1983) define them as the "initial attentional changes in response to a novel stimulus" (p.6). Typically, the animal turns its head towards the stimulus, brings the sense organs to bear upon it, thus investigating or exploring the stimulus. However, Birke and Archer (1983) suggest that some studies encompass a number of stages within this "orienting response"- the initial alignment of the animal, the analysis of the stimulus and finally recognition of the stimulus. That is, "orienting" may take various forms, each mediated by separate brain structures or mechanisms. Furthermore, orienting may be followed by a number of responses, including scanning the stimulus from a distance, sniffing with the body stretched out (often seen in rats in an approach-avaoidance conflict), direct investigation, or turning and ignoring the stimulus.

Again, Birke and Archer (1983) stress that in order to take adaptive significance in natural environments into account, researchers should recognise that orientation may not only occur in response to stimulus characteristics (*e.g.*, novelty), but also because the animal has a "searching image" for stimuli of that type. Ethologists suggest that animals have a hypothetical model or "search image" in their heads, which allows them to respond effectively to only certain stimuli. In other words, Birke and Archer (1983) maintain that psychological and ethological accounts of responses to stimuli in laboratory and natural environments should be synthesised to provide a more adequate account of exploratory behaviour.

Direct investigation (sniffing at, gazing at, or manipulating objects) may be the least ambiguous measure of exploration, according to Birke and Archer (1983), yet it may not be clear what is actually being measured. In particular, sniffing of objects by rats is commonly used to measure exploratory behaviour, but sometimes it may be a response to odour traces left by rats previously tested. Thus, researchers must be careful to control for such effects.

1.8.2 STIMULUS COMPLEXITY

Stimulus complexity refers to "the number of distinguishable elements and the dissimilarity of those elements", and animals are "tuned to deal with" stimuli that fall within the range of "complexity" typically encountered within the natural habitat (Russell, 1983, p.37). That is, maximal exploratory responses are elicited by stimuli of moderate complexity. In fact, animals tend to ignore or actively avoid highly complex stimuli. On the other hand, more exploration is elicited by complex stimuli than by simple ones, since more information must be "assimilated". Russell (1983) stresses that the typical laboratory psychology experiment utilises objects and visual patterns that are arbitrarily assigned a level of complexity. In natural environments, such stimuli may be "relatively meaningless" (Russell, 1983, p.37). Furthermore, the effect of complexity alone may not account for exploratory behaviour in natural environments, since ***stimulus content*** (*i.e.*, whether the object is a predator, conspecific or piece of vegetation) is likely to be the crucial determinant (Russell, 1983).

1.8.3 EFFECTS OF PRIOR EXPERIENCE AND HOUSING (IMPOVERISHED OR ENRICHED CONDITIONS)

Renner (1987) investigated the effect of housing conditions on overall activity level and interactions with objects in a test environment. Prior to testing, the rats were housed for 30 days in either an enriched environment (group housed in a large cage with stimulus objects) or an impoverished environment (solitary housed in a small cage with pine shavings on the floor). The stimulus objects used during testing were selected from a pile of "junk objects" kept in the lab. They were considered to be familiar (not novel) after the first day of presentation, and were either "manipulable" or "nonmanipulable". Testing took place in a large arena, with an attached start box.

Renner (1987) scored a wide range of non-object-related behaviours (sniffing of the arena, grooming, withdrawal into start box, freezing, immobility, locomotion, digging, rearing and propping with forepaws against the wall). His range of object-related behaviours was particularly extensive, and included low-risk investigation (sniff/nose contact), paw contact, climb/enter object, contact with mouth (bite/drag), accidental contacts and object behaviour (object moves or rocks). His findings have important implications for the study of exploratory behaviour. Exploratory behaviour may not be a unitary phenomenon in terms of "quantity and character". That is, rats may engage in similar amounts of exploratory behaviour, but there may be differences in the range of activities.

Renner (1987) found that irrespective of housing condition, each group of rats spent an average of 28% of testing time engaged in exploration of the arena (or test apparatus). Both groups displayed a wider range of object behaviours towards the nonmanipulable objects. However, the rats with experience in an enriched environment engaged in a broader range of object behaviours overall (*i.e.* greater behavioural diversity). They used their paws more and were more likely to climb onto the larger objects. Renner (1987) suggests that a more diverse repertoire of investigatory behaviours may have an impact on survival in natural environments. For example, monitoring of a broader range of possible information might increase environmental knowledge, which in turn may reduce the risk of predation.

1.8.4 BIOLOGICAL PREPAREDNESS AND EXPLORATORY BEHAVIOUR

As a result of evolutionary selection, each species is predisposed to learn certain responses more easily than others, namely those that have some adaptive value (Seligman, 1970). As Birke and Archer (1983) point out, Seligman's (1970) concept of "biological preparedness" must be taken into account when attempting to explain exploration in various species. There are likely to be species-specific differences with respect to all aspects of exploratory responses. Different species habituate to stimuli at different rates. If the stimulus is "irrelevant" in terms of survival in natural habitats, animals are likely to habituate to it rapidly (Birke & Archer, 1983). An animal may also tend to investigate objects that are more "relevant" to it, such as those that are marked with the scent of its own species. Thus, Seligman's (1970) "biological preparedness" theory may not only account for the traditional areas of "biological constraints of learning" (*e.g.*, instinctive drift, taste aversion, or even why humans are predisposed to develop certain phobias more readily than others), but also to studies of exploratory behaviour in the laboratory and natural environments.

1.9 INDIVIDUAL DIFFERENCES IN EXPLORATION AND OTHER BEHAVIOURS

When large numbers of rats are used, and group means are reported, individual differences may be overlooked. Laboratory rats have been found to show markedly different performances on a number of behaviours. Negrão and Schmidek (1987) subjected 37 young adult (>90 days of age) hooded rats (19 males & 18 females) to a battery of four tests on two separate occasions. Four different apparatus were used to determine performance for four categories of behaviour: burrowing (terrarium with loose earth), food hoarding (food pellets & nesting material available in two interconnected cages), exploration (multi-chamber apparatus) and insect predation (five adult cockroaches in a glass-fronted cage).

Negrão and Schmidek (1987) found that the behavioural performance of the rats was far from stereotyped. Instead the individual rats (without any particular training or conditioning) differed markedly in their performances for the four behavioural categories, although there were some differences between litters, and females scored higher on the burrowing and insect-predation measures. They suggest that individual differences in performance may have some biological relevance. That is, individual differences in wild social rats could be biologically advantageous, with individuals taking on particular roles in the community based on their skills (selective advantage of variability). Negrão and Schmidek (1987) conclude that:

> "performance individualization in a social species such as the rat might be advantageous by leading to spontaneous division of activities. Individual animals would thus tend to assume specific roles in the community on the basis of their specific motivations" (pp. 110-111).

1.10 BEHAVIOURAL DIFFERENCES BETWEEN WILD AND DOMESTIC NORWAY RATS IN LABORATORY ENVIRONMENTS

With psychology's increased awareness of adaptive significance of behaviours in wild environments, it is important to be aware of the many differences in behaviour that exist between wild and domestic (laboratory) Norway rats. That is, researchers must be careful not to assume that behavioural findings for domestic strains of rats are applicable to wild counterparts.

Wild and domestic rats differ in their responses to aversive stimuli. If they are blasted with air, wild rats vocalise more frequently (*e.g.*, squealing) and leap against the walls of the test apparatus, but cease grooming and freezing much earlier than domestic rats (Mason & Price, 1973). This may reflect the wild rats' attempts to seek an escape route as rapidly as possible, especially since they appear to move more rapidly and spend less time sniffing and scanning the test chamber (Mason & Price, 1973). If shocked through a grid floor (0.5-mA), wild rats show more intense and extreme responses. They initially respond with "rather intense leaping and jumping generally directed toward the lid of the conditioning chamber", whereas domestic rats "leap about the walls" (Price, 1972, p.54). Price (1972) suggests that wild rats tend to be smaller in body size (20% lighter), which may in part account for their heightened response to shock.

Differences in gnawing behaviour and platform jumping have also been found between wild (wild-caught parents) and domestic rats. Price (1973) presented rats (not food-deprived) with a wooden dowel into the home cage (only moved into this cage two days previously). The domestic rats gnawed the dowels significantly more. All of the wild rats marked their dowels with urine, whereas only a quarter of the domestic rats engaged in urine marking. When the rats were introduced to the gnawing tunnels/chambers (with wooden barriers & pegs), both wild and domestic rats gnawed wood to gain access to a narrow tunnel. If access to the tunnel was unrestricted, both groups engaged in little gnawing. When confined to the tunnel, wild rats were more likely to gnaw their way back to the safety of the home cage. In an experiment investigating jumping behaviour, Price (1973) found that only one domestic rat jumped off the platform (8 x 8 inches in diameter & set at varying heights of 6, 10 & 14 inches). By contrast, the wild rats were "strongly motivated to jump", after thoroughly exploring the platform and peering over the side. Price (1973) maintains that the differences in jumping and gnawing reflect the "heightened activity of wild rats when placed in a totally novel environment", but it is unclear whether these behaviours are linked to escape and/or exploration (p.316).

Studies by Galef (1970a) have found differences in responses to novelty between fourth-generation laboratory-bred wild rats and domesticated albino rats. Domesticated rats are far less aggressive towards human handlers, other rats, and small mice. Wild rats resist capture and are very aggressive towards humans, attack and kill introduced rats, and tend to kill mice. If domesticated rats fight with each other, these fights are more like the harmless wrestling observed in immature wild rats. If novel objects are placed into a familiar environment, domesticated rats readily approach the objects, whereas wild rats avoid them. Galef (1970a) suggests that wild rats' "timidity" (neophobia) and "savageness" are manifestations of the response to novelty. He found that stimulus novelty was a prerequisite for eliciting aggression and timidity, since only unfamiliar mice, rats or humans elicited aggression, and only novel objects produced avoidance behaviour.

In a study of shock-associated aggression, Galef (1970b) measured the number of attacks (bites) directed towards a target (familiar & unfamiliar) and the number of escape attempts (leaps toward the lid or attempts to hide in a food cup) by wild rats. The targets were hardwood balls mounted on aluminium poles. He found that shock delivered through the floor resulted in increased levels of escape-directed behaviour and attack. In the presence of the familiar object, attack was rare but escape-directed behaviour was frequent. The opposite effects were found in the presence of the novel object. If both targets were available (familiar & novel), more attacks were directed towards the novel target. Galef (1970b) concludes that stimulus novelty elicits aggression in wild rats in response to shock and directs it towards novel targets (inanimate objects).

1.11 EXPLORATORY BEHAVIOUR IN CAPTIVE CHIMPANZEES

Responses to novel stimuli have been investigated in chimpanzees in laboratory and zoo environments. This section will focus on studies conducted in laboratory situations, since the zoo studies are covered in Chapter 5.

1.11.1 KÖHLER'S EARLY EXPERIMENTS (1913-1917)

Over a period of four years, Wolfgang Köhler (1925) conducted a number of studies on the "psychology of chimpanzees" and ape intelligence (problem solving) at a research station run by the Prussian Academy of Sciences in Tenerife (Canary Islands). Nine chimpanzees were used (from three years of age upwards). Although exploratory behaviour as such was not investigated, Köhler (1925) devotes a chapter to "handling of objects" and many of the experiments conducted involve the use of sticks, boxes or other implements to reach food or solve problems. Köhler (1925) also describes the neophobic reactions of the chimpanzees to "primitive stuffed toys" (p.333). As Goodall (1986) points out, this early research was carefully conducted, and Köhler's descriptions of chimpanzee behaviour "remain among the most careful, perceptive, and important in the literature" (p.7).

1.11.1.1 OBJECT MANIPULATION

> "Experimental tests are not necessary in order to induce the chimpanzee to handle the objects of his immediate surroundings in a variety of ways...The various objects ready to the captive's hand are hardly more numerous or diverse than the products of nature in the forests of the Cameroons." (Köhler, 1925, p.69).

Köhler (1925) recognised the complexity of the "wild" chimpanzees' natural environment. Most of the object manipulation described by Köhler (1925) involved tool-use (*e.g.*, ant-dipping & digging for roots). Although the objects that were available to the chimpanzees were simple, the range of activities that they were used for was wide and the activities complex at times. Köhler (1925) suggests that most object manipulation in chimpanzees is "play", which in some cases can become tool-use. The captive chimpanzees initially used long poles or sticks as "jumping-sticks" or stilts, as a form of play. Later, it developed into tool-use, where the pole was used to reach objects or areas out of reach. Sticks, wire or straw were used to reach plants outside their enclosure. Straws, twigs and cloth rags were used to drink or soak up water. Twigs or blades of grass were used to dip for ants. Sticks were used to dig up roots or food (hidden by the experimenter). The chimpanzees used leaves, straw, rags and pieces of paper to remove faeces, water, oil or blood from their bodies. Sticks were also used as weapons (in displays) or to poke at lizards, dogs, human observers or chickens. Straw, grass, branches, ropes and wires were used to build nests.

The captive chimpanzees also carried objects around on their backs or shoulders (rope, rags, grass, twigs, leaves, bushes, stones, 9-pound blocks of lava), squeezed under their chins (string, rags), between the lower abdomen and upper thigh (food, wood, stones, rags, stones, photos), in their mouth (empty preserve tins) and draped around their necks (metal chain, string & pieces of rag). The chimpanzees used their mouths and hands to paint the beams, bars and walls of their enclosure with lumps of white clay (Köhler, 1925).

Most of the problem-solving experiments conducted by Köhler (1925) involved the use of tools to reach the "objective" (food) that was hung or positioned out of reach. The chimpanzees successfully manipulated a number of objects, in order to extend their reach, and obtain their goal. This included fashioning a "double-stick" (creating a long stick by inserting a thinner bamboo rod into a thicker bamboo rod), stacking boxes, and even using the keepers and experimenters as "footstools" (p.147).

1.11.1.2 NEOPHOBIA

After observing that the chimpanzees were thrown into a "perfect panic" by the sight of "large and uncommon" animals, such as oxen and camels, Köhler (1925) tested the chimpanzees' reactions to crude animal reproductions, or primitive stuffed toys. These toys were 40 cm tall, wooden framed, cloth covered, stuffed with straw and attached to a stand. The toys were roughly shaped like oxen or donkeys, but "most drolly unnatural" (Köhler, 1925, p.333). Although Köhler (1925) does not use the term neophobia, the chimpanzees' fear of the objects ("paroxysms of terror") is clearly neophobic. The fear reactions were less severe, if the stuffed animal was smaller. When Köhler (1925) approached the chimpanzees, with a cardboard mask of the "Cingalese plague demon" over his face, the chimpanzees fled. Köhler (1925) stresses that the chimpanzees were not afraid of every novel object, merely those that were "weird" or "frightful" (p.335).

1.11.2 PRESENTATION OF NOVEL STIMULI IN LABORATORIES

Bloomsmith and co-workers have conducted a number of studies using novel objects as enrichment devices at the University of Texas M.D. Anderson Cancer Center (*e.g.*, Bloomsmith, Finlay, Merhalski & Maple, 1990; Maki & Bloomsmith, 1989). Schapiro, Brent, Bloomsmith and Satterfield (1991) provide a list of potential enrichment devices (presented here as Figure 1.2), of which their class of "manipulable" devices is most relevant to the discussion of novel objects for captive chimpanzees. These researchers stress that objects should be exchanged or added over time (*i.e.*, to take into account habituation effects) and that there should be enough objects to allow subordinate individuals access. With respect to chimpanzees, the addition of novel objects can lead to decreases in abnormal behaviours (particularly if the chimpanzees are singly-housed), and some of the hard and "indestructible" dog toys can even remove plaque from chimpanzee teeth (Schapiro et al, 1991).

Manipulable novel objects are often provided to chimpanzees (& other primates) as a means of increasing the "complexity" of unstimulating captive environments (particularly laboratories). Responses to such novel objects include increases in activity levels, decreases in abnormal behaviours and aggression, increases in manipulatory behaviours (not surprisingly), and spontaneous use of the objects as tools (Bloomsmith et al, 1990). An inverse relationship between stereotypic behaviours and manipulatory behaviours appears to exist, although as

Bloomsmith et al (1990) point out, the noncontingent presentation of novel stimuli is not always an effective therapeutic technique.

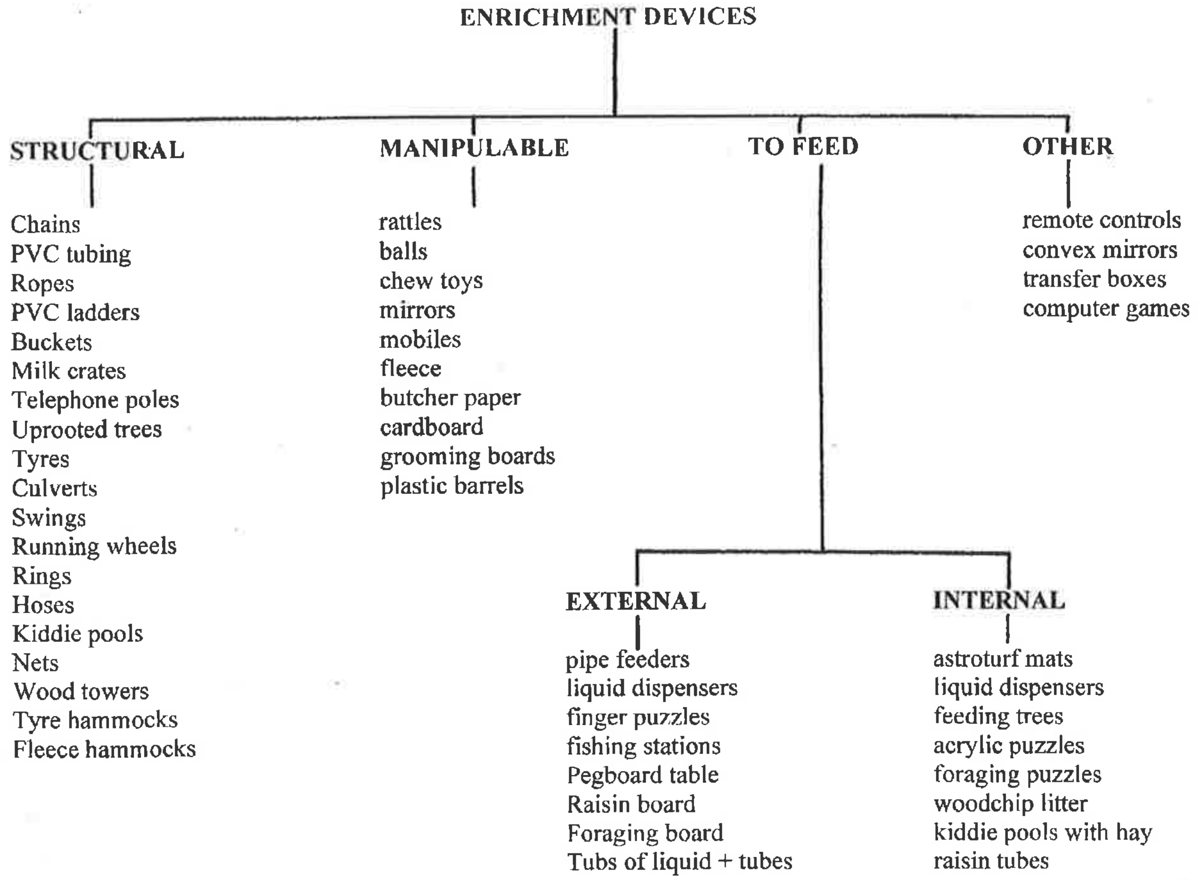


Figure 1.2. Some of the enrichment devices (including "manipulable" novel objects) presented to captive chimpanzees (& other primates) organised by function (Figure 1 in Schapiro et al, 1991, p.23).

Even the presentation of simple rigid plastic balls (10-inch or 6-inch diameters) can encourage physical activity in captive laboratory chimpanzees, helping "combat" the "problems of boredom and obesity" (Bloomsmith et al, 1990, p.321). Such balls are inexpensive, easily cleaned and are unlikely to cause injury (to either chimpanzees or human workers). Bloomsmith et al (1990) compared levels of ball use in sixteen chimpanzees. Balls were presented prior to data collection and left with the chimpanzees for three weeks, and observations took place from 7.30 a.m. to 11.30 a.m. (typically an active period). Seven of these subjects were housed in an indoor/outdoor enclosure, with observations (& ball use) restricted to the outdoor "corral" (22 m in diameter), which also contained movable objects, concrete culverts, uprooted trees, a large climbing structure and grass. This group of chimpanzees was presented with four balls. The remaining nine chimpanzees were housed in groups of two or three in more barren concrete-floored indoor/outdoor runs (2.4 m x 6.1 m x 2.4 m), with chain-link or cinder block fences or dividers, barred ceilings and containing resting boards. These chimpanzees were each given a ball.

Bloomsmith et al (1990) found that over the three weeks, the chimpanzees used the ball for an average of 7.1% of the total observation time (ranging from 0 – 19.6%). Most of this ball use took the form of "active use" (rolling, throwing, bouncing, hitting or kicking the ball represented 40% of ball use), "holding" (31%) and "resting on the ball" (19%). There was an effect of novelty (or habituation), but even after three weeks, ball use took up 2.5% of session time on average. Bloomsmith et al (1990) maintain that any item that occupies more than 2% of a captive chimpanzee's time (after 3-weeks of continuous exposure) must be considered worthwhile. They also stress that the younger subjects, and those housed in the more barren runs used the balls significantly more, and therefore these chimpanzees would benefit most from the introduction of such balls. A singly-housed juvenile male chimpanzee and a singly-housed adult male gorilla tested under the same conditions used the ball for more than 20 % of total session time (almost 30% for the gorilla). Unfortunately the study did not discuss effects on other categories of behaviour, although they did point out that eleven agonistic encounters (as a result of competition for the three balls) occurred during the first two days in one of the groups of three juvenile subjects housed in a run. They suggest that supplying a greater number of balls could reduce the likelihood of such aggressive incidents.

1.12 EXPLORATORY BEHAVIOUR IN CAPTIVE EXOTIC CATS

Not surprisingly, most of the information about exploratory behaviour (mainly responses to novel stimuli) in captive exotic cats, has come from studies conducted in zoos. A number of these studies will be examined in detail in Chapter 5. This section will deal with some general qualitative observations about responses to novel objects and odours.

Barren enclosures situated in buildings that house large cats (lions, tigers & pumas) have been shown to result in chronic levels of stress (urinary cortisol) and stereotypic pacing in leopard cats (Carlstead, 1998). Such enclosures provide no appropriate stimulation, nor any hiding places from perceived predators (big cats). Carlstead and her co-workers provided the four individually housed leopard cats in this environment with hollow logs, branches, boxes and platforms and the behavioural and physiological correlates of stress reduced significantly (Carlstead, 1998).

Mellen, Hayes and Shepherdson (1998) suggest that the presentation of "non-food-related" novel objects (*e.g.*, Boomer balls or other large plastic objects) can elicit elements of hunting behaviour in cats, such as stalking and pouncing. Even objects such as pumkins may be stalked and attacked (Lewis, 1992; Mellen et al, 1998). Mellen et al (1998) stress that objects such as Boomer balls can also incorporate food items (*e.g.*, bones wedged inside a cut in the ball), which encourages more extensive exploratory behaviour. They also suggest that habituation takes place less rapidly if the object is made of "natural" parts of prey items (*e.g.*, animal skins) rather than "unnatural" plastic.

Cats and other animals also use olfaction (to detect scent-marks left by urine, faeces & claw sharpening) to monitor information about conspecifics (Kitchener, 1991; Mellen et al, 1998). Therefore, novel odours can also be used effectively to encourage exploratory behaviour in captive felids. The range of odours used to enhance captive cat environments include faeces from prey species (*e.g.*, zebra faeces for lions), catmint or catnip, rose petals, lanolin, spices (mace, allspice, nutmeg & cumin) and hunter's commercial mule deer musk (Mellen et al, 1998). The way in which these odours are presented (spatially & temporally) can be varied, just as object or food presentation is (Mellen et al, 1998).

1.13 CHAPTER SUMMARY

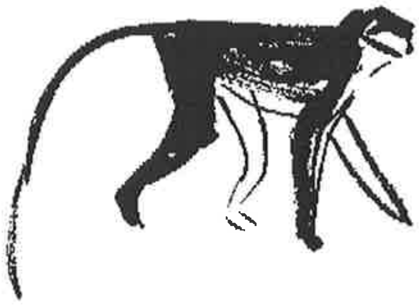
Although studies of exploratory behaviour ("curiosity", "play" or "stimulation-searching") have been conducted by psychologists for over a century, there is still no adequate generally agreed upon theory of exploration. Furthermore, significant problems regarding the distinction between play and exploration, as well as differences between the different categories of exploratory behaviour still exist. The existence of noticeable individual differences in exploration and other behaviours further complicates the issue.

Studies of exploratory behaviour within psychology typically take place within the laboratory and researchers have failed to choose stimulus configurations that are relevant to conditions likely to be encountered in natural environments, although researchers are aware of the many behavioural differences between wild and domestic rats. It is unclear whether the findings based upon the somewhat arbitrary stimuli chosen can be regarded as representing true stimulus determinants of exploratory behaviour under all conditions (*e.g.*, novelty & complexity).

Finally, research on exploratory behaviour in species other than the rat is perhaps even more problematical and unsystematic. Studies of object manipulation or responses to novel objects in captive chimpanzees and exotic cats are few in number and the findings are too general to allow a comprehensive analysis of exploratory behaviour. That is, the reports are somewhat qualitative in nature or the range of behaviours included for analysis is too narrow.

CHAPTER 2

ADAPTIVE SIGNIFICANCE OF EXPLORATORY BEHAVIOUR IN ANIMALS



2.1 ADAPTIVE SIGNIFICANCE OF EXPLORATORY BEHAVIOUR

Until recently, psychologists have largely ignored the adaptive significance of exploration, preferring to concentrate on its immediate situational determinants, eliciting stimuli and motivational mechanisms (Russell, 1983). Adaptive considerations have not been central to the development of methods and theories dealing with exploration in psychology. Russell (1983) states that Berlyne's (1960) epic and influential work in this area, as well as several major reviews since then, have recognised: "the information-supplying role of exploration" but "this aspect has had little heuristic impact" (p.25). Even Berlyne (1960) was more concerned with the effect that exploration has on psycho-physiological arousal. Russell (1983) maintains that the psychological theories of arousal, curiosity and boredom, which attempt to determine the nature of the proximate mechanism of exploration, could "in principle" be reconciled with adaptive considerations. Psychologists must begin to take the adaptive aspects of exploratory behaviour into account, since it obviously contributes to survival in natural habitats.

> "There is a fundamental rule governing animal behavior: In order to increase reproductive fitness, the individual must live in an environment predictable to itself, and one it can cope with. This rule is a consequence of the laws of least effort and the maintenance of homeostasis...*Animals strive to live in an environment predictable to themselves*. Conversely, we can claim that animals are structured by natural selection to live in predictable environments" (Geist, 1978, p.24 & p.27).

Exploratory behaviour provides information, which allows animals to maintain homeostasis, by ensuring that the social and physical environment remains predictable (Geist, 1978). Animals continuously monitor the stimuli in their environments. Geist (1978) suggests that when an animal confronts stimuli that are known and harmless, it is unlikely to respond. If a unique stimulus is encountered, which has "semblance" to known stimuli (particularly those that signal danger), an animal becomes aroused and investigates the stimulus. That is, animals must "clarify" strange stimuli, by investing some time, energy and nutrients, whilst remaining ready to fight or flee- or in other words, in a state of "excitation combined with curiosity" (Geist, 1978, p.25).

2.2 EXPLORATORY BEHAVIOUR AND SURVIVAL IN RODENTS

Cowan (1983) points out that exploratory behaviour increases an individual's chance of survival in two ways. Firstly, factors affecting mortality can be reduced, such as vulnerability to predation, trapping and poisoning. Secondly, factors directly affecting survival can be increased, such as foraging ability.

Small commensal rodents, not surprisingly, are subject to predation as soon as they leave their nests (Cowan, 1983). Predation can be avoided, if the rodents are familiar with their surroundings, and able to use under cover pathways and refuges. This has been tested in captive situations, with owls as the predators, and various mouse species as the prey. Those mice given a few days to explore the environment before introduction of owls were predated upon less, than those newly introduced, and unfamiliar with their new environment (Ambrose, 1972; Metzgar, 1967).

The adaptive significance of an animal's attachment to a familiar area is quite obvious (Russell, 1983). If an animal possesses information about the availability of food and water, places to sleep and hide, and the presence of conspecifics (including mates) and predators, then its chances of survival are enhanced. The mere establishment of a home range is not enough. It is also necessary for an animal to maintain its familiarity with this environment. This is especially important in areas that are subject to seasonal and climatic change, or changes due to man, or the behaviour of other animals.

2.2.1. PATROLLING AND "MENTAL MAPPING" OF THE ENVIRONMENT

Familiarity with the home range is maintained by regular inspections of the area. In rodents and small mammals, this has been found to take the form of environmental patrolling, which is a very systematic inspection of different areas in turn (Barnett & Cowan, 1976; Cowan, 1983; Jewell, 1966). Patrolling is highly ordered in time and space (Cowan, 1983). Russell (1983) suggests that the patrolling animal may be "refreshing its memory" of the home range. Various costs may be involved in patrolling, such as the possible short-term exposure to predators. However, these are outweighed by the benefits. Familiarity with the environment is vital to wild rats, if they are to avoid predators. Barnett (1975) states, that in wild rats:

> "the principle means of avoiding predators are the use of pathways under cover, and flight to a burrow or other place of concealment. These actions depend on previous experience of the topography of the living space. Given such experience, they can run from any one point to any other, by the shortest route and in the least possible time" (p.49).

Cowan (1983) reports that in animals, which live in colonies or groups, the dominant male or female is usually the only one to patrol the entire home range. He also states that patrolling has been observed in a "plus-maze" in both wild and laboratory rodents.

Apart from affording protective advantages, by remaining familiar with home ranges, patrolling and exploration can contribute directly to survival. In order to survive, animals must search for food, water, shelter, mates and other resources. Optimal foraging is linked to exploratory behaviour. A study by Bider, Thibault and Sarrazin (1968) found that "exploratory wanderings" of satiated racoons, resulted in efficient and rapid use of new food sources, which had been discovered in areas not usually associated with food (Cowan, 1983). Cowan (1983) points out that a number of studies have shown that:

> "foraging animals explore and sample their environment continuously and can use the information when the environment changes; less profitable food patches are sampled more than expected, and when patch quality is changed, foraging behaviour changes appropriately" (p.158).

Systematic search and exploration, or patrolling, has been shown to have an effect on optimal foraging in birds (pied wagtails), in a study by Davies and Houston (1981). As well as allowing prey abundance to increase to a "profitable level" in depleted areas, patrolling also resulted in early eviction of intruders (Cowan, 1983).

Exploratory behaviour in natural habitats can also be linked to "homing" and "exploratory migration" (Cowan, 1983). Many small mammals maintain home ranges. In addition, they may explore areas well beyond these ranges. Cowan (1983) posits that the additional information gleaned from these exploratory forays, results in homing, or the ability to return to home ranges if they are displaced beyond normal range-lengths. Exploration beyond the home range, but where the ability to return to this familiar area is retained, can be considered "exploratory migration". Far from being a pointless meandering, Baker (1978) suggests that such exploratory behaviour may serve a role:

> "in resource exploitation in patchy habitats based on ranking of habitats visited during such exploration; animals then patrol ranked habitats primarily to reassess their suitability" (Cowan, 1983, p.157).

2.2.2 NEOPHILIA AND NEOPHOBIA

Approach and contact behaviour has adaptive implications similar to those for patrolling. That is, it brings the animal into contact with essential resources, necessary for survival. However, Russell (1983) stresses that there are times when approach and contact can be harmful, or indeed fatal. For example, a new object in the home range could be a trap or toxic in some way. Similarly, an area beyond the home range may be deficient in resources, and thus, best left alone. Behaviours, which help prevent contact with potentially dangerous changes in the environment, are those that are generally incompatible with exploration. These include protective or fear responses, such as withdrawal, fleeing, hiding and freezing.

Cowan (1983) postulates that exploratory behaviour in wild and laboratory rats varies with respect to the balance between approach (neophilia) and avoidance (neophobia). This balance is crucial, since it: "determines the nature and extent of exploratory behaviour" (Cowan, 1983, p.171). Two major protective behaviours displayed by commensal rats (*Rattus norvegicus* & *R. rattus*) are: new-object reaction; and poison shyness. These behaviours have obvious survival value, since they afford protection from traps and poison. New-object reaction refers to the avoidance of unfamiliar objects in familiar environments (an unlearned response). Poison shyness concerns the avoidance of noxious foods (a learned response). The wild rats studied by Cowan (1977) often starved themselves for days, rather than approach the new objects in the familiar "food arm" of the plus-maze. Commensal rats also display a reluctance to eat new foods (Cowan, 1983). Domesticated laboratory rats, on the other hand, do not display neophobic (new-object) reactions, but do demonstrate poison shyness (Cowan, 1983). Wild, non-commensal Australian rats (*R. fuscipes* & *R. villosissimus*) do not display neophobia either.

Cowan (1983) maintains that the avoidance of new objects in familiar surroundings observed in the two commensal species can be attributed to selection pressures during the rats' association with humans. Such selection is likely to have occurred in man-made environments, where human predation via traps and poison bait is commonplace. Thus, some protection is afforded these species by the neophobic reaction to newly laid traps and bait, which prevents the rapid investigation of new objects, so typical of laboratory rats. Similarly, rats that have not been consistently predated upon by humans do not tend to avoid new objects (*e.g.*, Australian *R. fuscipes* & *R. villosissimus*). Lack of success in recent field poisoning of rabbits, in Australia and New Zealand, has been attributed to neophobia. Selection pressures have favoured animals that avoid baits, which were new objects (Cowan, 1983). Cowan (1983) points out that no such inter-species differences exist with respect to new-place exploration. All the rats (*i.e.*, Australian indigenous species, commensal & domesticated laboratory rats) displayed rapid investigation of unfamiliar places.

2.2.2.1 EARLY FIELD STUDIES OF NEOPHOBIA AND NEOPHILIA IN WILD RODENTS

Whilst the Norway or brown rat (*Rattus norvegicus*) has been a popular laboratory subject around the world, outside the laboratory it has been considered a destructive pest. Crowcroft (1991) devotes a chapter to field studies of rats conducted during World War II, in both urban and rural areas. From 1939 to 1945, the *Bureau of Animal Population* (Oxford University) led by Charles Elton studied the natural history of three rodent pest species, and means of controlling them. The three species were: the Norway or brown rat (*R. norvegicus*); the black/ship/roof or plague rat (*R. rattus*); and the house mouse (*Mus musculus*). Such pests were understandably of particular concern to a country at war. These rodents fed on, and spoiled grain and other food kept in storage, and in the field.

As Crowcroft (1991) points out, very little was known about the behaviour and ecology of wild rodents, or about poisons and other means of pest eradication. The researchers knew nothing about food or taste aversion in brown rats. "Could a rat remember the food associated with the pains of a sublethal dose of poison? Could a rat discriminate between poisoned and unpoisoned food" (Crowcroft, 1991, p.30)? Methods of estimating the size of rat populations before and after poisoning had to be developed. Census baiting was used to ascertain how much unpoisoned bait the rats would consume. This offering of a new source of food led to the discovery of neophobia in wild rats.

2.2.2.2 NEOPHOBIA OR AVOIDANCE OF NOVEL OBJECTS IN SURFACE-DWELLING WILD BROWN RATS *(Rattus norvegicus)*

In 1940, Ranson discovered "new object avoidance" behaviour in rats that were provided with a new source of food (Crowcroft, 1991). The *Bureau of Animal Population* had a research station, or semi-naturalistic laboratory, set up in an old shack on a pig farm in Oxford. Ranson discovered that if a loaf of bread was placed in the shed with the wheat pile that was previously there, most of the 39 rats that entered the shed turned around and left.

> "Only one rat, in fact, seriously attempted to pass the bread. It first crept up behind and showing great hesitation, attempted to get between the loaf and the wall. After two attempts, which brought it level with the loaf, it gave up and went around to the other side. Here there was plenty of floor space for it to keep well away from the loaf, but after again getting level with it the rat went back and out of the shed" (Crowcroft, 1991, p.32).

In summary, the researchers of the *Bureau* found that "new object reaction" in brown rats was elicited when:

(i) new objects were placed near a food supply;
(ii) different containers were used for the food;
(iii) familiar objects were moved to a new position;
(iv) the type of food was changed;
(v) there were changes in illumination;
(vi) there was intermittent noise;
or (vii) other disturbances or changes in the environment occurred (Crowcroft, 1991).

The rats habituated to the novel objects or situations over time. This knowledge of neophobia was then applied to increase the effectiveness of the pest control programme. The manner in which poison was used was altered. The first stage involved offering non-poisoned food to rats, until they had habituated to it, and were feeding "confidently". Later, poison was added to the same food, which was less likely to evoke neophobia. This new method resulted in less poisoned food being consumed. Previously, when only poisoned food had been available, the rats had suffered "warning symptoms" and then stopped feeding altogether (Crowcroft, 1991).

Rats that had survived poisoning, exhibited an aversion to the food in which the poison was contained, even if poison was not present subsequently. That is, the food base (with or without poison) was refused. However, if the same poison was placed in a new food base, it was usually taken. If a new poison was placed in a new food base, it was also accepted. This knowledge of food aversion was also applied to the pest control programme, and the poisoning techniques were altered. Follow-up poison treatments used different poison, and different bait bases from those used in the initial treatment (Crowcroft, 1991).

2.2.2.3 NEOPHOBIA OR AVOIDANCE OF NOVEL OBJECTS IN SEWER-DWELLING WILD BROWN RATS *(Rattus norvegicus)*

As Crowcroft (1991) asserts, during World War II rats were a problem above ground as well as in the sewers of Britain. Researchers from the *Bureau* also studied the biology of sewer rats, and then attempted to bait them with poison. Three main findings about the biology and behaviour of these sewer rats emerged. Firstly, the distribution of the rats was correlated with the distribution of humans in the buildings above. Secondly, sewer-dwelling rats also exhibited neophobia. Thirdly, only brown rats inhabited the sewers, despite the prevalence of black rats in the London dock areas (Crowcroft, 1991).

Sewer rats eat food that is flushed into the sewers, and not human faeces, as was sometimes believed. During the 1940s, many fears of rats leaving sewers to invade houses were held. Public health authorities were afraid that the open sewers and abandoned buildings of heavily bombed London would lead to "hordes of rats" leaving their sewer environments and infesting the dwellings above (Crowcroft, 1991, p.36). However, as Crowcroft (1991) points out, these fears were unfounded.

2.2.2.4 NEOPHILIA, OR APPROACH OF NOVEL OBJECTS, IN WILD BLACK RATS LIVING IN DOCK AREAS *(Rattus rattus)*

Once the *Bureau of Animal Population* had made progress in reducing numbers of brown rats in wartime Britain, they sought to use similar control measures for black rats (Crowcroft, 1991). However, this species of rat differed significantly with respect to its reaction to novel stimuli. Consequently, the Bureau was unable to transfer the methods of rat control it had already developed.

> "The black rat behaved, in some ways, like a big form of house mouse; it was more curious about new objects than afraid of approaching them, and more erratic in its visits to baits left in place for a number of days" (Crowcroft, 1991, p.39).

Despite these findings, financial and logistical factors prevented necessary changes being made to the existing pre-baiting procedures. Thus, black rats in dock areas were baited in the same way as brown rats. Recent studies have discovered that wild black rats demonstrate neophobia and poison shyness under laboratory conditions (Cowan, 1983).

2.2.2.5 REASONS FOR DIFFERENCES IN NEW OBJECT REACTIONS OF BROWN AND BLACK RATS

A variety of ecological or environmental factors may have influenced the new object reactions observed in the two closely related species of rat. ***Neophilia***, or approach of novel objects, might be considered an adaptation to environments that are constantly changing. Black rats living in dock areas are subjected to constant human activity and noise (*e.g.*, movement of ships, pallets of goods). In order to obtain the necessary resources for survival, black rats must approach novel objects in their ever-changing environment. Their contact with humans and the associated activity and noise in dock areas might be far higher than that of brown rats living in underground sewers or in terrestrial environments.

Neophobia, or avoidance of novel objects, on the other hand, might be expected to arise in environments that are less changeable, with less human activity. Brown rats living in more stable home ranges might be more likely to regard novel objects, or indeed any novel stimuli as more "suspicious". The general physical topography of a sewer, farm, house, or terrestrial area would be less likely to change on a daily, weekly or even monthly basis, whereas, the physical topography of dock areas could change quickly and regularly. The rats in terrestrial habitats (*i.e.*, brown rats) may also have been more subject to encountering traps and poison bait during their association with humans. Thus, neophobia may be attributed to such selection pressures (Cowan, 1983).

Since laboratory rats are typically brown rats (*R. norvegicus*), it is important to be aware that this species in natural or wild environments has been shown clearly to demonstrate neophobic reactions.

2.2.2.6 NEOPHILIA IN SURFACE-DWELLING WILD HOUSE MICE (*Mus musculus*)

During World War II, the house mouse (*Mus musculus*) also posed a serious threat to food stores and supplies in Britain. Crowcroft (1991) points out that the Ministry of Food only held two weeks worth of flour and grain in storage or buffer depots (at any given time). The buildings in which these food supplies were stored were easily accessible to rodents. Grain was simply placed in hessian sacks, and then piled into stacks. According to Crowcroft (1991), each:

> "stack was a mouse paradise, providing superabundant food, shelter, and nesting material. When the mice nibbled at the sacks, whether for the grain or the fibers, the grain bled out, causing the stacks to slump, even to collapse" (pp.40-41).

Not surprisingly, once the grain had leaked out, most was re-bagged and used as animal feed instead. However, even this re-bagged grain was "suspect", since it may have been mixed with the poison bait set out for the mice.

The control methods that had been used successfully for brown rats were unsuccessful with mice. Unlike brown rats, the house mice quickly approached novel objects (neophilia) in their environment, even if these objects were traps (Crowcroft, 1991). In addition, mice readily sampled new food sources. However, only small amounts of food from any one source in the resource-rich buffer depots were eaten. Thus, mice tended to ingest only sub-lethal doses of poison, from which they recovered. Trap avoidance or shyness did eventually appear in populations of mice that were heavily trapped.

Southern (Chitty & Southern, 1958), also discovered that the home range of house mice is very small (Crowcroft, 1991). The size of the home range, coupled with the rapid rate of reproduction, meant that control programmes had to greatly increase the number of poison bait points set out, if every mouse was to be reached. Even at the end of World War II, the "war against mice in buffer depots" continued, since strategic stocks of flour and grain were kept for another 15 years in Britain, whilst the Cold War with Russia was at its peak (Crowcroft, 1991, p.41).

2.2.2.7 CHANGES IN HUMAN BEHAVIOUR BASED ON THE FINDINGS OF WILD RODENT BEHAVIOUR

The wartime research of the *Bureau of Animal Population* showed that human behaviour influenced rodent activity (Crowcroft, 1991). Not surprisingly, if less rubbish was left piled up in factories or stores, less cover was provided for rats. Similarly, if food scraps were removed rather than left at work, then a source of rat food was also eliminated. Swift repairs were encouraged, since leaking water faucets and taps provided rodents with water. All quite mundane and seemingly obvious suggestions, but until rodent behaviour had been properly studied, these practical problems had not been dealt with.

2.2.3 PLAY AND OBJECT MANIPULATION IN RATS

The various forms of "playful" behaviour that have been reported for rats appear at particular developmental stages (Hole & Einon, 1984). "Popcorn" behaviour (sporadic hopping, jerking & jumping) begins to appear at about 15-days of age, whilst play-chasing and rough-and-tumble play takes place from about 21 to 40 days. After this period of time, rats gradually show "not very serious fighting" (or NVSF) and sexual play: "until the cessation of clearly-playful behaviour at about 60 days" (Hole & Einon, 1984, p.112). Although rats engage in social rough-and-tumble play, predatory object play is restricted to some carnivores (e.g., cats, dogs & ferrets), and object manipulatory play appears to be exclusive to primates (Einon, 1983).

Most of the studies that include observations of object manipulation in wild rats have already been discussed. Typically, these studies have investigated reactions to novel stimuli (usually neophobia) in wild (*e.g.*, Crowcroft, 1991) or laboratory environments (e.g., Galef, 1970a; Cowan, 1977).

2.3 NEUROPHYSIOLOGICAL EVIDENCE FOR THE IMPORTANCE OF EXPLORATION: A CRUCIAL SURVIVAL BEHAVIOUR IN RATS

Winson's (1990) research on memory processing indicates that theta rhythm (a regular signal in the hippocampus) appears in animals that are awake when they engage in behaviour that is crucial to their survival. That is:

> "theta rhythm appeared when they exhibited behavior that was not genetically encoded - such as feeding or sexual behavior - but rather as a response to changing environmental information. Predatory behavior in the cat, prey behavior in the rabbit, and exploration in the rat are, respectively, most important to their survival" (Winson, 1990, p.88).

Interestingly, theta rhythm also occurs during REM sleep, in the hippocampus, which is the area of the brain involved in memory processing. Winson (1990) suggests that information essential to survival is collected during the day (when theta rhythm is activated by exploration in the rat). It is then encoded by theta rhythm into memory during REM sleep. If a lesion was made in a rat's septum, so that theta rhythm could no longer be activated, then spatial memory was destroyed. "Rats that had previously learned, using spatial cues, to locate a particular position in a maze were no longer able to do so" (Winson, 1990, p.90). Further studies found that spatial memory was stored in the rat hippocampus during sleep. Individual CA1 neurons fire vigorously, mapping a location when the rat moves to a particular place during exploration (coding space). These same neurons that had mapped space during the day, fired at a significantly higher rate (than previous sleeping baseline) in REM sleep. Winson (1990) posits that spatial information that is encoded when the rat is awake and exploring its environment is reprocessed or strengthened during sleep.

> "With the evolution of REM sleep, each species could process the information most important for its survival, such as the location of food or the means of predation or escape - those activities during which theta rhythm is present. In REM sleep this information may be accessed again and integrated with past experience to provide an ongoing strategy for behavior" (Winson, 1990, p.94).

Perhaps the most important finding to emerge from Winson's (1990) research is that exploration (& the resulting spatial or memory map) is the "pivotal" behaviour for a rat's survival. This crucial survival behaviour alone activates theta rhythm in rats, and clearly the memory-processing mechanisms that take place during REM sleep, show how important memory or spatial maps are to a rat's survival.

2.4 EXPLORATORY BEHAVIOUR, HOME RANGES AND SURVIVAL IN CATS

As mentioned previously, exploratory behaviour increases an individual's chance of survival (Cowan, 1983). Like rodents, cats also have a home range, which provides all the necessary resources. This area includes hunting sites, water, places to sleep and rest, lookout positions, and dens, which are linked together by a series of trails (Kitchener, 1991). Information about these sites, as well as the presence of conspecifics enhances the cat's chances of survival (Russell, 1983). It is also necessary for a cat to maintain its familiarity with its environment, monitor changes (seasonal & climatic, human-induced, prey density, behaviour of other animals), and defend it from intruders (conspecifics).

Kitchener (1991) asserts that the home range can vary temporally and spatially, and may overlap with those of conspecifics. However, for some cats, there is a core area within the home range that does not vary, and which is fiercely defended. For example, in a study of domestic cats on a farm in Cornwall, Panaman (1981) found that females ranged over areas as large as 1.5 hectares, but that over 80% of their time was spent in the core area of 0.2 hectares (Kitchener, 1991).

The home range appears to serve different functions for male and female cats (Kitchener, 1991). Female home ranges are smaller and incorporate dens and sufficient prey sites, to allow for the successful rearing of kittens, no matter how low the prey density is. The presence of males within this home range is tolerated, but not of females. Male home ranges, on the other hand, are larger and overlap with two or more female home ranges. The larger area provides sufficient food, as well as the opportunity to mate with as many females as possible. As Kitchener (1991) states male home ranges tend not to overlap, although there are exceptions (*e.g.*, some bobcats, jaguars, pumas, & Iriomote cats).

Most cats use chemical (scent marking) and visual warnings to alert potential intruders of their presence, rather than physical threats and aggression (Eaton, 1987). If a cat's home range is particularly large, then it may be impossible to defend it against intruders (of the same sex). In such cases, a "time-plan" system of spacing, rather than a "fixed territory" may exist (Eaton, 1987). That is, if the area is too large to have absolute boundaries, then a temporal system "with boundaries that move as the warnings lose their effect" separates cats, such as cheetahs (Eaton, 1987, p.106).

The size of the home range can vary extensively within and between cat species, but typically, the larger species occupy larger territories. The size of the home range, and the pattern of habitat use within the home range is influenced by a number of factors, including, prey availability or density; season; age of kittens (for females); and dominance. Kitchener (1991) emphasises that:

> "far from having a chaotic, random system of home ranges driven by the need for 'solitary' cats to avoid each other at all costs, most wild cats maintain a predictable system of land tenure, which promotes social stability and maximises the reproductive success of both males and females" (p.155).

Estimates of home range size for caracals are based on very small sample sizes (four females & one male in the Cape Province, South Africa). The average female home range was 18.2 km^2, and the male ranged over an area of 65 km^2 (Stuart & Wilson, 1988). These ranges may not be representative, since the size of a home range is affected by a number of factors, including resource availability (*e.g.*, of prey) and the level of persecution by humans.

Caracals in the Negev Desert (Israel) have much larger home ranges, with females covering 100 km^2 and males 200 km^2 (Stuart & Wilson, 1988). Compared with the figures from South Africa, these ranges are approximately five times greater for females and almost four times greater for males. Weisbein and Mendelssohn (1990), presumably the researchers referred to by Stuart and Wilson (1988), suggest that at least 20 caracals range over an area of 100 km^2 in the northern Aravah Valley of Israel. Some of these caracals range outside this area, which is classified by Weisbein and Mendelssohn (1990) as: "farming areas and wadis near settlements" (p.22). In fact, the average home range size for five males and four females tracked by Weisbein and Mendelssohn (1990) is even larger. Males were found to hold home ranges of 220.6 km^2 (+/- 132 km^2), which is four times the size of the home ranges of females, given as 57.3 km^2 (+/- 55 km^2).

The greater size of the male's home range may ensure that he has access to a greater number of possible mates. Weisbein and Mendelssohn (1990) point out that this explanation is only valid if caracals are polygamous. These researchers found that the size of a caracal's home range is related to two variables, namely, body weight and availability of food. When food is readily available, the size of the home range decreases, but home range increases with increases in body weight. Size and shape (& utilisation) of home ranges for male caracals do not appear to be affected by seasonal factors. Female home ranges, on the other hand, are likely to vary in size and shape whilst progeny are being reared (Weisbein & Mendelssohn, 1990).

Weisbein and Mendelssohn (1990) provide a measure of "home range stabilisation" for caracals of both sexes. By plotting this measure as a graph/curve, it follows an asymptotic course for males after 10.25 (+/- 2.36; N=4) tracking periods of 24-hours (503 location points). Females with their smaller home ranges, reached this asymptote after only 8.3 (+/- 1.53; N=3) periods of 24-hour monitoring. Far from being mutually exclusive, the home ranges of caracals in this study tended to overlap. Most male home ranges incorporate a large proportion of several female home ranges. Male home ranges overlap with other male home ranges as often as 50% of the time, whereas, female home ranges only overlap each other 27% of the time. Weisbein and Mendelssohn (1990) suggest that females can more easily defend their smaller home ranges against other females, thus ensuring the greatest possible success of rearing offspring. Males on the other hand, appear to have to "sacrifice" parts of their home range in order to occupy a larger territory, thus affording greater mating opportunities. Nine of the thirteen caracals studied were "permanent residents" of the area, with the others "wandering about" as transients or temporary residents (Weisbein & Mendelssohn, 1990, p.21). One of these transients was an old male, who had "lost" his home range, and the other three were young caracals in the process of migrating away from the maternal home range.

The typical caracal home range may be large. However, like other medium-sized cats, several preferred areas or activity centres often exist, which provide shelter, water and prey (p.224). Weisbein (1988) tracked a re-located, spayed and radio-collared female caracal. He found that she utilised a number of activity centres in the new home range (34 km^2). Interestingly, the main activity centre was just 1.5 km away from the release point, and near her initial preferred area. It is likely that she thoroughly explored the area around the release site, and then gradually explored beyond that point. Two secondary centres (North & South of the release site) existed, in farming areas (vineyards & pine groves) with plenty of shelter (ruins, caves, vegetation), prey (hares & birds), and water sources. The hilly and bare areas between the activity centres were passed through, but otherwise unutilised.

Preferences for certain areas of the home range, in the field study by Weisbein and Mendelssohn (1990), show how difficult it is to separate caracal habitats into "natural" or "influenced by/living with humans". Few caracal habitats appear to be unaffected by human activities and settlement. In the Aravah Valley of Israel, caracals preferred to "congregate" near fishponds or other water sources, and wadis near human settlements and farming areas (Weisbein & Mendelssohn, 1990).

Caracal's food preferences may be subject to seasonal variations. Weisbein and Mendelssohn (1990) are unable to provide unequivocal evidence for this, but they do suggest that in the colder months of winter and early spring caracals show a preference for food items that are easily acquired (*i.e.*, low energy expenditure). Such items include: trap baits; carcasses; and domestic animals. In order to save energy, which is needed for body warmth, the caracal may become a scavenger or even raid human settlements.

Weisbein and Mendelssohn (1990) calculated the average 24-hour walking distances for caracals. Males travelled approximately 10.4 km daily (+/- 5.2km; N=40), whereas females travelled only 6.6 km (+/- 4.1km; N=37) over the same period of time. This daily distance of travel varied little over the course of a year, but the distance travelled during the daytime was influenced by whether the caracal was hungry or satiated, sexually active, or rearing young (for females). The paths used during the daytime also varied, as did the resting sites.

2.4.1 PATROLLING AND "MENTAL MAPPING" OF THE ENVIRONMENT

Since the male caracals monitored by Weisbein and Mendelssohn (1990) had such large home ranges (on average 220.6 km^2), showed preferences for certain areas, and travelled only 10.4 km daily (on average), it is unlikely that they would be able continually to defend their home range. However, it is likely that they patrol the home range periodically, and scent mark (urine & faeces) at various locations along the trails, to deter potential intruders (Kitchener, 1991). Although no study investigates patrolling of the home range in caracals, ocelots completely patrol their small home ranges (between 1.2 & 8.1 km^2 in size) every couple of days (Emmons, 1988; Kitchener, 1991).

Familiarity with, and utilisation of cover, in its home range is one adaptive function of a cat's exploratory behaviour (in the form of patrolling & mental mapping). Many cats also cache prey, if they are unable to completely devour their kill in one feeding session (Kitchener, 1991). Caching helps prevent the kill being discovered by other predators. Leopards are known to cache prey in trees, as are Scottish wildcats. Caracals use grass to cover prey (reedbuck), Canadian lynxes use snow, and other cats (*e.g.*, pumas, bobcats, feral cats) use whatever loose materials (*e.g.*, leaves, earth) are available to cover their prey (Kitchener, 1991). Cats must be able to find the cache again. A "mental map" of their environment would allow them to do so.

If prey densities are low or food is absent altogether (e.g., feral cats in urban environments), then cats may be forced to scavenge (Kitchener, 1991). Clearly, actively searching for caches, carcasses or other food sources involves exploratory behaviour, and successful location of food is the key to survival. Up to 17% of a Canadian lynx's diet may be scavenged, and as high as 75% of a male lion's food may be scavenged from lionesses in Rwenzori National Park in Uganda (Kitchener, 1991; van Orsdol, 1986).

Thus, patrolling the home range, in search of prey and other resources, and monitoring any changes is linked to survival. Further, a clear "mental map" of caches, cover, dens and other resources would also facilitate survival.

2.4.2 SEARCH STRATEGY AND PREDATION

Small cats use two main hunting strategies (Kitchener, 1991). The ***mobile strategy*** (M) is one in which the cat actively moves towards prey. The cat may patrol the home range until it encounters prey. The second hunting strategy is the ***stationary strategy*** (S). As its name suggests, this involves the cat remaining stationary (or waiting in ambush) until prey approaches. The former strategy, involving ***active exploration of the surroundings***, or patrolling, is a far more successful strategy. Thus, exploratory behaviour is linked to hunting success. Corbett (1979) found cats (feral & domestic) used the M and S strategies equally, but the M strategy was twice as successful (4.2 kills per hour, compared with 2.1 kills per hour). Thus, although extra effort is required to actively search for prey, this is rewarded with a higher hunting success rate (Kitchener, 1991).

Not surprisingly, dominant cats usually employ the more successful M strategy (Corbett, 1979). If subordinate cats were to use this more active strategy, they might be more open to attack from more dominant cats, and have an even lower hunting success rate (Kitchener, 1991; Kruuk, 1986). However, when prey densities are low, cats that usually use the S strategy are forced to search for prey, since it is unlikely to just pass by (Kitchener, 1991).

Lions of Ngorogoro National Park in Tanzania appear to use three different hunting strategies (Elliott, McTaggart Cowan & Holling, 1977). The first of these (Type I) involves killing prey that has been encountered. The second (Type II) involves the lion stalking and killing prey. Both of these strategies are quite opportunistic, and would be successful when prey densities are high. The third strategy (Type III), however, involves actively searching for prey. This is a hunger driven strategy and necessary when prey densities are low (Kitchener, 1991).

The S strategy can be successful, in areas that provide plenty of cover for cats to hide from their prey. Lions hunting in dense riverine habitats have been found to have a higher hunting success rate compared to those in areas affording little cover (Schaller, 1972). With dense cover available, the success rate was 41%, compared with only 12% (Kitchener, 1991). The hunting success rate of pumas in the Idaho Primitive Area can be as high as 82% in winter, when snow and rough bluff areas provide heavy cover (Hornocker, 1970; Kitchener, 1991).

Actively exploring the home range for prey is linked to a cat's hunting success rate, and ultimately to its survival. When prey densities are low, this form of exploratory behaviour is vital to survival. Once a successful kill has been made, cats often explore their immediate surroundings before they begin to feed. Kitchener (1991) suggests that such exploration would detect other predators or scavengers in the area, and allow time to drag the prey into cover.

2.4.3 NEOPHILIA AND NEOPHOBIA

Little information about wild cat reactions to novel stimuli appears to exist. However, a series of experiments document reactions of lions to thorny objects associated with food (bait). Kortlandt (1980) suggests that early hominids may have developed the use of thorn branches as defensive weapons against carnivores, since lions (& other carnivores) show "excessive fear of suddenly moving thorn bushes" (p.79). He conducted a number of experiments with approximately 12 free-ranging (but provisioned & considered tame by George Adamson) lions at Kora National Reserve (Kenya), and a pride of wild lions on the shores of Lake Ndutu (Ngorongoro Conservation Area, Tanzania), using large chunks of meat and live sheep as "test models", to investigate the lions' responses to thorns (p.90).

In the first of Kortlandt's (1980) experiments, three lions (accustomed to being fed) encountered three large chunks of meat covered by loosely placed thorns or spiny branches, when they arrived to be fed. The lions stopped near the baited objects, circled around them, sniffed, looked for an opening in the thorns, "hesitatingly made batting movements with their paws in the air", and tried to probe their muzzles "gingerly" through small gaps in the thorns for up to 30 seconds (p.91). Although the lions could easily have batted the thorny branches away with their paws, they were "much too afraid to do so", and eventually used their muzzles to push under or through the thorns (p.91).

In a second experiment, Kortlandt (1980) presented eight wild lions (two adult males, four adult females & two subadult cubs) at Lake Ndutu with a live sheep contained in a mesh cage (105 x 40 x 118 cm), covered with whistling thorn branches (held together with wire & twine). He maintains that this object resembled a natural bush. The baited object was set down about 30 m away from the lions (& 50 m away from the experimenters' cars) that were still consuming a sheep that had been offered (injured but alive & anchored down with a small boat anchor) thirty minutes earlier. It should be noted, that a lioness killed the sheep, but a male took it from her and trotted away with it. "Then, however, the anchor became caught behind a tree. As the male felt the rope tightening he threw the sheep high up into the air, with a loud growl, and ran away, apparently panicked by the sudden interference of what must have been to him some kind of witchcraft" (Kortlandt, 1980, p.92).

The lions were considered to be “less shy” than before the offering of the first sheep (Kortlandt, 1980, p.92). After three or four minutes an adult female walked towards the cage, hesitated and stopped within 0.5 m “ready to jump away” (p.92). Thirty seconds later, a second lioness joined her and they both “started to saunter around the cage, although in an agitated manner, investigating it from all sides, but keeping their noses about 0.3 m away from the thorns” (Kortlandt, 1980, pp. 92-92). The visual inspection continued for up to 90 seconds, and then the lionesses began to poke their noses through gaps in the thorns and made “hesitating patting” movements with one paw (p.93). After several minutes of investigation, and the arrival of another lioness (& departure of the second), a “lull” or rest took place (another lioness approached, looked & then withdrew).

For the next 80 minutes, 11 lions participated in the test or merely looked on. Although some of the lions succeeded in clawing and biting through the mesh and even dragging the whole contraption by a rope for a couple of metres (like a sled), they were unable to reach the sheep, and it was subsequently released onto a farm without a scratch. The lions growled and angrily “swished” their tails, but Kortlandt (1980) stresses that they did not use powerful bites, were extremely awkward in their manipulations of the object, and apparently easily fatigued. He suggests that the thorny object was approached and manipulated (paws & mouth) with “extreme caution”. At no time does Kortlandt (1980) consider that some of the lions may have exhibited “trap shyness”. There is no mention of whether lions in that area have been poached, or subjected to tourists or other humans (inside or outside the reserve) or domestic livestock. As Turner and Meister (1988) point out, only experienced cats recognise and attack immobile prey. Typically, a cat’s movement towards prey, is elicited by a moving or moved object that is “neither too large, nor too fast and is moving more or less in a straight path” (Turner & Meister, 1988, p.113).

The third experiment was really rather bizarre. The same group of lions was presented with the same live sheep bait, but this time a framework (to which the sheep was harnessed), with four rotor blades on top, with a thorny branch attached to each was presented to them. A motor, switched on by a pedal in the observer’s car, allowed the rotor blades and branches to turn, thus forming a protective shield. Not surprisingly, the lions did not respond. Kortlandt (1980) moved the sheep closer (to a distance of 20 metres), and even tried to arouse the lions by driving a vehicle up behind them. This did not succeed in making the lions approach the object. A follow-up study using blades (& attached thorny branches) mounted low over meat fed to the tame lions at Kora National Reserve, succeeded in frightening the lions. They initially jumped and fled and then some made attempts to approach the food. Their approach/avoidance reactions were as expected (although not by Kortlandt), following an aversive stimulus.

Kortlandt's (1980) experiments were far from ideal (& in fact unethical in many respects- *i.e.*, use of an injured sheep unable to escape & use of another sheep in two stressful encounters with predators), and did not interpret any of the evidence in terms of reactions to stimuli (familiar or novel) presented in natural and familiar environments. The object or situation was so artificial, so novel and aversive (in the case of the motorised shield), that the neophobic reactions or complete disinterest were not at all surprising. Furthermore, the wild lions may have had aversive experiences with humans in the past. Yet, Kortlandt (1980) was surprised and attributes the fear and avoidance reactions to the "suddenly fast-moving thorny branch" rather than to the motor and the unnatural stimulus presented (& way in which it was presented). "Each time I pressed the button the lions leapt away much more wildly and much further than I had ever seen a lion do when a conspecific's paw struck out at it. Four sweeps, without making a hit, sufficed to elicit the "looking-away reaction" and to induce the lions temporarily to withdraw under the shade of a tree" (Kortlandt, 1980, p.99). The only time that he mentions the terms familiar or unfamiliar is when he suggests that future experiments could use familiar or unfamiliar control test stimuli, presented beneath whistling thorns. This research highlights the fact that even field experiments have contributed little to our understanding of neophobia and neophilia in wild cats, and the few observations that exist are qualitative/anecdotal in nature.

2.4.4 PLAY AND OBJECT MANIPULATION

Researchers have examined play in a number of cat species, including, the domestic cat (Martin & Bateson, 1988), the cheetah (Caro, 1987) and the lion (Schaller, 1972). As Kitchener (1991) states, play forms a significant part of kitten behaviour. It emerges as co-ordination and motor skills develop. The adaptive function of play is still unknown, but various hypotheses have been put forward, centred around its possible role in: "physical training, developing competitive skills for fighting or predation, developing cognitive skills or for promoting socialisation" (Kitchener, 1991, p.193). Play may in fact serve more than one function. Even solitary animals, such as, bears engage in play as cubs and later on their own as adults, which Poole (1985) uses as evidence to reject the socialisation hypothesis (Kitchener, 1991).

Play is not without its costs and risks to both kittens/cubs and mothers, suggesting it may serve an important developmental role if the benefits are to outweigh the costs. Kitchener (1991) points out, that the potential costs of play include risk of injury to the young, and increased energy and milk demand from the mother. Of the hunts that were unsuccessful in a study of cheetahs (Caro, 1987), 16% of failures were attributed to intervention by the cubs (Kitchener, 1991). Schaller (1972) found that play in lion cubs peaked at dawn and dusk, as did adult activity (Kitchener, 1991).

Most of the information on play in felids comes from research on domestic cats, not cats in the wild. As a kitten develops, different types of play emerge at different developmental stages (Kitchener, 1991). Martin and Bateson (1988) discuss the age at which three types of play appear in kittens, namely, social play, object play and locomotor play. From four weeks of age, until 12-14 weeks of age social play predominates, but declines after this period. Social play-fighting is not without its risks as the kittens mature, as by three months of age, these play-fights can develop into serious incidents.

Eye-paw coordination is necessary for kittens to interact with small moving objects. Therefore, it is not surprising, that object play does not emerge until 7-8 weeks after birth, along with locomotor play. Martin and Bateson (1988) suggest that play changes markedly at the time of weaning, near the end of the second month of life, a time when behavioural reorganisation appears to occur. At weaning (7-8 weeks of age), a sharp increase in play with inanimate objects is observed. After weaning is completed (8-12 weeks of age), many measures of play are very different from those observed in the same kittens prior to weaning.

Some of the behaviours that form part of a kitten's social play repertoire (approaching, pawing, holding & biting other cats) are positively correlated, whereas others (rearing, arching & chasing) are negatively correlated with adult predatory behaviour and the attention paid to prey (Caro, 1979). Rearing, arching and chasing may be linked to adult agonistic behaviour instead.

Social play and object play appear to be separately organised and controlled, as indicated by the lack of inter-correlations between the measures of the two types of play, as well as, the different developmental stages they emerge at (Martin & Bateson, 1988). Object play and social play also differ with respect to the motor patterns used, with repetitive motor patterns frequently occurring during object play, but not during social play (Martin & Bateson, 1988).

Barrett and Bateson (1978) investigated the development of play in 13 litters of kittens (14 males & 14 females), from four to twelve weeks of age. Each family of cats was provided with a sawdust tray, up-turned box, small stuffed toy dog and table tennis ball in an observation room. The kittens were observed for 30 minutes with the mother present and 30 minutes without the mother present. One of the categories measured was "object contact" or object play (physical contact- by patting the object with a paw or biting the object). During the 8-12 weeks period, the males made significantly more "object contacts", but this difference was less marked in females that had a male in their litter. Of all the play measures scored, "object contact" occurred most frequently, with a massive increase from the fourth to the twelfth week. Barrett and Bateson

(1978) suggest that as cats get older, "object contact" becomes more associated with exploration and prey catching (hunting).

As mentioned previously, one hypothesis concerning the function of play postulates, that play provides a means of practice for adult predatory skills. Martin and Bateson (1988) suggest that despite the similarity of play motor patterns and prey capture and kill patterns, play experience is not a necessary prerequisite for development of the basic elements of predatory behaviour. Even cats reared in isolation ("Kasper Hauser" cats), with no opportunities for visual or play experience, directed "normal" predatory behaviour towards a moving "prey-dummy" at 11 weeks of age (Martin & Bateson, 1988; Thomas & Schaller, 1954). Play may not be a necessary prerequisite for development of predatory behaviour, but it may enhance predatory skills (Martin & Bateson, 1988).

Domestic cats and many species of wild cats play with prey that is either dead or alive. Kitchener (1991) posits an important role for prey play in the development of prey capture skills, and recognition of prey species, in kittens or cubs. Behaviours, such as, stalking and handling of prey can be practised when the mother felid brings back live prey for the kittens or cubs to play with. Prey play is not only observed in young cats, but also in adult wild cats (*e.g.*, servals). Geertsema (1985) found that servals in the Serengeti play with rodent prey (Kitchener, 1991). According to Leyhausen (1979), prey play behaviour can be divided into three categories. The first category of "restrained play" involves low intensity catching behaviour, which is "modified playfully" (Kitchener, 1991, p.79). The most common form of prey play involves chasing, and catch and throwing of prey, and is termed "overflow play". This category of play may be observed in very hungry cats, but directed towards non-prey objects. Finally, "play of relief" involves leaping in high curves over and around the dead prey. Such "prey play" is typically elicited by large or dangerous dead prey items (Kitchener, 1991).

During the first weeks of life, the mother felid brings the kittens, or cubs, prey that she herself has killed (Turner & Meister, 1988). Live prey is then brought home to the kittens when they are at least four weeks old. The prey play that ensues is considered to "help the kittens reach the motivational threshold required to apply the killing bite" (Turner & Meister, 1988). Prey play also occurs if the adult cat is in a conflict situation- hungry but facing a large or difficult prey animal. Such play may help tire the prey animal and reduce the risk of injury to the cat.

2.5 EXPLORATORY BEHAVIOUR, HOME RANGES AND SURVIVAL IN CHIMPANZEES

Chimpanzees live in a variety of different habitats, from continuous forests to open savannah grasslands with scattered trees (Wrangham, 1992). Thus, it is likely that the type of habitat, and therefore, the home range will affect the way in which chimpanzees explore their home range and peripheral areas. The home range is often lacking in well-defined boundary lines, such as streams or ravines, and the peripheral areas typically form an overlap zone between neighbouring chimpanzee communities (Goodall, 1986). Nishida (1979) states that home ranges of the K-group and M-group of chimpanzees at the Mahale Mountains (Tanzania) have "well-delineated and traditional" boundaries, with an apparently "invisible barrier" that results in the chimpanzees turning back (p.82). Although each chimpanzee home range has its boundaries, these can change from year to year, with the expansion or contraction of the home range (Goodall, Banddora, Bergmann, Busse, Matama, Mpongo, Pierce & Riss, 1979). Irrespective of habitat type, chimpanzees live within a home range with boundaries and areas that overlap with other chimpanzee home ranges.

2.5.1 PATROLLING AND "MENTAL MAPPING" OF THE ENVIRONMENT

Chimpanzees at Gombe (Tanzania) visit the peripheral areas of the home range periodically. Goodall (1986) suggests that they visit these boundary areas for three major reasons. Firstly, chimpanzees that have formed a "consort" relationship may "go on safari" for as long as one month. During this time, the male leads the oestrus female (& her dependants) to a more remote and isolated part of the home range (Goodall, 1986; Nishida, 1979). Typically, this area is part of the overlap zone. Excursions to the peripheral areas of the home range are also made to feed on seasonal and abundant sources of food. Thirdly, and perhaps most importantly, chimpanzees patrol or monitor the peripheral areas of the home range. Males typically undertake patrols, but may be accompanied by females (usually in oestrous). Patrolling behaviour exhibited by adult males is linked to territoriality, or the maintenance, defence, and enlarging of the home range (Goodall, 1986).

Chimpanzees on "patrol" tend to travel in compact groups, moving cautiously and silently. Goodall (1986) maintains that vocal silence (which can be maintained for more than three hours) is the most striking aspect of patrolling behaviour. Dry leaves and rustling vegetation are avoided, male charging displays take place without the usual accompanying pant-hoots, and female copulation calls are suppressed. Goodall (1986) found that calls or noises made by others were suppressed by adult males (adolescent Goblin was hit or embraced), or by mothers (an infant with hiccoughs was repeatedly embraced). Noisy human observers may be threatened

(Goodall, 1986). As Goodall (1986) points out, these observations: "suggest that the chimpanzees have some concept of the need for silence at such times" (p.580).

Although patrolling has been described in detail for the chimpanzees at Gombe (Goodall et al, 1979; Goodall, 1986), details are sketchy for other study areas. Nishida (1979) observed, "scouting" (patrolling) in adult males at Mahale (Tanzania), as well as charging displays directed at "enemy groups". Ghiglieri (1984) suggests that the higher rates of travel observed in the male chimpanzees at Kibale may result from: "the need to patrol their communal home range and to increase their opportunities to locate and mate with estrous females" (p.68). Chapman and Wrangham (1993) found that male chimpanzees at Kanyawara (Kibale National Park, Uganda) were seen in boundary areas four times as often as females, and used an area up to twice as large as females.

Ghiglieri (1984) maintains that chimpanzees with their specialist's diet of relatively rare fruit dispersed in discrete patches require superior abilities to locate and exploit such patchy (spatial and temporal) resources. Further, one would:

> "expect them to exhibit unusual abilities of resource location. Chimpanzees with the best developed spatial sense and memory, form sense (for recognising plant species), and time sense (for understanding the phenomenon of synchronous fruiting) will have a competitive advantage over other apes and sympatric monkeys" (Ghiglieri, 1984, pp.94-95).

Fruit may ripen and disappear on a weekly basis. However, unless humans interfere (*i.e.* destroy the area), the actual spatial distribution of the plants or food species would only slowly change over an individual's lifetime (Ghiglieri, 1984). If optimal foraging were indeed linked to exploratory behaviour, then efficient and rapid use of fruit would require chimpanzees to have a spatial mental map. This would be periodically updated to allow for changes in the environment. Ghiglieri (1984) reports that chimpanzees at Kibale tested figs visually, and by gently squeezing them. Once ripe, fruit was systematically harvested.

> "The interesting psychological questions on mental maps in animals are not *whether* they exist, but *how* exactly the individual maps reality and derives behavioural rules from them" (Boesch & Boesch, 1984, p.160).

Wild chimpanzees in western Africa (Tai National Park, Ivory Coast) use hammers (stones or wooden clubs) to crack nuts on anvils (tree roots or stone outcroppings). Of the five species of nuts cracked, Boesch and Boesch (1984) collected data for two, *Panda oleosa* and *Coula edulis*.

These researchers analysed the spatial mental map of chimpanzees by investigating the transport between different tree locations of hammers used for cracking the two species of nuts.

Unlike the *Coula* trees, which are abundant and often within sight of others, the *Panda* trees are relatively rare and widely scattered. In addition, *Coula* nuts can easily be opened by wooden clubs, whereas, *Panda* nuts are very hard and can only be opened with stones. Since stones are a rarity at Tai National Park, the stone hammers are often transported between the different anvil or tree sites. Boesch and Boesch (1984) marked and numbered the *Panda* trees, and weighed and marked all stones found at anvil sites and elsewhere. It was then possible to follow the transport of the stone hammers between the various *Panda* trees, and measure the distance such stones were transported. Hammer transport was also measured for *Coula* trees, but in a restricted area, since the trees were so abundant.

Boesch and Boesch (1984) report that chimpanzees transport harder hammers (stones), of greater weight, and for longer distances for the harder *Panda* nuts. An optimal *Panda* hammer is heavier than an optimal *Coula* hammer, which leads Boesch and Boesch (1984) to conclude that: "chimpanzees are prepared to carry an optimal tool over a longer distance than a suboptimal one, as if they compared the benefits and costs of various choices" (p.162). The analysis suggests that chimpanzees appear to remember where stones are located, and choose stones that minimise transport distance. A "least-distance" principle would make sense, since carrying a heavy stone (over 3kg) in one arm, whilst walking on three limbs is a more difficult form of locomotion. "A chimpanzee typically first selects a tree - either by actually going there or mentally - and then the optimal stone, suggesting that tool quality might be less crucial than tree quality" (Boesch & Boesch, 1984, p.166).

Chimpanzees appear to use a mental map that allows them to compare distances, and the weight of the hammer is also combined in some cases. Importantly, chimpanzees bring stones to goal trees, even though the stone and Panda tree cannot be seen at the same time. Boesch and Boesch (1984) argue that chimpanzees demonstrate four mental operations, namely: measurement and conservation of distance; comparisons of several distances; permutation of objects in this map; and permutation of the point of reference. These researchers suggest that only an evolved mental map could account for the simultaneous presence of these four operations, which according to Piagetian criteria, belong to the "concrete operations period". Furthermore, Boesch and Boesch (1984) maintain that the Euclidian level of spatial representation, and stage IIIB of the concrete operations level are evident in the wild Tai chimpanzees (appearing in humans at the age of nine years). That is:

> "the Tai chimpanzees seem to demonstrate an Euclidian mental map, using straight lines to measure distances" (p.168), and Boesch and Boesch (1984) postulate, that: "the exploitation of a particularly rich and patchy food source under conditions of poor visibility contributes to the high development of spatial capacities in the Tai chimpanzees" (p.169).

2.5.2 NEOPHILIA AND NEOPHOBIA

Young chimpanzees "use a variety of objects, almost anything that they can get hold of, in both self-stimulation and social interaction" (McGrew, 1992, p.183). Yet, few examples of wild chimpanzee reactions to novel objects have been documented. Unless an investigator conducts a field experiment, in which novel objects are introduced into the wild environment, or "accidental" encounters with objects occur (Figure 2.1), "natural" encounters with objects rarely occur within sight of an observer. For example, chimpanzees of the Kanyawara community at Kibale National Park (Uganda) are known to leave the forest and enter adjacent human settlements (to crop-raid), and also encounter illegally set snares and traps within the forest (many have snare wounds), but researchers rarely have the opportunity to observe their reactions to objects in these situations (personal observation).

Goodall (1986) points out that chimpanzees use twigs or sticks to investigate objects that they are "afraid to touch with their hands" (pp.548-549). She describes how eight-year old Fifi used a long palm frond to touch the bloodied head of a dead python that had been placed in the feeding area at Gombe. The head was touched with the frond and then withdrawn, and sniffed. She only investigated the snake after staring at it for "some time" (Goodall, 1986, p.549).

2.5.3 OBJECT MANIPULATION, PLAYAND TOOL-USE

McGrew (1977) posits that object manipulation is vital to the survival of all primates, since they all engage in this activity during maturation, and it may develop into tool use. "In all known cases, both in the wild and in captivity, spontaneously developing chimpanzee tool-use behaviors began as object manipulation in infancy" (McGrew, 1977, p.262). Exploratory behaviour is often directed towards objects (especially novel ones), object play in chimpanzees is particularly complex (McGrew, 1977), and tool-use in chimpanzees is varied and requires a great deal of manipulative skill (Matsuzawa, 1996).

2.5.3.1 OBJECT MANIPULATION

Although there were accounts of object manipulation in captivity, until McGrew's (1977) analysis of Gombe records of object manipulation (collected since 1960) for six older infant chimpanzees (1.5 to 5-years old), there were no baseline norms of "normal object manipulation" in wild chimpanzees (or indeed other primates). He calculated how often the young chimpanzees handled objects ("palmar contact by at least one or both hands with an object"), what these objects were, and whether there were differences in the way in which object were manipulated (McGrew, 1977, p.270). The rate of overall object manipulation was high. The chimpanzees manipulated objects during 75% (group mean) of the observation minutes (for 368 observation hours). Most of the objects manipulated (67%) were classified as "attached vegetation" (i.e. living & flexible parts of plants- trees, shrubs, herbs, vines & grasses). The other category (non-attached objects) included solid food (fruit, bananas, palm nuts), loose vegetation (sticks, grass, leaves) natural objects (stones, soil) and artificial objects (cloth, paper).

The female chimpanzees tended to manipulate the movable detached objects rather than the living vegetation. McGrew (1977) stresses that the subject numbers were low, but points out that sex differences in tool-use (females use tools more often to obtain termites & ants at Gombe) and object manipulation (captive females interact with inanimate objects more often) have been found in a number of studies. McGrew (1977) concludes that wild chimpanzee infants spend a large amount of time manipulating objects in their physical surroundings.

2.5.3.2 USE OF OBJECTS DURING SOLITARY AND SOCIAL PLAY

Objects that are found in the natural environment are often incorporated into bouts of play. Goodall (1986) provides a number of examples. At Gombe, young chimpanzees treat the large round strychnos fruit, stones and other fruits as if they were balls- carried, thrown up into the air, juggled from one hand to the other, rolled along the ground and then retrieved. Prized objects (such as strips of skin or hair from old kills, pieces of cloth or twigs laden with fruit) are draped over the shoulders or carried around tucked between the neck and shoulder or thigh and belly. Goodall (1986) states that juvenile or adolescent females in particular sometimes use large stones or short sticks for long bouts of "self-tickling" (accompanied by loud laughter). Twigs or palm fronds may be used to initiate social play or form part of a chasing game or tug-of-war.

2.5.3.3 TOOL USE AND META-TOOL USE

"Tool use is a kind of object manipulation in a broader sense" (Matsuzawa, 1996, p.204). McGrew (1992) defines a tool as a "moveable, inanimate object used to facilitate acquisition of a goal" (p.177), and devotes a whole book to the subject of chimpanzee tools as "material culture" (& implications for our understanding of human evolution).

Chimpanzees use a variety of tools in their natural environments, but the repertoires of tool-use (& tool-kits) vary markedly across populations (McGrew, 1992). Since the first anecdotal

Figure 2.1. Occasionally field researchers may observe ***neophilia*** or "object approach and contact" behaviour in "wild" free-ranging animals. A spotted hyaena regularly tipped over traps (set by a researcher in 1997 to catch & weigh/measure his mongoose subjects at Queen Elizabeth National Park, Uganda) to successfully obtain the morsels of food inside (top). A chimpanzee at Kibale National Park in Uganda (Kakama) inspects a notebook and paper left unattended by a researcher (not me!), and vervet monkeys immediately approach any unattended items at the Uganda Wildlife Education Center in Uganda (bottom left & right respectively).

account of use of "hammer-stones" in 1844, and the headline-catching accounts of tool-using by Goodall in the 1960s, 32 populations of free-ranging chimpanzees in Africa have been reported to use tools (McGrew, 1992). However, only 12 populations show 43 types of "habitual" tool-use, or " patterns shown repeatedly by several members of a group" (McGrew, 1992, p.179). No single pattern of tool-use is observed at all sites. Of the 43 types of habitual tool-use, approximately half are subsistence activities. That is, they are used to acquire or process food, particularly social insects (*e.g.*, termites & ants) or nuts. The other types of tool-use are related to weapon-use, self-directed behaviours (self-tickle, leaf-napkin) or communicative signals (play-start, leaf-groom, leaf-clip). Despite the impressive list of tool-kits and repertoire of associated behaviours, McGrew (1992) points out that many more tool-use behaviours have been observed in captivity (or in the wild as anecdotal evidence), but have yet to be systematically documented and analysed for wild chimpanzees.

Arguably the most complex use of tools by wild chimpanzees is that of stone tool use, since it requires the skilled use of two detached objects (Matsuzawa, 1996). Across West Africa, a number of populations of chimpanzees use a hammer (tool) to crack open a hard nut (goal-object) resting on an anvil (fixed object; McGrew, 1992). Almost ten years of learning and practice are needed to attain the skill level demonstrated by adult chimpanzees, with one-third of infants starting to use the pair of stones as tools by the age of 3.5 years (Matsuzawa, 1996). The most advanced stage of tool use observed in wild chimpanzees to date, is the use of a "meta-tool" (a tool used to "improve the function of another tool") to crack open nuts (Matsuzawa, 1996, p.201). At Bossou (Guinea), Matsuzawa (1996) observed three chimpanzees (including a 6.5-year old) using a stone to wedge underneath the anvil stone, so that the anvil remained flat and stable.

2.5.3.4 USE OF OBJECTS AS WEAPONS

Apart from humans, the only real predators that chimpanzees encounter are large carnivores (leopards, lions & hyaenas). Kortlandt (1980) maintains that carnivores have had an impact on the survival strategies (particularly defensive behaviours) of not only chimpanzees, but also early hominids. Although many species have evolved anti-predator defensive behaviours (*e.g.*, watchfulness, alarm calls, concealment, flight & mobbing), some primates have evolved more active forms of defense. Since the 1960s, Adriaan Kortlandt and his co-workers have conducted a number of studies with baboons and chimpanzees, in which a stuffed leopard was presented to them (Kortlandt, 1980). Male baboons in Uganda reacted by knocking the dummy off the tree trunk, jumping on it and attacking it. Kortlandt (1980) removed the leopard before it was completely destroyed. In a number of different experiments, chimpanzees threw objects at the stuffed leopard (Kortlandt, 1980).

When a stuffed leopard was placed under a tree, chimpanzees responded by throwing large dead branches at it. Kortlandt (1980) states that forest-dwelling chimpanzees were even more aggressive and threw branches more often (but less accurately), when they encountered an animated stuffed leopard placed in a clearing. When the same dummy was presented to savanna-dwelling chimpanzees, the chimpanzees not only resorted to throwing branches, but also used large sticks (up to 2 m long & 4 cm thick) as clubs to deal the leopard a number of ferocious blows (70-150 km/h). When confronted with a live leopard (kept out of reach), wild-caught chimpanzees also engaged in extremely aggressive use of weapons. Kortlandt (1980) stresses that at the time of these tests, leopards were still common in the test areas. He maintains that the slow reproductive rate of chimpanzees and inability to rely on using trees to escape the predators in all situations, helped evolve the “armed fighting techniques” observed (Kortlandt, 1980, p.83).

Goodall (1986) provides a number of accounts of “generalized” hurling of rocks and branches by males during their displays (usually at other males). One male (Mike) incorporated two or three empty kerosene cans into his charging displays. This noisy display (without any physical violence) so intimidated his rivals, that he rose from a low social position (in a hierarchy of 14 males) to become alpha male. Chimpanzees, particularly adult males, also throw (“aimed throwing”) stones, rocks or sticks at baboons and humans (Goodall, 1986). Sticks, branches and stones have also been used to hurl at or hit monitor lizards, mice, bushpigs, leopards and lions. Over a six-year period (when there was competition over bananas in camp), Goodall (1986) found that males threw objects most frequently at conspecifics, whereas females tended to throw objects at baboons. She observed that young chimpanzees began to start throwing objects during “aggressive” play with young baboons. Typically, the baboons runaway, with the chimpanzees in pursuit, and “brandishing sticks or throwing stones” (Goodall, 1986, p.553).

2.6 EXPLORATORY BEHAVIOUR IN WILD AND CAPTIVE ANIMALS

For rats, at least, there are differences in a number of behaviours (including exploration) between wild and laboratory strains. One might also expect that there are differences in the amount and type of exploratory behaviour (& other behaviours) observed in wild rodents, felids and primates when compared with their captive counterparts (held in zoos). This section will investigate an early (& extensive) study of exploratory behaviour (responses to novel objects) conducted in a zoo environment.

2.6.1 GLICKMAN AND SROGES' (1966) STUDY OF "CURIOSITY" IN OVER TWO HUNDRED ZOO ANIMALS

In an extensive and ambitious study of "curiosity", Glickman and Sroges (1966) investigated the responses of over 200 zoo animals towards a variety of novel objects. The huge range of species (>100), coupled with the standardised set of objects (scaled to the size of the animal), results in a psychological study of exploratory behaviour that is truly comparative in nature. Furthermore, besides discussing effects of captivity on behaviour, these researchers consider the evolutionary aspects of "curiosity", and what its adaptive significance in natural habitats might be.

The study was carried out at Lincoln Park Zoo in Chicago (187 mammal subjects & 20 reptile subjects) and at the Bronx Zoo in New York (35 primate subjects). Male-female pairs (of each species) housed in the same enclosure were tested individually, in the "home" or adjacent enclosure. Testing sessions took place when the zoo was closed to the public (between 5p.m. & 11 p.m.). Since the daily feeding time for mammals was between 1p.m. and 4p.m., these subjects were usually satiated when tested. The reptiles, on the other hand, were fed weekly and their level of hunger or satiation would have varied when tested.

Glickman and Sroges (1966) adapted the size of the novel objects (with the exception of the paper ball) to the size of the species being tested (large objects for the large cats, donkey, guanaco, crocodiles, python & sea turtle; small objects for the small rodents; & medium sized objects for the other species). Wherever possible, the researchers provided every subject with his/her own set of objects, so that odour and other potential intervening variables would not interfere. Thus, the objects had to be simple, inexpensive and easily replaced. The set of objects consisted of nine items, which were always presented in the following order: two wooden blocks, two pieces of steel chain (ranging in length from 3-24 inches), two pieces of wooden dowel, two pieces of rubber tubing (ranging in length from 3-24 inches), and a ball of crumpled-up paper. Objects were presented as pairs (or singly in the case of the paper ball) for a 6-minute test session, removed, and then the next pair was introduced (after a delay of 5-20 minutes). Thus, there were usually 5 test sessions per subject.

Interestingly, of the over 100 species studied, Glickman and Sroges (1966, p.156) state, that large hoofed animals were not sampled (too difficult to separate from the herd), and neither were adult great apes ("for fear of the damage they might do to their glass-fronted cages with the stimulus objects"). The reptile sample was somewhat biased towards engaging in object-directed behaviour. That is, the species selected by the zoo curators were: "those deemed most likely to react" (Glickman & Sroges, 1966, p.156), and the reptiles were usually food-deprived to some extent (fed once a week). Other subjects were omitted from the report if they failed to complete at least four of the five tests. Tests were halted if the subject ate the crumpled paper (approximately 10% of subjects attempted to eat the paper ball), or risked injury from splinters or possible choking. The total number of subjects used in the final analysis was: 100 primates, 45 carnivores, 30 rodents, 13 "primitive" mammals, and 20 reptiles.

Data were collected using data sheets, which divided each 6-minute test session into 5-second intervals, giving 72 sample intervals. Details about the topography of object-contact responses were also recorded qualitatively (*e.g.*, biting, chewing, use of forepaws, sniffing *etc*). The two main categories of exploratory behaviour directed at the stimulus objects used were: ***orienting towards object*** (turning eyes towards object, or "visual exploration"); and ***contact with object*** ("intentional" not accidental, if, for example, the animal was pacing). The latter category often included visual orientation as well, but was only scored once as "contact".

Glickman and Sroges (1966) describe a number of interesting differences in the topography of object-manipulatory responses in the different taxonomic groups. For all groups, the most common "contact" behaviour was ***chewing*** of the objects. Rodents typically gnawed the objects, and in some instances objects were hoarded (either deposited in certain locations or buried with sawdust). "Aggressiveness of approach" appeared to differ between the suborders. Glickman and Sroges (1966) highlight the similarity between object-directed behaviours and prey-capture and consumatory responses in carnivores. Objects were stalked, chased, swatted with paws, bitten, "worried" and tugged at (against the paws). Object approach was also "vigorous" and "relatively fearless" (Glickman & Sroges, 1966, p.185).

Extensive manipulation of objects was observed in the primates, with hands being used to grasp and manipulate, along with visual inspection. Idiosyncratic patterns of object manipulation were most common in the macaques and baboons. Such varied manipulatory responses were rarely observed in the Prosimians. Almost 20% of the adult primates tested, displayed fear towards the objects. Three species appeared to use specialised anatomical features as part of their object manipulation techniques. That is, the giant anteater used its snout and tongue, the spider monkey utilised its prehensile tail, and the guanaco used its lips.

Differences were also observed in the total amount of investigatory behaviour displayed towards objects, by the different taxonomic groups. Amongst the mammals, no significant sex differences were noted, but an effect of age was observed. Subadults were more reactive towards objects than adults of the same species, but adults made more "orienting" responses. "Primates and

Carnivores exhibited more investigatory behavior than Rodents or a group of "primitive" mammals" (Glickman & Sroges, 1966, p.184). With the exception of a crocodile (who "lunged at", pushed & bit the objects), the 20 reptiles tested showed little response to the objects.

The three suborders of rodents differed in the amount of reactivity to objects shown (Hystricomorpha > Sciuromorpha > Myomorpha). Few differences in amount of exploratory behaviour directed at the objects were observed in the carnivores. However, the meerkats were less "immediately reactive", and as a group, the smaller cats (*Felis*) were less reactive than the larger cats (*Panthera*). Amongst primates, a number of differences were found. The Colobinae showed more visual-orienting responses, but less investigatory responses than the Cercopithecinae (both belong to the "Old World" monkeys). Then, within the Cercopithecinae, the guenons and patas monkeys displayed more visual-orienting responses, but less investigatory behaviour than the baboons and macaques. The more "primitive" Prosimians and "highly-evolved" Colobinae differed little in total reactivity (Glickman & Sroges, 1966, p.185).

The mean total responses (orienting + contact) varied depending on the type of object used in the test. Part of Glickman and Sroges's (1966) Table 4 is included here (as Table 2.1) to show these differences. Although, the primates displayed significantly more "orienting" responses than the carnivores, when the "orienting" and "contact" responses are combined, the mean total responses are higher for carnivores with all objects, except the chain. Not surprisingly, the lowest values are found for the chain. This is perhaps the least "naturalistic" object. The wooden blocks and dowels, and paper ball can all be chewed or easily destroyed. The rubber tubing could hide possible food items. The steel chain, however, is cold and indestructible.

Table 2.1
The mean frequency of total responses towards novel objects (Orienting + Contact) per six-minute test session. The "paper" test was discontinued for nine primates, three carnivores and one rodent (taken from Table 4, Glickman & Sroges, 1966, p.159).

	Primates	**Carnivores**	**Rodents**
No. of subjects	100	45	30
Blocks	33.79	38.49	19.30
Chain	24.43	19.07	7.80
Dowel	28.39	29.58	12.90
Tubing	26.21	38.98	16.93
Paper	26.24	33.19	20.55

Despite the quite short length of test sessions (6 minutes), habituation towards the novel objects was observed even after the first minute, in all taxonomic groups. Glickman and Sroges' (1966) Figure 1 is included here (as Figure 2.2) to illustrate this habituation effect, and the differences in mean reactivity towards objects ("orienting" + "contact"/4) in the different groups.

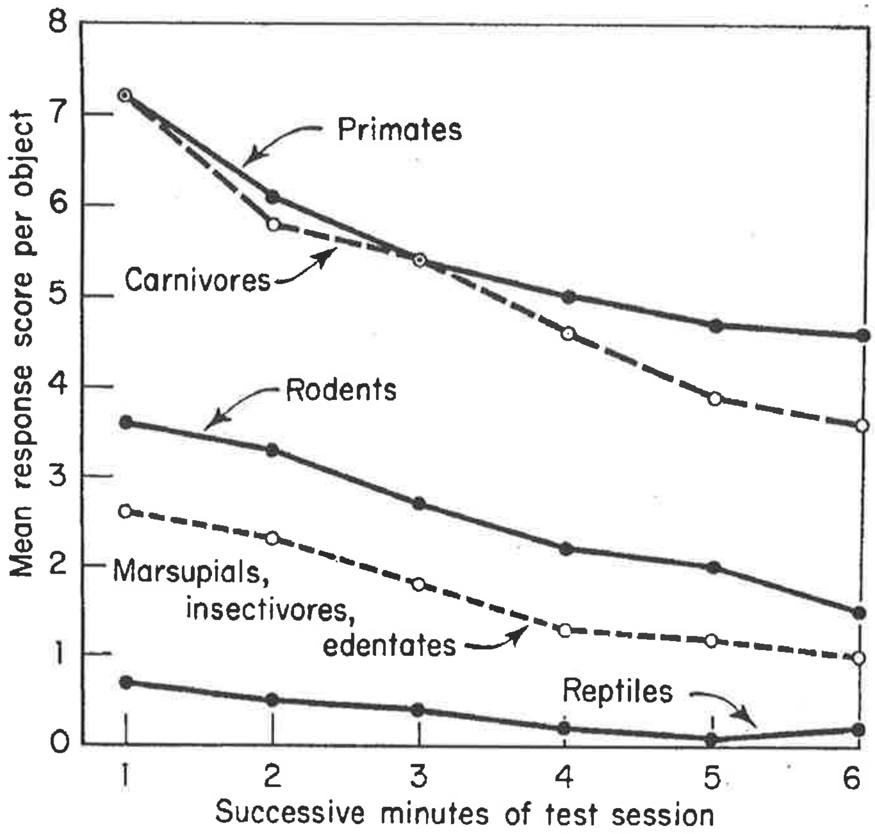


Figure 2.2. The habituation to novel objects over successive minutes of the 6-minute test sessions, as shown by the mean reactivity ("orienting" + "contact"/4) to test objects (taken from Figure 1 in Glickman & Sroges, 1966, p.161).

Although, general observations regarding amount of exploratory behaviour and topography of response across taxonomic groups have already been mentioned, the responses of rodents (particularly the Myomorphs- mice & rats), cats and great apes in Glickman and Sroges' (1966) study will be described in greater detail over the next few pages.

2.6.2 RESPONSES TO NOVEL OBJECTS BY RODENTS IN GLICKMAN AND SROGES' (1966) STUDY

Of the three suborders of rodents tested, the Myomorphs (Kangaroo Rat, Lesser Egyptian Jerboa, Lesser Egyptian Gerbil, Fat Dormouse) displayed the lowest amounts of total response towards the objects, with a mean raw score of 4.33. By comparison, the mean total response (raw scores) of the Sciuromorphs (squirrels, marmots) was more than double (11.0), and the mean total response (raw scores) of the Hystricomorphs (porcupines, agoutis) was 20.76. This was almost five times as high as the Myomorph score.

The vigorous gnawing (Hystricomorphs), burying and hoarding of objects observed in the other two suborders, was noticeably absent in the Myomorphs. "Where there was gnawing, it was of briefer duration, and the entire approach of these smaller animals was one of greater caution on those occasions when object contacts were made" (Glickman & Sroges, 1966, p.174). This may reflect a greater object-avoidance (neophobia) in these smaller rodents. If the test sessions were longer, or there were more of them, perhaps the Myomorphs would also display more responses to the objects.

Glickman and Sroges (1966) stress, that the rodent sample size was far too small to draw any major conclusions. However, the possible adaptive significance of the various behaviours observed can be discussed. The most reactive rodents were the porcupines and agoutis, which are much larger and "better armed" than the small and shy "mouse-like" Myomorphs sampled. Glickman and Sroges (1966) suggest, that this: "would fit with the attempt to relate quantity of reactivity to danger from predators" (p.180). That is, rodents in natural environments might be exposed to greater danger from predators, if they were to investigate an object in an open area. These researchers also point out, that the hoarding behaviour or large amounts of gnawing exhibited by some of the rodents was probably a reflection of the type of behaviour observed in these species in their natural environment.

2.6.3 RESPONSES TO NOVEL OBJECTS BY CATS IN GLICKMAN AND SROGES' (1966) STUDY

Ten species of cats, divided into two genera (not taxonomically correct in a couple of cases): *Felis* (Bay Lynx, Serval, Golden Cat, Ocelot, Mountain Lion) and *Panthera* (Leopard, Lion, Tiger, Jaguar, Snow Leopard) were included in Glickman and Sroges' (1966) final analysis. Other carnivores were also included in the analysis, but this section will focus on the behaviour of the cats.

"Object-oriented behaviour" was predominantly chewing or mouthing responses. However, there were also high percentages of "playful" behaviours, such as: "vigorous swatting, chasing, "worrying" activities" (Glickman & Sroges, 1966, p.171). Objects were "batted" around the cage with "mobile" paws, and forepaws were used to hold down or "cradle" objects whilst being chewed. When eating, larger cats (*Panthera*) tend to use their forepaws to "cradle" the food, whereas, smaller cats (*Felis*) tend to eat the food off the floor, without use of forepaws (Leyhausen, 1956). Glickman and Sroges (1966) found similar differences in use of forepaws when chewing the test objects. In addition, the *Panthera* treated test objects like food, but in a more "playful" manner. As with food, objects were carried in the mouth to shelves at the rear of the enclosure, where they were licked and chewed, whilst the cat was lying down.

The mean response (raw) score was much higher (more than double) for the genus *Panthera* (45.1), than for the genus *Felis* (17.9). Interestingly, the mean response score for the *Panthera* was the highest of all the carnivores tested (cats, foxes, raccoons, coatimundis, weasels, minks, skunks, & meerkats). By contrast, only the meerkats scored lower than the *Felis*. Thus, the larger cats were the most "reactive" to the novel objects. However, the range of behaviours displayed towards the objects was similar. Like the domestic kittens observed by Leyhausen (1956), both genera exhibited: " 'artificial' stalking and pouncing, sometimes after exaggerated crouching; rolling on the back, holding the object in the forepaws, and kicking at it vigorously with the hind legs; and …swatting and holding in the mouth and shaking" (Glickman & Sroges, 1966, pp.172-173). Three cats (two lynx & one cougar) licked each object, and then rubbed their heads against the object whilst lying on the back or side. The duration of this behavioural sequence was sometimes one minute or longer.

Glickman and Sroges (1966) suggest that the high reactivity towards objects displayed by the carnivores is compatible with the environmental demands made upon these animals in their natural habitats. In order to hunt successfully and capture prey, carnivores must be active and employ complex and vigorous behavioural patterns. Competition for prey between carnivore species, or even individuals is intense, and survival may be enhanced in species or individuals that are: "more reactive and capable of sustained reactivity" (Glickman & Sroges, 1966, p.179). The object-directed behaviours observed in the study, were similar in topography to those behaviours directed towards prey items. Glickman and Sroges (1966) point out that the manipulatory play behaviours observed in young mammals have adaptive significance, since they allow the animal to hone the skills it will later require as an adult. Whereas, these "playful" behaviours are usually only observed in young wild carnivores, in the zoo situation, adults also engage in these behaviours.

2.6.4 RESPONSES TO NOVEL OBJECTS BY GREAT APES IN GLICKMAN AND SROGES' (1966) STUDY

As mentioned previously, no adult great apes were included in Glickman and Sroges' (1966) analysis. However, two infant gorillas, two young chimpanzees and one adolescent chimpanzee were included. The adult mean total response (raw) scores ranged from 6.75 to 54.25 for the old world primates, and the adult mean total response (raw) scores ranged from 6.75 to 36.55 for the new world primates. For the younger great apes, the mean response (raw) scores were high (between 45.0 & 71.2), with the young female chimpanzee scoring highest. The female and male gorilla scores were 66.4 and 45.0 respectively. The scores for the young female chimpanzee, young male chimpanzee, and adolescent male chimpanzee were as follows: 71.2, 58.6 and 55.4.

The young female chimpanzee was "generally reactive to all the objects", which is reflected in her high score (Glickman & Sroges, 1966). The blocks were licked, swung, and both hands and feet were used simultaneously. The black rubber tube evoked a fear response from her, which Glickman and Sroges (1966) suggest may be attributed to the tube's snake-like appearance. She did, however, touch it five times, "bark", and eventually withdraw to the back of the enclosure. The young male chimpanzee showed no fear of the rubber hose. Instead, he bit and stretched it, and attempted to fit the smaller tube into the larger one. The blocks were sucked and bitten, and also waved and twirled around. The crumpled paper was chewed, removed, and chewed again, "like chewing gum" (Glickman & Sroges, 1966, p.171). The adolescent male chimpanzee used hands, feet and mouth extensively to manipulate the objects. He tended to sit with his back to the cage wall, and rock backwards and forwards whilst manipulating the objects. The infant gorillas (both approximately one year old) also scored highly, but were described by Glickman and Sroges (1966) as being "much more slow moving in their approach" than the chimpanzees (p.171). All objects were manipulated with the hands (not feet) and also chewed.

Primates, with their binocular vision, engaged in relatively large amounts of visual exploration (Glickman & Sroges, 1966). Object reactivity was highest in those primates that are known to actively search for sparsely distributed food in their natural habitats. Chimpanzees, in particular, would be expected to show high object reactivity scores. In the wild, their diet centers around fruit, which is not always in plentiful supply. Fruit trees are scattered around the forest, and fruits ripen at different times of the year (Litchfield, 1997). They may travel many kilometers per day. Chimpanzees are equally at home on the ground or in trees. Apart from fruit, chimpanzees also eat terrestrial herbaceous vegetation (*e.g.*, ginger stems & elephant-grass pith), use tools to fish for ants and termites or crack open nuts, and also hunt monkeys and small mammals. These skills all require great manual dexterity, and hand-eye co-ordination.

2.6.5 EFFECTS OF CAPTIVITY ON RESPONSES TO NOVEL OBJECTS

As Glickman and Sroges (1966) assert, it is difficult to determine what effect captivity has on a particular animal's (or species') reactivity to novel stimuli. On the one hand, captive animals often have more spare time than their wild counterparts, who would spend most of the day foraging. There are no predators to avoid, and novel objects are unlikely to be harmful. Reactivity in the less complex and changing captive environment could be enhanced. On the other hand, if captive animals have developed stereotypic behaviours, which are likely to "block" attention to novel stimulation, then reactivity could be reduced. Further, for many species, very little is known about their behaviour in natural environments, so it is not possible to determine what effect captivity may have.

This early work by Glickman and Sroges (1966) clearly still remains the most comprehensive comparative study of exploratory behaviour in captive animals, and has helped psychologists take a more ecological approach to the study of behaviour. Timberlake (1993) states that:

> "Glickman and Sroges (1966) investigated the exploratory behavior of zoo animals, looking for overall phylogenetic grades in reactivity. However, the data compelled a different interpretation relating exploratory behavior to the ecological variables of food variety, predator pressure, and the importance of social communication" (p.690).

2.7 CHAPTER SUMMARY

Exploratory behaviour is a vital survival behaviour for rodents, felids and primates. This has been demonstrated in a number of behavioural and neurophysiological studies. Rats are subject to predation, which can be avoided if they are familiar with their environment (able to seek refuge quickly). Rodents maintain familiarity with their home ranges through regular patrolling. Wild brown rats display neophobic reactions to novel objects, unlike other species of rats.

Few studies of wild felids specifically investigate reactions to novel objects or ways in which objects are manipulated in wild environments. However, a number of studies have shown how important exploratory behaviour is with respect to effective patrolling and monitoring of home ranges, and successful hunting strategies. Research has shown that gender differences exist: males have larger home ranges, and male kittens appear to engage in more object play (in captivity). The many field studies of chimpanzees provide a rich source of material on exploratory behaviour: patrolling, object play, object manipualtion and tool-use. However, evidence for reactions to novel objects is usually anecdotal in nature. Again, there appear to be gender differences: males have larger home ranges, and females engage in more tool-use (unless it is use of weapons).

Finally, Glickman and Sroges' (1966) comparative study of responses of over 200 zoo animals towards a variety of novel objects is discussed, as well as the effects of captivity on behaviour.

CHAPTER 3

SCHEDULES OF REINFORCEMENT, EXPLORATION AND ADJUNCTIVE BEHAVIOURS

3.1 SCHEDULES AS TOOLS TO STUDY BEHAVIOUR

In the late 1970s, a trend of operant studies that examined responses other than the instrumental response alone emerged, with operant techniques being widely used as "tools". Honig and Staddon (1977) maintain that technological advances in observational and recording equipment allowed operant researchers to monitor simultaneously various responses apart from the operant behaviour itself. This led to more interesting and less restricted "controlled environment" studies. Honig and Staddon (1977) stressed that this extension:

> "provides a bridge to the ethological study of animal behavior, a field whose avowed interests sometimes appear very different from those of operant psychology...but whose methods are quite similar. Thus, while the pressing of the bar has not passed, it has been supplemented by other concurrent observations" (p.4).

By 1979, Fantino and Logan were suggesting that behavioural psychologists were becoming aware of the need to understand how an animal behaves in its natural environment, in order to understand an animal's behaviour in any situation, including the laboratory setting.

In the 1980s, schedules *per se* were no longer of general interest to many researchers, but rather became tools used to investigate more interesting phenomena. Zeiler (1984) suggested that this lack of interest in and understanding of schedules could be attributed to a dearth of theoretical innovations and conceptual integration. He criticised the existing theories, such as Herrnstein's absolute rate matching law, for having a molar orientation, and looking for "overriding" rules. That is, only descriptions of overall or relative response rates were given, whilst the moment-by-moment behaviour was lost. Cumulative records had largely disappeared from experimental reports, reflecting a "shift in focus from behavior as it occurs in real time to behavior averaged over extended time periods" (Zeiler, 1984, p.491).

Thus, in the 1980s a new approach to schedules emerged, which attempted to integrate learning theory within general evolutionary theory. As a result, adaptation was "reinstated" as the key issue underlying learned behaviour, since such behaviour is an animal's way of coping with its environment. Zeiler (1984) summises that: "schedule performance, then, is properly viewed as a foraging strategy rather than as an invariant" (p.492). He concludes that psychologists, and more specifically "schedule enthusiasts", should realise the importance of a biological orientation. If this is accomplished, then the "sleeping giant" (*i.e.*, schedule research) will be "reawakened by the freeing of the experimental analysis of individual behavior from the orthogonal conceptual biases of the past" (Zeiler, 1984, p.492).

A decade later, researchers such as Dall, Cuthill, Cook and Morphet (1997) continue to discuss schedules of reinforcement as tools to study animal foraging behaviour. They point out that the integration of psychological principles (behavioural analysis) with theoretical frameworks developed by behavioural ecologists (*e.g.*, delay-reduction, optimal choice) has led to the use of laboratory tasks that are "functionally similar to foraging tasks that would be faced in the wild" (p.181). Dall et al (1997) point out that lever pressing and search effort in rats is "equivalent" (Dallery & Baum, 1991) and search effort can be modelled by variable-ratio schedules (Hanson, 1987).

When operant approaches are used to test optimal foraging theory in the laboratory, the ecological relevance of schedules of reinforcements still poses a problem (Dall et al, 1997). Schedules of reinforcement tend to model general foraging strategies rather than experiences faced by specific animals in natural environments (or ecologically realistic foraging strategies). Dall et al (1997) maintain that research should be based on knowledge about ecological problems that a species is likely to encounter in the wild. Important ecological features should then be incorporated into a well-designed experiment that manipulates the key variables in an ecologically relevant way.

Dall et al (1997) conducted a study of starlings foraging for topsoil invertebrates, that combined a field study with a laboratory experiment. The field study was used to determine the aggregation of earthworms on a sheep pasture. The laboratory experiments then used this information to choose schedules of reinforcement that simulated the observed scales of prey aggregation, or "potential natural search-effort-prey-encounter contingencies" (Dall et al, 1997, p.182). The schedules of reinforcement were ratio based, so that the "dependence of prey encounter on active searching" could be simulated (Dall et al, 1997, p.182). Experimental testing took place in an operant cage containing a feeder, drinking fountain and operant perch. The food trough was covered by a plastic door that was pushed in by the starling's beak, a behaviour that was topographically similar to a bird probing topsoil for earthworms.

Dall et al (1997) shaped the responses of hopping on the operant perch, and probing at the feeder (chained FR 3 hops & FR 2 probes) during training. The hopping response was designed to emulate the bounding or short walks that starlings demonstrate when they probe for topsoil invertebrates. However, only probing was directly reinforced, since probing is required to obtain prey items in the wild. Two schedules of reinforcement were used that simulated a "dispersed" (reinforcer delivered after either 10 feeder probes or one perch hop) and "clumped" (after 50 feeder probes or 5 perch hops, the next five probes were reinforced- a chained FR50 FR1 schedule) aggregation of prey items. The "clumped" schedule of reinforcement represented the field situation in which a starling's reinforced probe would guarantee that the next few probes would also be reinforced. The "dispersed" schedule of reinforcement represented a field situation in which a starling's reinforced probe is unlikely to be followed by reinforcement for the next few probes. The field sampling study had shown that more prey was likely to be found within one step (4cm) and less likely to be found after 16 steps (64cm).

Dall et al (1997) found that starlings quickly "adapted" to both schedules of reinforcement, as demonstrated by efficient responding that minimised the number of responses to reinforcement. Performance was slightly more efficient in the simpler "dispersed" situation. Dall et al (1997) conclude that starlings are able to exploit patchy prey types, since they demonstrate "flexible learning of the extremes of the reinforcement schedules (ratio based) that will be encountered when foraging for such prey" (p.190).

The most important finding of the study conducted by Dall et al (1997) is that an ecologically relevant foraging problem was simulated by schedules of reinforcement in the laboratory, based on factors elucidated by an ecological sampling field study. They refer to Fantino and Logan's (1979) work as presenting a "biologically informed" approach, and maintain that such an approach can be enhanced by combining the precise methods of experimental psychology with the external validity of field ecology (p.191).

Combining experimental and observational techniques, and studying behaviour in a variety of settings will be discussed further in the next chapter. Other examples of schedules of reinforcement as models of foraging will be discussed near the end of this chapter.

3.2 SCHEDULES OF INTERMITTENT REINFORCEMENT

The publication of Ferster and Skinner's (1957) book, *Schedules of Reinforcement*, is often considered to be the starting point of current work on schedules of intermittent reinforcement. However, fixed-ratio and fixed-interval schedules were already in use (albeit under different names) at least two decades earlier, as formulated in Skinner's (1938) book, *The Behavior of Organisms*. This work does not use the current terminology of schedules of reinforcement. Instead, fixed-interval and fixed-ratio schedules are referred to respectively as: periodic reconditioning and reconditioning at a fixed ratio.

Two concepts fundamental to Skinner's early (1938) work are the *reflex* and *reflex reserve*. The former represents the "observed relation" between a stimulus and response, whilst the latter refers to "a hypothetical entity" which is "a convenient way of representing a particular relation that obtains between the activity of a reflex and its subsequent strength" (Skinner, 1938, p.26). Within a year of its publication, *The Behavior of Organisms* was being hailed as "an extensive theoretical treatment of behavior" with a novel approach (Ellson, 1939, p.566). However, the "new and rather radical" *reflex reserve* concept and its "subsidiary principles" were heavily criticised for being illogical, restrictive and impossible to measure directly (*ibid*, p.566). In addition, Ellson (1939) questioned Skinner's use of the *rate of response* parameter to the exclusion of all others (except a brief mention of *amplitude of response*). The *reflex reserve* principle was never upheld, or indeed referred to in Skinner's later works.

Despite its flaws, outdated terminology, and the fact that it has been largely superseded by *Schedules of Reinforcement*, Skinner's (1938) study used *rats* exclusively as subjects rather than *pigeons*, which predominate in the 1957 work. Thus, it lays the basic groundwork for any study examining schedules of reinforcement with rats serving as subjects.

Zeiler (1977) emphasises that: "schedules of reinforcement are among the most powerful determinants of behavior", each with its own characteristic and orderly effects (p.201). So influential have stable and systematic performances been, that Sidman (1960) posits the use of schedules to test the adequacy of experimental control. If a typical schedule performance is not achieved, then extraneous variables of some description are interfering and preventing the experimental situation from being adequately "controlled" (Sidman, 1960). However, apart from the order and replicability of results generated by schedules, Zeiler (1996) emphasises that "schedules play a major role in the life of animals. To understand why animals behave, we must know how schedules work" (p.549). As will be discussed subsequently, Zeiler (1996) also maintains that "(b)iological thinking is the most promising source we now have for finding a correspondence-like principle that could provide meaning to the past half-century of schedule research" (p.550).

3.3 FIXED-RATIO SCHEDULES AND EXPLORATORY BEHAVIOUR

Litchfield (1987) examined exploratory behaviour in the laboratory rat under conditions of intermittent food-reinforcement (FR 30 schedule), continuous reinforcement and extinction. An "open-field" style exploration (Skinner) box was used, with a soft substrate (sawdust). Two groups of three removable objects were clipped onto the floor of the exploration box when required. A number of behavioural measures (frequency & duration) were used to score: exploratory behaviour directed at the stimulus objects; exploratory behaviour directed at the peripheral areas of the apparatus; behaviour directed at the bar and food-trough area; and displacement behaviour. Observations were recorded for three schedule and three extinction sessions. Stimulus objects were either present during schedule running (FR 30 or CRF) or present only during extinction sessions (after FR 30 or CRF).

A substantial amount of each of the behaviours scored occurred during the post-reinforcement pauses (PRPs). The frequency and duration measure of each of the behaviours during the PRPs represented at least a third of the total value. All behaviours examined were present during the PRPs. Typically, these findings would be accounted for in part by the aversive nature of the PRPs (Dinsmoor, Lee & Brown, 1986). The stimuli present during the PRPs are held to be negative predictors of food. They have aversive properties, which tend to suppress operant responding. PRPs had typically been considered as aversive periods of "non-responding".

Unlike the schedule-induced behaviours reported by researchers such as Falk (1971), the behaviours observed by Litchfield (1987) were considered to be of adaptive significance to rats, and not "out-of-context". Importantly, this study shows that rats do not remain passive during PRPs. Instead, a variety of behaviours were shown to occur, which are largely exploratory in nature. The PRP provided rats with an opportunity to explore their surroundings, or to engage in other behaviours. Once a food pellet has been consumed, the animal is able to investigate the objects and other areas of the apparatus, in an effort to locate alternative sources of food, maintain familiarity with surroundings, or seek sources of novel stimulation. After a while, the rat then returns to the manipulandum and its known food source.

3.4 EXTINCTION AND EXPLORATORY BEHAVIOUR

Skinner (1938) describes extinction as the "act of withholding reinforcement", which is the reciprocal process of conditioning (p.65). Millenson and Leslie (1979) state that extinction of the instrumental response occurs when: "a previously reinforced operant is no longer followed by its usual reinforcing consequence", resulting in a decline in the frequency of the operant (p.49). These researchers point out that psychologists tend to use the term *extinction* in two different ways. One refers to the actual experimental *procedure* which breaks the response-reinforcer contingency, whilst the other refers to the *process*, or observed decline in the frequency of the instrumental response as a result of the procedure (Millenson & Leslie, 1979, p.50). In the following sections, the word *extinction* will primarily be used with respect to the experimental procedure of withholding reinforcement.

Forster (1986) points out that few studies have concentrated on both exploration and extinction. Fewer still have considered exploration as an outcome of the extinction process. Harcourt (1983) demonstrated a strong relationship between exploratory behaviour and extinction in *Rattus norvegicus*. His study reinforced and extinguished exploration as the operant, or instrumental response. Reinforcements were delivered at the stimulus objects in an exploration box, thereby strengthening exploratory behaviour. During extinction the reinforcements were withheld, resulting in a reduction of exploration. Forster (1986) reinterpreted these findings by positing that the exploratory behaviour, which decreased, was not the behaviour that had previously been reinforced. She suggests that *novel* exploratory behaviour occurs at the onset of extinction, and thus exploration of a different *topography* may have been present (& unaccounted for) in the Harcourt (1983) study.

Exploratory behaviour was found to be an outcome of extinction by Forster (1986). Over three extinction sessions, the behavioural measures pertaining to exploration and bar-related activity decreased significantly. Such declines were seen to reflect decreasing novelty coupled with the effectiveness of extinction. Litchfield (1987) expanded upon these studies by investigating a schedule of intermittent reinforcement (FR), exploration, and extinction (with similar findings for the extinction sessions).

In a follow-up study, Forster (1992, 1995) investigated exploratory behaviour in association with the extinction process. However, in this instance, rats were either conditioned to bar press (with paws) or key push (with noses). A control group was not conditioned to perform either operant response. She found that during extinction, the rats trained to perform an operant task engaged in more exploratory behaviour in the form of "nose contacts" (included biting) than the control rats (no training). However, this effect did not extend to the other measures of object-directed exploration ("sniffing objects" or "touching objects with paws"). As expected, the operant responses declined over extinction sessions, as did exploratory behaviour (as a result of habituation). During the first 15-minute extinction session, the animals trained to key-push with their noses, contacted objects more with their noses than the other groups (response generalisation), but this effect was not observed in subsequent sessions.

3.5 CHARACTERISTICS OF SCHEDULES OF INTERMITTENT FOOD-REINFORCEMENT

Schedules of intermittent food-reinforcement are characterised by a number of properties, which will be discussed in this section (*e.g.*, aversive nature of stimuli occurring early in the interval between reinforcers, patterns of responding, rates of response, & amplitude of response).

> "The importance of the intermittent reinforcement procedure rests on the facts that first, each schedule of reinforcement produces its own characteristic pattern of responding: this tells us something about the way the organism adapts to reinforcement contingencies, and secondly, response rates on intermittent reinforcement schedules are usually higher than with continuous reinforcement; this gives a sound baseline on which the effects of other variables (for example, drugs) can be assessed" (Davey, 1981, p.43).

3.5.1 AVERSIVE PROPERTIES OF STIMULI OCCURRING EARLY IN THE INTERVAL BETWEEN REINFORCERS

Dinsmoor et al (1986) postulate that stimuli constantly preceding the reinforcer by a very *short* interval of time become *positively* reinforcing. Likewise, those stimuli that are characteristically present early in the interval between reinforcers, that is, preceding the reinforcer by a *long* amount of time, become *aversive* reinforcers. Some stimuli are more aversive (or negative) than others depending on their temporal position with respect to the reinforcer (Dinsmoor et al, 1986). These researchers used "retired" White Carneaux breeding hens in a task that presented a series of colours on the keys (to be pecked) before each reinforcer delivery. They suggest that parallels could be drawn between their task and Ferster and Skinner's (1957) chained schedule.

Stimuli occurring early in the interval between reinforcer deliveries are negative predictors of food, and consequently produce an inhibitory effect on operant responding. Dinsmoor et al (1986) suggest that this is reflected in a decreased rate of pecking in the presence of the initial stimulus (in a series of stimuli preceding reinforcement), which serves as a negative reinforcer. These researchers maintain that the same "relative-time" theoretical construct can be used to explain the post-reinforcement pause, which precedes responding on large fixed-ratio or fixed-interval schedules of reinforcement. Again the early part of the interval between reinforcers is considered to be aversive, and stimuli associated with this part of the interval suppress operant responding in their presence (Dinsmoor et al, 1986). Other studies dealing with schedule-induced or adjunctive behaviours support the suggestion that the stimuli present during the post-reinforcement pause have aversive properties. For example, Gentry (1968) found that "aggressive" behaviour is usually produced during the post-reinforcement pause.

Dinsmoor et al (1986) state that various explanations for the aversive nature of stimuli at the start of a ratio or interval have been posited. These include frustration, fatigue, the size of the forthcoming ratio or interval, and the energy cost of the required responding. Dinsmoor and his coworkers stress that each of these postulations is in some way inadequate. They conclude that the duration of the post-reinforcement pause is in part determined by the time to the next delivery of a food-reinforcement. In summary, Dinsmoor et al (1986) state:

> "Stimuli arising early in the interval between food deliveries appear not only to be inhibitory but also to be aversive to the subject in a wide variety of experimental contexts" (p.277).

3.5.2 RATE OF RESPONSE

This parameter has always played a major role in Skinner's operant studies. He aimed his 1938 study at demonstrating "that the rate of responding is the principle measure of the strength of an operant", emphasising:

> "that the main datum to be measured in the study of the dynamic laws of an operant is the length of time elapsing between a response and the response immediately preceding it or, in other words, the rate of responding" (p.58).

Despite the fact that Skinner (1938) justified his preoccupation with the rate of response on the grounds of practical and time constraints (the study took six years to complete), he was immediately criticised upon publication of *The Behavior of Organisms*:

> "Only one characteristic of the response is measured: the interval between responses, or 'rate of response'. Responses are graphed cumulatively against time so that the rate of response at any point is indicated by the slope of the curve" (Ellson, 1939, p.567).

The rate of response of key pecking (in pigeons) or bar-pressing (in rats), being "emitted by a freely moving organism" remains a central issue in Ferster and Skinner's 1957 study (p.7). In fact, this parameter again forms the "basic datum", being readily determined from their cumulative records, which show any change in rate.

Ferster and Skinner (1957) attribute the difference in rate of responding on fixed-ratio and fixed-interval schedules to the fact that only fixed-interval schedules differentially reinforce longer inter-response times (*i.e.*, time between individual instrumental responses). This occurs on fixed-interval schedules because the lower rate of responding, the longer time between responses and consequently the greater the probability that the next key-peck or bar-press will be reinforced. Davey (1981) adds that reinforced inter-response times on fixed-interval schedules tend to become progressively longer. Herrnstein (1970) suggests that fixed-interval schedules implicitly "penalize" rapid rates of responding, since this would unnecessarily increase the work expenditure per reinforcement. By contrast, fixed-ratio schedules "may favor rapid responding by arranging a direct proportionality between the rate of responding and the rate of reinforcement" (Herrnstein, 1970, p.244). Thus, the faster the responding on fixed-ratio schedules, the greater the rate of reinforcement. Eventually, the response rate reaches a "ceiling", beyond which the rate cannot increase further (Davey, 1981).

3.5.2.1 WITHIN-SESSION DECREASES IN RATE OF RESPONSE

Although there is a typical pattern of responding for each of the "simple" schedules of intermittent reinforcement, the rate of response can vary within sessions. McSweeney and Roll (1998) suggest that the rate of response within a session can increase or decrease, or increase and then decrease. A variety of "failed" explanations have attempted to account for such within-session changes, including muscular warm-up and fatigue, interference from exploration or adjunctive behaviours, changes in attention or motivation, and more. McSweeney and Roll (1998) maintain that the most likely explanation for late-session decreases in rate of response is that the effectiveness of the operant reinforcer (or Pavlovian unconditioned stimulus) decreases as a result of satiation or habituation. That is: "reinforcers lose their ability to support instrumental responding as subjects satiate or habituate to them" (McSweeney & Roll, 1998, p.428). These researchers maintain that since a reinforcer is a stimulus, then repeated presentation of (or prolonged exposure to) that stimulus can result in habituation (as occurs with other stimuli). That is, habituation to food (a positive reinforcer) can occur, which may limit consumption, or serve as one of many factors that contribute to satiation.

McSweeney and Roll (1998) provide a number of examples, and discuss (& reject) a number of definitions of satiation and habituation. They suggest that research has not convincingly supported satiation as the factor responsible for late-session decreases in operant responding, nor for early-session increases. McSweeney and Roll (1998) found that "within-session changes in operant responding share 12 characteristics with habituated responding" (p.432), which suggests that these processes share a common mechanism. The critical variable for within-session changes as a result of habituation is "exposure to the sensory aspects of the reinforcer", or stimulus specificity (McSweeney & Roll, 1998, p.434). They point out that habituation occurs to both ingestive (*e.g.*, food or water) and noningestive (*e.g.*, lights or tones) stimuli, whereas satiation is usually only associated with ingestive stimuli. Habituation and extinction also share similar empirical properties (*e.g.*, dishabituation or disinhibition, spontaneous recovery). McSweeney and Roll (1998) stress that researchers must abandon the assumption that habituation only occurs for "reflexive" or "biologically irrelevant" stimuli. They conclude that habituation can account for temporal changes in responding in both Pavlovian and operant conditioning situations.

3.5.2.2 FIXED-INTERVAL SCHEDULE RATES OF RESPONSE

Skinner (1938) describes periodic reconditioning (*i.e.*, a fixed-interval schedule) as a process in which "the periodicity of the reinforcement" is "held constant", or in other words, where "reconditioning is periodically repeated at some interval" (p.117). Ferster and Skinner (1957) describe a fixed-interval (FI) intermittent schedule of reinforcement as one in which:

> "...the first response after a designated interval of time is followed by a reinforcing stimulus. It is programmed by a timer which starts from zero after each reinforcement (or from the start of the session) and closes a circuit ("sets up" a reinforcement) at the end of a designated time. The first response following this period operates the magazine" (p.133).

As these researchers point out, the reinforced response does not always immediately follow the designated time interval, but may take place some time after the required time has elapsed. Researchers and programmers must therefore decide whether to time the interval from the end of the previous interval, or from the reinforcement (which may be some time after the set interval). The fixed intervals used by Ferster and Skinner (1957), were timed from the reinforced response. They stress that fixed-interval schedules are characterised by bursts of responding near the "time of reinforcement", and thus there is typically little difference between the two timing strategies.

Fixed-interval schedules are characterised by a pattern of responding: "in which a pause follows each reinforcement, after which the rate accelerates to a terminal (usually moderate) value" (Ferster & Skinner, 1957, p.134). This results in the distinctive "scalloped pattern" of cumulative records for this schedule of reinforcement (Davey, 1981). At the beginning of the interval, when the animal will not be reinforced, there is a low rate of responding, whereas, towards the end of the interval, when reinforcement is likely, there is typically a higher rate of responding. In fact, fixed-interval schedules tend to reinforce differentially low rates of responding, and lengthen pauses, since: "the longer the interval since the last response, the more likely the next response is to be reinforced" (Ferster & Skinner, 1957, p.134).

On an FI one-minute schedule of reinforcement, run over five sessions, Ferster and Skinner (1957) found that the pause-after-reinforcement was usually between fifteen and thirty seconds in length, and was subsequently followed by a smooth acceleration of responding to a terminal rate. However, a PAR did not follow all reinforcements. Instead: "...the terminal rate is assumed immediately following the reinforcement and is maintained until the next reinforcement" (Ferster & Skinner, 1957, p.157). In another case, during the 56th session of FI one minute (after CRF), the pigeon usually paused for between ten and thirty seconds after reinforcement. However, on a number of occasions the bird responded immediately after reinforcement and continued responding throughout the one-minute interval (Ferster & Skinner, 1957, p.197).

> "To the extent that the bird's behavior is an event varying in time and correlating consistently with the FI schedule, it can be thought of as a clock by which the bird may modify its behavior with respect to reinforcement. The terminal rate at the end of the fixed interval represents the most optimal setting of the clock, and the curvature represents intermediate clock-settings. With a perfect clock an interval should contain only a single response. The bird's own behavior, however, is a relatively poor clock" (Ferster & Skinner, 1957, p.266).

Ferster and Skinner (1957) conducted an experiment in which a "clock" was added, consisting of a projected spot of light, which grew in size as the interval lengthened and approached reinforcement. This uniformly changing external stimulus was added in order to investigate the "control exercised by the bird's own behavior" on various FI schedules of reinforcement (Ferster & Skinner, 1957, p.266). On a FI ten-minute schedule, Ferster and Skinner (1957) found that initially the small size of the "clock" was a novel stimulus and suppressed the bird's responding for a period of time (p.267). After a few sessions with the clock, the PAR was greater than half the interval in length (in some cases 85% of the interval). The PAR was followed by rapid acceleration of responding to the terminal rate (over 10 responses per second, after 25 hours), which was up to 35 times greater than before the clock was introduced. The clock was found to control the bird's rate and pattern of responding even during extinction (Ferster & Skinner, 1957, p.269).

There is a noticeable absence of the mention of any pauses (PARs) on FI schedules in Skinner's (1938) early work. In fact, the pattern of responding on FI schedules is depicted as a "fusion of successive extinction curves following the reinforcement of single responses" (p.118). He even suggests, that "it is not possible to tell from the recorded behavior where the successive reinforcements occur" (p.118). Skinner (1938) investigated the bar-pressing response of rats on four FI schedules, with fixed-intervals of three, six, nine and twelve minutes. He suggests, that the rate of responding is a function of the interval between reinforcements or "successive reconditionings", with shorter fixed-interval schedules correlated with greater total numbers of responses (p.120), and lower rates of responding on schedules with "lower frequencies of reinforcement" (p.126).

Skinner (1938) alludes to the possible existence of a PAR, when he discusses the constant rate of response on higher fixed-interval schedules, suggesting that the: "constant rate is attained only through a *reduction* in the rate immediately following reinforcement" (p.126). He goes on to suggest, that a temporal discrimination by the rat is involved in cases where a constant rate manifests itself. The constant rate of response on FI schedules leads Skinner (1938) to suggest that something akin to an "internal clock" exists, allowing the rat to alter its pattern of responding accordingly if the interval is changed. That is, the: " state of the reflex quickly adjusts to a change from, say, five to six minutes between reinforcements, and the organism might therefore be said (inaccurately, I am contending) to distinguish between five- and six-minute intervals" (Skinner, 1938, p.164).

The post-reinforcement pause and the fixed-interval "scallop"

The distinctive "scalloped pattern" of the fixed-interval cumulative records is considered to be a robust phenomenon, since it occurs with a variety of reinforcers and responses, and has even been observed in pigeons run on FI27-hour schedules (Davey, 1981). Davey (1981) suggests that typically it is held to "reflect a temporal discrimination on the part of the animal" (p.63). There appears to be a direct relationship between the duration of the post-reinforcement pause and the fixed-interval value (as long as it is greater than 10 seconds). The length of the post-reinforcement pause is usually two-thirds of the fixed-interval value (Davey, 1981; Schneider, 1969). Davey (1981) states that that there are three main hypotheses relating to the fixed-interval scallop. The first of these suggests that scallops occur as a result of response chaining. The second hypothesis posits delay of reinforcement as the factor responsible for the scallop. Temporal control by the reinforcing stimulus is the third reason given for the FI scallop.

Davey (1981) concludes that experimental evidence favours the view that temporal control of responding by the reinforcing stimulus is the most likely explanation for the development of the "scalloped" pattern of responding on fixed-interval schedules.

3.5.2.3 VARIABLE-INTERVAL SCHEDULE RATES OF RESPONSE

Unlike the "fixed" schedules, which establish "a correlation between behavior and reinforcement", the variable-interval schedule "is designed to produce a constant rate by not permitting any feature of the bird's behavior to acquire discriminative properties" (Ferster & Skinner, 1957, p.326). The intervals between reinforcements vary randomly (or almost randomly in some cases). Variable-interval schedules with the same mean interval may have different distributions of intervals. The largest and smallest (usually zero or close to zero) intervals may be different, as may be the size and number of steps in a series to be randomised. Ferster and Skinner (1957) describe three types of VI schedules. An "arithmetic" VI schedule specifies the largest and smallest intervals. A "geometric" VI schedule specifies the mean interval of reinforcement, as well as the shortest interval and progression of intervals in a series. The third type is the "Fibonnacci" VI schedule, which specifies that successive terms in the interval series can be obtained by adding the previous two numbers together (Fibonnacci numbers).

Ferster and Skinner (1957) use a number of different types of variable-interval schedules (with arithmetic, geometric & Fibonnacci series of intervals), and stress that strict randomisation of the sets of intervals is not attempted, since this increases the probability of many long or short intervals occurring in a row. These researchers found that pigeons responded at fairly uniform rates for long periods of time on variable-interval schedules. Typically, there is no pause after reinforcement. In fact, there may be an increase in the rate of response immediately after reinforcement, which then declines to an intermediate rate for the remainder of the interval. In a 14-hour session approximately 87,000 responses were made by a pigeon which was "fully under control of the schedule" and a "performance of this magnitude may be repeated on a daily schedule" (Ferster & Skinner, 1957, p.338). The typical cumulative record is quite linear in appearance, but with "oscillations" in rate depending on the way in which reinforcements are grouped on the variable-interval schedule.

Ferster and Skinner (1957) ran pigeons on a VI one-minute schedule of reinforcement after continuous reinforcement (arithmetic series of intervals ranging from 0 to 2 minutes in steps of 10 seconds). Over 16 sessions, apart from "slight oscillations", the bird's performance was at an "approximately constant rate of responding with no rate change correlated with any feature of the schedule" (Ferster & Skinner, 1957, p.327). The overall rate between birds varied from about 0.8 to 1.5 responses per second. In another case, two birds were run on a VI one-minute schedule (after CRF) for three sessions of 60 reinforcements. The overall rate for the last session was 0.35 responses per second, and a mean of 20 responses were made per reinforcement.

In one experiment, Ferster and Skinner (1957) fed two food-deprived birds just prior to an experimental session (on a geometric VI 7-minute schedule of reinforcement). The amount of food provided before the session varied from 10 to 80 grams. The latter amount was 20% of the bird's body-weight. Surprisingly, pre-feeding had no apparent effect on the performance during the variable-interval schedule (except for a decline in the rate of one bird when fed the maximum amount of 80 grams). Ferster and Skinner (1957) conclude that the variable-interval schedule seems "to be less sensitive to variables such as level of deprivation and drugs" (p.372).

3.5.2.4 VARIABLE-RATIO SCHEDULE RATES OF RESPONSE

Ferster and Skinner (1957) describe a variable-interval schedule of reinforcement as one in which "reinforcement occurs after a given number of responses, the number varying unpredictably from reinforcement to reinforcement" (p.391). Further, like fixed-ratio schedules "it arranges for differential reinforcement of high rates" with "few instances where a reinforcement occurs after a pause" (Ferster & Skinner, 1957, p.391). These researchers ran birds on arithmetic VR40 and VR50 (approximately) schedules following continuous reinforcement. The largest ratio was about 100, and successive responses were sometimes reinforced. High overall rates developed rapidly. As Ferster and Skinner (1957) assert, high rates of responding result in high frequencies of reinforcement, which sustain high rates of responding. After the mean ratio was increased to 360 (over 16 sessions), the pigeons' responding increased immediately after reinforcement. This period of high response rate was then followed by a period of responding at a lower rate, or a pause (prior to another run of responses). Thus, pauses may occur, but not immediately after reinforcement. Such pauses can be very long (a one-hour long pause was reported by Ferster & Skinner, 1957).

In one study, Ferster and Skinner (1957) changed the schedule of reinforcement from VR 360 to FR 360 and then back again. They suggest that both schedules should result in a differential reinforcement of high rates, but that "the bird's own behavior may serve as a counter with FR" (Ferster & Skinner, 1957, p.407). Only during the third session on FR 360 do post-reinforcement pauses regularly appear. Overall rates of responding fall as the session progresses, and post-reinforcement pauses become longer. Prior to the third session, reinforcement was followed by a "priming" run of responses. That is, the bird responded at a high rate following reinforcement before pausing. For one of the birds, when the FR 360 schedule was changed back to the VR 360 schedule, less than 10 reinforcements were received before the transition to variable-ratio performance was accomplished. The longer pauses disappeared and the high rates of responding immediately after reinforcement reappeared. After 18 sessions of VR 360 the schedule was again changed to FR 360. Throughout the session following the change, a post-reinforcement pause and acceleration to a terminal rate gradually appeared. Initially, reinforcements were followed by 25 to 75 responses at the terminal rate (a "priming" run).

3.5.2.5 DIFFERENTIAL REINFORCEMENT OF LOW RATES SCHEDULE RATES OF RESPONSE

A differential reinforcement of low rate schedule requires a minimum amount of time to elapse between two responses before a reinforcer is delivered. To obtain a reinforcer (*e.g.*, food pellet) on a DRL15-s schedule, for example, the animal must wait at least 15 seconds since the last response. If a response is made before the 15 seconds has elapsed, that response is not reinforced, and the timer is reset to zero. As their name suggests, DRL schedules tend to produce low rates of responding (Davey, 1981), or very slow and accurately timed responses (Barker, 1997). Millenson and Leslie (1979) describe the DRL schedule as a fifth "simple" schedule (after FI, VI, FR and VR schedules), which is often used to study an animal's ability to time intervals precisely, as well as, the ability to patiently wait for reinforcement. Ferster and Skinner (1957) only used DRL criteria in conjunction with other simple schedules (*e.g.*, a VI 1-minute DRL 6-s schedule- VI 1 drl6- where no response is reinforced unless it is preceded by an IRT of six seconds).

Davey (1981) points out that two characteristic patterns of responding emerge. During the typical experimental session there are periods when the animal receives a constant flow of reinforcers, because the responses are accurately spaced. That is, the IRTs exceed the DRL criterion. However, at other times during the session, the subject emits "bursts" of responses. This results in IRTs that are well below the DRL criterion, and therefore, go unreinforced. If a frequency histogram of IRTs is constructed, Davey (1981) states, that two modes emerge, with one for very short IRTs ("bursts" of responding) and another for IRTs around the DRL criterion (reinforced responses, indicating accurate temporal discrimination). A DRL schedule:

> "might be called a 'single state' schedule in that it generates only states that we call 'pausing'. Most other schedules could be labelled 'two-state' in that they generate a state of pausing followed by a state of responding" (Davey, 1981, pp. 86-87).

Spaced responding on DRL schedules

The fact that a large percentage of IRTs are emitted around the DRL criterion, resulting in the subject receiving a reinforcer, suggests that the animal is able to make a temporal discrimination and accurately space its responses. Davey (1981) maintains that two explanations may account for this ability to space responding. Firstly, mediating or collateral behaviours may aid efficient DRL responding. Secondly, temporal discrimination may be taking place.

Collateral or mediating behaviours are stereotyped patterns of behaviour that appear when animals are trained on DRL schedules. Davey (1981) points out that a number of researchers maintain that these stereotyped chains of behaviour have been "adventitiously" or "superstitiously" reinforced (p.83). Collateral behaviours help the animal "fill" the temporal interval that is specified by the particular DRL schedule, and may aid in efficient and accurate operant responding. Wilson and Keller (1953) found that after every bar press, a rat run on a DRL schedule:

> "went to the water bottle and climbed on it, climbed the ventilation holes in the rear of the cage, poked its nose at the glass cover over the cage, and returned to the bar" (Davey, 1981, p.83).

Barker (1997) found that after being run on DRL-15s schedules for several weeks, *Rhesus macaques* become "incredibly efficient" (p.250). During a four-minute session, one monkey produced only one nonreinforced response (14:97 seconds). The other interresponse latencies ranged from 15:02 to 15:14 seconds. Barker (1997) suggests that such a schedule produces "fine control over local rates of response", and is analagous to behaviour that requires "rhythm and pacing" (p.250). One of the *Rhesus* monkeys studied by Barker (1997) in the 1960s was so accurate in her timing that responses were within hundredths of a second of the required 15 seconds. He suggests that the collateral behaviours, a "sequenced pattern resembling rhythmic counting", observed helped the monkey achieve such accuracy (Barker, 1997, p.438). He even states that the monkey was counting:

> "After making a reinforced response, this seated monkey would (a) rhythmically chew the pellet for a few seconds; (b) then begin to sway from side to side, metronome-like, for the next few seconds; (c) then still swaying, with her left hand begin to rhythmically tap the upper center section of the performance panel positioned in front of her; (d) then, as the end of the 15-second interval approached, with exaggerated intensity her sway switched from side to side to front to back, and her tapping speeded up to about two taps per second; and (e) finally, with her right hand she deftly slapped the appropriate lever located on the lower left-hand portion of the performance panel. She would then pick up her sucrose pellet and begin the sequenced pattern again" (Barker, 1997, p.438).

Barker (1997) is careful to point out that the rigorous methodology and framework adhered to by Skinner and other behaviourists has accounted for animal learning and behaviour "without formally acknowledging the cognitive processes of *paying attention*, of *remembering*, and of *memory*" (p.439). However, Barker (1997) posits that such cognitive processes, if used cautiously, may help explain complex animal behaviour (*e.g.*, counting, timing, maze learning, rule learning *etc*) and "bridge the gap" between human and animal behaviour.

Davey (1981) suggests that overt collateral behaviours are not observed in all cases where efficient DRL responding has been established. Furthermore, superstitious reinforcement (which may have built up chains of collateral behaviour) is not considered to be a major determinant of behaviour. Mediating behaviour may aid in the acquisition of efficient DRL behaviour, but the animal must still be making some kind of a temporal discrimination. Davey (1981) states that:

> "In view of the extremely efficient and stable DRL performances that animals exhibit it seems highly unlikely that such a 'fragile' process as superstitious reinforcement could be solely responsible...mediating behaviour cannot really act as a substitute for temporal discrimination" (p.84).

As Davey (1981) points out, both fixed-interval and DRL schedules specify fixed temporal contingencies, and produce pauses, which suggests that temporal discriminations are being made. On fixed-interval schedules, the occurrence of the reinforcer acts as a temporally predictive stimulus. On DRL schedules, however, animals also appear to be able to space responses efficiently after non-reinforced responses. Thus, Davey (1981) asserts that these non-reinforced responses are also able to "act as stimuli exerting temporal control" (p.84). He concludes that the spaced responding observed on DRL schedules may be controlled by responses that act as "temporal inhibitory stimuli" (p.85).

"Bursts" of responding or very short inter-response times (IRTs) on DRL schedules

As Davey (1981) reports, short IRTs (*i.e.*, 2 seconds or less) are the category furthest from the DRL criterion, and yet such "bursts" of responding (which are never reinforced) are persistent on DRL schedules. Again, there are two main explanations for this phenomenon. Firstly, such "bursts" occur as a result of frustration. Secondly, the "bursts" provide the subject with response feedback.

Amsel's (1958) ***frustration theory*** suggests that an organism's history of reinforcement sets up an "expectation" concerning the consequence of responding. If these expectations are "thwarted", for example putting the organism on extinction after continuous reinforcement, then frustration may occur (Barker, 1997). That is, an "expected" reward is omitted (Davey, 1981). As Davey (1981) states, response bursts on DRL schedules tend to occur after non-reinforced inter-response times just short of the DRL criterion, or after a non-reinforced response has followed a run of reinforced responses. In these cases it is possible that the animal was expecting the reward, which was not forthcoming, resulting in a "frustrative burst" (Davey, 1981, p.86). However, Davey (1981) stresses that the concept of frustration is hypothetical and has been criticised by a number of researchers.

Response bursts may provide response feedback to the animal, and as such facilitate more accurate timing behaviour. The "animal can be confident that he has made a response and can time the interval from this point" (Davey, 1981, p.86). If an audible "click" is provided as feedback for each response, bursts are found to decline, lending support to the suggestion that these bursts provide feedback (Davey, 1981; Kelleher, Fry & Cook, 1959).

Davey (1981) maintains that both factors (frustration & response feedback) may account for the response bursts observed during DRL schedules. He also points out that "bursts" of responding are found on other schedules of reinforcement, and as such may just be a "facet of behaviour which is insensitive to schedule control" (p.86).

3.5.3 AMPLITUDE OR "STRENGTH" OF RESPONSE

Skinner (1938) instigated the investigation of the intensive properties (*i.e.*, force) of responses. In his early studies using albino and hooded rats, he employed a rather primitive method of measuring the force of a rat's bar press. Every time the rat pressed the lever down, a ballistic pendulum would correspondingly move, with the "excursion of the pendulum" being a "function of the force with which the lever is pressed (Skinner, 1938, p.310). This apparatus was in turn connected to a "force-recording" kymograph, a forerunner of the cumulative recorder. Skinner (1938) suggests that the mean force remains relatively constant throughout reinforced responding, but the force of individual responses varies.

Skinner (1938) states that the following variations in force (& hence achievement of a criterion response) prevail under conditions of continuous reinforcement. Firstly, a successful response is made (*i.e.*, criterion is reached). Then the force decreases, and the next response is unsuccessful (*i.e.*, criterion is not reached). Finally, as a consequence of non-reinforcement the force increases, and the next response is reinforced (Skinner, 1938). In addition, rats "tend to adjust to a force which secures only slightly above the reinforcement of every other response" (Skinner, 1938, p.317). During extinction the force of a response also varies. Skinner (1938) states that initially an increase in force occurs, which subsequently declines to a very low value. Furthermore, this change in force observed during extinction is, in general, independent of the rate of response. Skinner (1938) concludes that changes in the intensity of a response are less dramatic than changes in the rate of response. Consequently, the "intensity of the response in an operant is significant only in relation to the differentiative history of the organism", where differentiation refers to the "discrimination of the form of the response" (Skinner, 1938, pp. 340 & 309).

3.6 MAJOR EXTINCTION EFFECTS FOLLOWING SCHEDULES OF INTERMITTENT REINFORCEMENT

Skinner (1938) describes extinction as the "act of withholding reinforcement", which is the reciprocal process of conditioning (p.65). Millenson and Leslie (1979) state that extinction of the instrumental response occurs when "a previously reinforced operant is no longer followed by its usual reinforcing consequence", resulting in a decline in the frequency of the operant (p.49). These researchers point out that psychologists tend to use the term extinction in two different ways. One refers to the actual experimental procedure, which breaks the response-reinforcer contingency. The other refers to the process or observed decline in the frequency of the instrumental response as a result of the procedure (p.50). In this chapter, the word extinction will primarily be used with respect to the experimental procedure of withholding reinforcement.

3.6.1 RATE OF RESPONSE

"The decline in rate of the once-reinforced response is the best-documented effect of extinction" (Millenson & Leslie, 1979, p.50). Towards the end of extinction rats typically respond at a rate that is just above the "operant-level" rate. Millenson and Leslie (1979) state that in addition to an overall decline in rate of responding, there is often a short transitory period of increased rate of response at the start of extinction. This occurs while the response-reinforcer contingency is "broken", and these researchers use the notion of "time allocation" to explain this finding. That is, much of a rat's time during reinforcement for bar pressing is spent in actually retrieving and consuming the food reinforcers, rather than in producing the instrumental response. Once reinforcements are withheld during extinction, the rat's "retrieval and consumption" time can be allocated to, or "released" for, other behaviours (including instrumental responses). Millenson and Leslie (1979) conclude that the transient increase in the rate of response at the onset of extinction is a result of more time being allocated to bar pressing than during reinforcement.

Ferster and Skinner (1957) did not systematically investigate the rate of response during extinction following each of the major schedules of intermittent reinforcement. For example, they did not systematically study extinction after running pigeons on a variable-interval schedule. Instead, they discuss the extinction curves that occurred as a result of "apparatus failures" (p.346). During variable-interval schedules higher rates of response after reinforcement may be followed by rates that "oscillate" greatly during the longer intervals. Ferster and Skinner (1957) suggest that the rate of response "oscillates" in a similar way during the first part of extinction. This is followed by periods of high rate of response separated by long periods of slow (or near zero) responding. These researchers found that just one reinforcement after hours of extinction following a variable-interval 7-minute schedule, was enough to reinstate the highest rate and result in responding that was not distinguishable from the previous variable-interval responding.

According to Ferster and Skinner (1957), the responding observed during extinction following variable-ratio running reflects the previous variable-ratio responding. That is, most responses occur in sustained runs, which are separated by pauses. Low rates of responding may only be reached after 1000s (as many as 8000) of non-reinforced responses have been made. Nevertheless, extinction occurs fairly rapidly, with most of the responses made early, before rapidly declining to zero. Ferster and Skinner (1957) point out that this is quite different to the extinction curve observed after variable-interval running, which shows a fairly continuous decline in response rate (p.413).

3.6.2 AMPLITUDE OR "STRENGTH" OF RESPONSE

During extinction the force of a response also varies. Skinner (1938) states that initially an increase in force occurs, which subsequently declines to a very low value. Furthermore, this change in force is generally independent of the rate of response. Skinner (1938) suggests that "normal" reinforcement is "made contingent upon the depression of the lever to approximately the mid-point of its excursion", and as a result, only the strong responses that reach this criterion are reinforced (p.323). However, during extinction the weaker (or non-criterion) bar presses may not be recorded, and could only be "checked by watching the rat" (Skinner, 1938, p.323). Skinner (1938) concludes that changes in the intensity of a response are less dramatic than changes in the rate of response.

3.6.3 CHANGES IN THE TOPOGRAPHY OF THE INSTRUMENTAL RESPONSE

During extinction marked changes in the form or topography of the instrumental response occur. One of the earliest reports of a breakdown in response stereotypy during extinction is found in the Guthrie and Horton (1946) study of "pole-tilting" in cats and dogs (Millenson & Leslie, 1979). Various studies using rats and pigeons illustrate this. Antonitis (1951) found that rats, which were conditioned for nose-poking (through a slot in the wall), showed stereotyped responses during reinforcement. Once placed on extinction, the instrumental response became far less stereotyped with respect to its position and angle. Eckerman and Lanson (1969) found that pigeons also demonstrate less stereotyped key-pecks during extinction. Forster (1986) reinterpreted the variations in the instrumental response as "a kind of exploratory behaviour – the pigeons investigate new and different ways of responding" (p.8).

Frick and Miller (1951) report another topographical consequence of extinction in a study using rats as subjects. These researchers found that a breakdown in a conditioned, sequential chain of bar-pressing/food-tray visiting occurred during extinction. Instead of a single bar-press being followed by a single tray visit, and so on in a continuous "loop", the rats began to remain and respond at the bar area or tray area for longer. Thus, as Millenson and Leslie (1979) suggest, placing animals on extinction results in a decline in the frequency of the instrumental response, as well as an increase in the variability of its topography, and a breakdown in the sequential structure of behaviour.

3.6.4 THE *DISCRIMINATION HYPOTHESIS* AND RESISTANCE TO EXTINCTION

The ***discrimination hypothesis*** postulated by Church (1963) states that the greater the similarity between the conditions of conditioning and extinction, the greater the ***resistance to extinction*** will be. That is, it will take longer for the instrumental response to extinguish, if the animal was previously run on a large intermittent schedule of reinforcement than if it was run under conditions of continuous reinforcement. An animal can readily distinguish between the conditions of reinforcement for every bar-press and those of extinction. By contrast, an animal previously run under conditions of intermittent reinforcement may less readily discriminate between the schedule and extinction conditions. This can be attributed to the fact that intermittent schedules of reinforcement incorporate a certain degree of "extinction" anyway, since sequences of unreinforced responses occur regularly. The larger or more variable the schedule the longer it will take for extinction of the instrumental response to occur.

3.7 POLYDIPSIA, AGGRESSION AND OTHER ADJUNCTIVE BEHAVIOURS

Polydipsia (excessive drinking), wheel-running, aggression and pica (*e.g.*, ingestion of wood-shavings) are examples of ***adjunctive behaviours***. Such behaviours typically occur after reinforcement delivery on schedules of intermittent food reinforcement, and at times when food is unavailable (Davey, 1981). Killeen (1975) suggests that these adjunctive behaviours exemplify the: "hyperreactivity to stimuli occurring after reinforcement" on intermittent schedules of food reinforcement (p.89).

Adjunctive behaviours are not only schedule-induced, but can also be induced as a result of extinction. Millenson and Leslie (1979) suggest that the frequency of grooming and investigatory behaviour, or exploration, is lower when an instrumental response is reinforced, but then increases again during extinction. In addition, novel behaviours may appear during extinction. Any of the adjunctive behaviours described by Falk (1971) may appear during extinction, if the opportunity to engage in them is available. Although the behaviours discussed in the following section (3.7.1 – 3.7.4) focus on studies of laboratory rats, there are many other behaviours that can be included in the list of adjunctive behaviours observed in captive environments (e.g., excessive chain-manipulation observed in individually confined pigs, which will be discussed subsequently).

3.7.1 POLYDIPSIA

Polydipsia was first reported by Falk (1961), who discovered this phenomenon in rats responding (bar pressing) on a variable-interval one-minute (VI1-min) schedule of food reinforcement. The animals used were not water-deprived, but nevertheless, they took in amounts of water (from a concurrently available source) equivalent to almost one-half their body weight. Whenever a food pellet was delivered, the rat would consume it rapidly before immediately drinking about 0.5ml of water. The excessive drinking occurred during the post-reinforcement pauses, and took a few sessions to develop properly. Davey (1981) maintains that the occurrence of polydipsia depends mainly on the parameters of the intermittent food schedule. It does not occur on schedules with short "inter-food" times, such as, Fixed-interval <5 seconds and Fixed-ratio 1 (or CRF), and similarly, has an upper limit of two to three minute (mean) inter-food times.

Falk (1971) states that this phenomenon has been confirmed by a number of researchers in a variety of animal species, such as, the rhesus monkey, chimpanzee and pigeon. He describes polydipsia as a food-schedule by-product, suggesting that this finding:

> "was not only an unusual finding-it was an outright absurd one...It is absurd for an animal to drink itself into a dilutional hyponatremia bordering on water intoxication. But perhaps most absurd was not the lack of a metabolic or patho-regulatory reason for the polydipsia, but the lack of an acceptable behavioral account. That is, the behavior is absurd in the sense of philosophical existentialism. Now most animals are probably not philosophical existentialists, but perhaps we have run across a class of behaviors in animals which was imputed to man as his exclusive, if obscure property" (p.577).

Whilst Falk's (1971) philosophical musings may be somewhat bizarre, his study opened up a whole new field of interest, with respect to intermittent schedules of reinforcement. He points out that polydipsia, and other adjunctive behaviours, are not elicited by the schedule conditions or indeed generated as new responses. Rather, certain schedules (coupled with the appropriate environmental conditions) increase the probability of a particular behaviour occurring.

Skinner (1987) in particular was very supportive of Falk's recent work (*e.g.*, Tang & Falk, 1987), describing him as an outstanding authority, whose work overcomes the barriers of several disciplines by examining: “similarities between adjunctive behavior and many of the rituals studied by ethologists on the one hand and by anthropologists on the other” (p.505).

Interestingly, Small and Lillard (1973) maintain that rats drink at a relatively constant rate of six or seven licks per second, across a “wide range” of water-deprivation levels. They suggest that a single “limbic pacemaker mechanism” may control this biological timing, or rhythm of licks and pauses (harmonic intervals or inter-lick intervals), just as it may also control theta activity, vibrissae twitches and heart rate.

Holme (1990) ran twelve rats on an FI120-s schedule of food-reinforcement, in an open-field apparatus (approx. 50 cm x 49 cm x 25 cm) with a soft substrate (wood shavings). Each session was three-hours long, six water bottles were present (only one of these served as a water source), with discrimination stimuli (cards) behind the spout of each bottle. Nine of the rats developed polydipsia (level of water intake was used to measure drinking). Holme (1990) calculated the percentage of total frequency of drinking that took place immediately after reinforcement (*i.e.*, immediately after consumption of the pellet) for four of her rats. Two of these rats had the water bottle positioned close to the feeder, and they drank sustantially more immediately after reinforcement (78.57% compared to 31.82%). The rat that drank the least immediately after reinforcement, drank twice as much during the session as the other rats, and the peak level of water intake varied noticeably between individuals (up to almost 50%). Thus, excessive drinking did not always take place immediately after reinforcement.

3.7.2 “NORMAL” PATTERNS OF FOOD-ASSOCIATED DRINKING IN RATS

Kissileff (1969) investigated the patterns of spontaneous drinking in rats that were neither food-deprived nor water-deprived.The rats lived in the Skinner-box for 12 days (24-hours per day), during which time their feeding and drinking patterns were recorded. Preliminary observations had shown that rats spent about five seconds to eat a food pellet, so in order to “discourage accumulation of pellets, a maximum 5-sec. delay was imposed between pellet delivery” (Kissileff, 1969, p.286). That is, pellets were only dispensed if a barpress occurred at least five seconds after the previous barpress (*i.e.*, a DRL-15s schedule, although he does not refer to it as such). Only the patterns for the “normal” or “intact” rats will be discussed in detail here (*i.e.*, not the desalivate neurolically normal rats or recovered lateral rats).

The “intact” rats fed in short discrete bursts (3 – 6 minutes in length), with lengthy pauses between “meals” (Kissileff, 1969). Typically these discrete “meals” took place at night. Although there were occasional drinks during meals, and there was a close temporal relationship between eating and drinking, drinking also took place in discrete bursts. Rats drank periodically "until a considerable quantity of water was taken" (Kissileff, 1969, p.289). Rats drank between 0.5 and 2.5 ml of water for most (>60%) of the drinking bouts. In addition, almost all (94%) drinking bouts took place within an hour (before or after, although usually after) of meals. Meals were typically only interrupted by the operant (bar pressing) and by short bursts of grooming. By contrast, the other groups of rats (desalivate neurolically normal rats & recovered lateral rats) displayed a "prandial" pattern of drinking. That is, they drank and eat in short alternating bursts (in rapid succession).

3.7.3 AGGRESSION AND ESCAPE BEHAVIOURS

Aggression and escape behaviours are also classified as adjunctive behaviours. Falk (1971) suggests that behaviourists view attack and escape as two mutually exclusive responses, whereas ethologists classify them together as agonistic behaviours (with threat & appeasement behaviours also falling into this category). He suggests that the broader classification recognises the various behavioural outcomes, which may arise from basically the same stimulus situation.

Gentry (1968) found that aggression in pigeons occurred as an adjunct to a fixed-ratio 50 (FR 50) schedule. As with polydipsia, the aggressive behaviour took place during the PRPs. Similarly, Hutchinson, Azrin and Hunt (1968) reported that squirrel monkeys directed biting attacks at a rubber hose during the PRPs when placed on various FR food schedules. Such experiments usually present a target to induce aggression, which for pigeons can be another bird (restrained & alive, or stuffed models). Rats also direct aggression at other animals during the PRPs (Davey, 1981).

Extinction-induced aggression is one of the most spectacular of the adjunctive behaviours. Azrin, Hutchinson and Hake (1966) studied this phenomenon on food-deprived pigeons that were conditioned to key-peck. Once the instrumental response had been successfully conditioned, an immobilised "target" bird (in a specially designed box) was placed into the experimental apparatus. Any attacks at the exposed body of the target bird were recorded. These researchers found that whenever extinction was imposed, vicious and aggressive attacks occurred in bouts that lasted up to ten minutes.

Intermittent schedules of food-reinforcement have also been found to induce adjunctive escape behaviour. Falk (1971) states that pigeons and rats produce self-imposed time-out periods on fixed-ratio schedules, in order to terminate the schedule. In addition, the excessive time spent in these time-outs increases as a function of the FR ratio size. Falk (1971) concludes that attack and escape behaviours appear to be induced by the aversive properties of food schedule parameters.

The rats in Holme's (1990) study did not only demonstrate polydipsia, but they also engaged in aggressive behaviour (vigorous biting &/or pawing) directed at the water bottles. This aggressive behaviour was not only directed at the water source, but rather at any of the six bottles. The rat (5) which attacked its water source the most was not polydipsic. She concluded that the closest bottle(s) provided a convenient target, and aggression was not directed towards the water source. Aggressive behaviours tended to occur "towards the end of the run", as a result of the "accumulating aversiveness of the situation" (Holme, 1990, p.96). Interestingly, the levels of escape-oriented behaviours far exceeded the levels of aggression in Holme's (1990) study, and one rat successfully escaped from the apparatus by climbing out (after pushing the lid aside with its nose). This rat was also polydipsic, engaged in up to three times as many operant responses as the other rats, and also returned to the apparatus after escaping, as a result of "hunger and/or its limited life history" (Holme, 1990, p.102).

3.7.4 PICA, WHEEL-RUNNING AND AIR-LICKING

Villareal (1967) carried out a study in which Rhesus monkeys were placed on a fixed-time 15-minute schedule of food-reinforcement (Falk, 1971). Following the ingestion of a reinforcement pellet (*i.e.*, during the post-reinforcement pauses), these animals ingested large amounts of wood-shavings present on the floor of the experimental apparatus. Pica was only observed during the intermittent schedule sessions, and never at other times (even when similarly food-deprived). The schedule induced levels of pica decreased to zero during extinction.

Falk (1971) states that concurrent wheel-running in food-deprived rats occurs more often on variable-interval one-minute food schedules than on fixed-ratio one (CRF) schedules of reinforcement. This behaviour typically occurs during the middle of inter-food periods, rather than during the post-reinforcement pauses. Davey (1981) maintains that these findings reflect properties of a complex and more general relationship between food and activity, rather than being a post-reinforcement phenomenon. Thus, wheel-running may in fact be a measure of general activity.

Air-licking was a later addition to the list of adjunctive behaviours. Mendelson and Chillag's (1970) study of this behaviour was carried out with rats on a fixed-time one-minute food schedule (Falk, 1971). A continuous stream of air was available from an otherwise empty drinking tube. Licking of this air-stream developed during the post-reinforcement pauses. These researchers found that when the deprivation level of rats was increased, a corresponding increase in air-licking was observed (Davey, 1981).

3.7.5 EXPLANATIONS FOR ADJUNCTIVE BEHAVIOURS

Davey (1989) presents three different explanations for the development of adjunctive behaviours. Firstly, some researchers have proposed that adjuctive behaviours may "become accidentally correlated with the delivery of reinforcement", that is, as a result of *superstitious reinforcement* (Davey, 1989, p.87). However, Davey (1989) suggests that this explanation is unlikely (he provides extensive evidence). Other researchers have favoured the suggestion that adjunctive behaviours occur as a result of *unconditioned elicitation by reinforcement*, since such behaviours typically occur immediately after reinforcement. Again, Davey (1989) maintains that this explanation is unlikely (& provides evidence for this). The third main explanation for adjunctive behaviours, suggests that stimuli correlated with nonreinforcement help induce these behaviours, that is, *induction by periods of reinforcement*. However, again, the evidence for this is inconclusive (Davey, 1989).

As with explanations of stereotypic behaviours (these will be discussed in detail subsequently), attempts to find a unidimensional construct or explanation appear to have failed. "Complexity has to be accepted as such rather than being masked by simple constructs" (Dantzer & Mittleman, 1993, pp.166-167). Nevertheless, the following sections will investigate some of the explanations for adjunctive behaviours.

3.7.6 POLYDIPSIA AND THE "DRY MOUTH" THEORY

Although it may be appealing to try and account for these behaviours in terms of emotional factors, such as: "the animal's way of producing emotional pacification", Falk (1971) stresses that such concepts are largely untestable (p.578). Instead, he maintains that the various adjunctive behaviours generated by intermittent food schedules should be examined, and consistencies between (or correspondences among) them stated empirically. Behavioural explanations are favoured, since physiological ones have so far been singularly unsuccessful. For example, the "dry-mouth" theories (such as the one posited by Teitelbaum, 1966) are inadequate and discredited by the fact that polydipsia is of such an excessive nature. Teitelbaum (1966) postulates that: "feeding causes dehydration by pulling water into the stomach from the tissues" which "should produce a state of thirst accompanied by a dry mouth. Chewing and swallowing a dry pellet may be difficult for a thirsty animal, so he drinks to help wash each pellet down" (p.589). However, the amounts of water consumed far exceed those necessary to "rinse" an animal's mouth, or replace dehydrated tissue fluids (Davey, 1981).

3.7.7 ADJUNCTIVE BEHAVIOURS AND THE POST-REINFORCEMENT PAUSE

Adjunctive behaviours typically occur immediately after a reinforcement is received, that is, during the post-reinforcement pause. As mentioned previously, the post-reinforcement pause is characterised by a low probability of reinforcement, and accompanied by aversive properties. Falk (1971) states that polydipsia, extinction-induced aggression and schedule-induced escape have all been found to sustain fixed-ratio schedules. In these instances the adjunctive behaviour functions as a reinforcer. Adjunctive behaviours do not only occur during PRPs, but also at other periods of non-reinforcement. For example, they have occurred at times when stimuli that signal extinction are present during multiple schedules of reinforcement (Davey, 1989).

Gilbert (1974) has shown that schedule-induced polydipsia only occurs immediately after food reinforcement, if post-prandial drinking is possible. In fact, he has demonstrated the "ubiquity of schedule-induced polydipsia, *i.e.*, the phenomenon's capability of appearing anywhere in the interval" (Gilbert, 1974, p.280). After 15 daily sessions (2-hour duration) on an FI60-s schedule of food reinforcement (with water concurrently available), two rats were observed for 23 or 24 daily sessions (120 pellets delivered per session). For the first three sessions (FI60-s schedule), water was continuously available. For the following six sessions, water availability was restricted to the final 30 seconds of each interval. Water was then again available continuously for four sessions, before being restricted to the final 10 seconds of each interval. Gilbert (1974) found that polydipsia occurred irrespective of whether water was available throughout the interval, or only during the last 30 seconds or 10 seconds of every interval. When water was continuously available, the rats engaged in more licks during the first half of each interval. Interestingly, the rate of drinking was approximately the same irrespective of whether water was available during the last 30 seconds or last 10 seconds of the interval. (Other procedures were also used in the latter sessions of Experiment 1, but these will not be discussed here).

In a second experiment, Gilbert (1974) attempted to discover the "locus of maximum induced drinking", by restricting water availability to different parts of the interval (p.280). Pellets were spaced by either 60 seconds or 210 seconds. If the inter-pellet interval was 60 seconds, then one of the rats drank most during the third or fourth sixth of the interval, whereas the other rat drank most during the second sixth of the interval. For one of the rats, water consumption was actually higher when availability was restricted. When the inter-pellet interval was 210 seconds, only one of the two rats remained polydipsic. Gilbert (1974) points out that bar pressing and pellet ingestion may have prevented excessive drinking at times (i.e., during the final and early parts of each interval, respectively). That is, there may have been competition between the bar pressing and licking responses. In addition, local satiation factors may inhibit drinking after a certain amount of water has been consumed. That is, the rat may drink its fill early in the interval. Clearly, Gilbert's (1974) studies show that polydipsia need not be restricted to the period immediately following pellet delivery on a fixed-interval schedule of reinforcement.

3.7.8 SUBSTITUTING ONE ADJUNCTIVE BEHAVIOUR FOR ANOTHER

Falk (1971) maintains that an adjunctive behaviour may be substituted for another, since the link between the schedule of reinforcement and the particular adjunctive behaviour produced "is probably not one of high specificity" (p.583). He found that if water and a wheel were provided simultaneously, then both polydipsia and wheel running were performed excessively. Thus, the adjunctive behaviour(s) engaged in excessively are a function of the environmental opportunities available to the animal, and "time-sharing" between behaviours is common. Falk (1971) discusses observations made during polydipsia studies, which clearly indicate the substitutability of various chewing-manipulatory behaviours for polydipsia (such as, the pulling up, shredding & manipulation of absorbent paper towels from underneath the metal bar floor of the experimental box).

3.7.9 IS ADJUNCTIVE BEHAVIOUR ANALAGOUS TO DISPLACEMENT BEHAVIOUR?

Adjunctive behaviour is persistent and difficult to satiate if the environmental conditions leading to its production are maintained (Falk, 1971). Falk (1971) directs attention to the many ethological studies of displacement behaviours, which define such behaviours as: "irrelevant, incongruous, or out-of-context" (p.585). More specifically, displacement behaviours appear to be out-of-context with respect to both the stimulus situation and the previous/following behaviour.

Tinbergen (1952) defines displacement activity as: "an activity belonging to the executive motor pattern of an instinct other than the instinct(s) activated" (Falk, 1971, p.585). Falk (1971) rephrases this definition, so that displacement behaviour becomes: "a response sequence which is ordinarily a function of variables other than those which presumably dominate the current situation", where variables refer to the: "major deprivation operations or stimulating conditions" (p.585). This researcher's main justification for drawing the analogy between displacement behaviour and adjunctive behaviour is the underlying fact that these behaviours occur in situations where consummatory behaviour is "thwarted". Displacement activities arise in other situations as well, but adjunctive behaviours typically occur in food-deprived animals that receive a food pellet, and are prevented from eating further by the intermittence of the feeding schedule. The adaptive significance of adjunctive behaviours remains unknown. Falk (1971) concludes that:

> "In both adjunctive behavior and displacement activity situations, the interruption of a consummatory behavior in an intensely motivated animal induces the occurrence of another behavior immediately following the interruption which is facilitated by environmental stimuli" (p.585).

Not all researchers agree that adjunctive behaviours are essentially "laboratory analogues of the displacement activities observed by ethologists" (Dantzer & Mittleman, 1993, p.153). However, there is still no conclusive evidence to suggest that these two types of behaviours are/are not linked. The following section discusses stereotypic behaviours and displacement activities in some detail.

3.7.10 ADJUNCTIVE BEHAVIOURS AND STEREOTYPIC BEHAVIOURS

Ladewig, de Passille, Rushen, Schouten, Terlouw and von Borell (1993) point out that a number of researchers have drawn comparisons between adjunctive behaviours and stereotypic behaviours on a behavioural level. Both "include a routine type activity and both develop over time under conditions of apparent stress" (Ladewig et al, 1993, p.109). However, they cite a number of studies by Dantzer and coworkers in the 1980s, that suggest stereotypic and adjunctive chain-manipulation behaviours (nibbling & chewing on a metal chain covered with cloth strips, rubber hose, leather & nylon straps) in post-weaning pigs are not equivalent. These behaviours were accompanied by differences in patterns of plasma cortisol levels depending on whether the behaviour was "adjunctive" or "stereotypic" (Ladewig et al, 1993). Ladewig et al (1993) state that "chain-manipulation following delivery of food in a massed form rather than intermittently was accompanied by a rise in plasma cortisol" (p.110).

Researchers have also attempted to draw similarities between stereotypic behaviours and displacement activities. That is, adjunctive behaviours, stereotypic behaviours and displacement activities seem to share some properties, but do not appear to be analogous. Duncan, Rushen and Lawrence (1993) point out that stereotypies and displacement activities differ in at least four ways. Unlike stereotypic behaviours, displacement activities occur frequently in natural environments, take up a relatively small amount of an animal's time, do not appear to be "addictive", and remain unchanged with repeated performances. Thus, one must conclude that they are different categories of behaviour, and cannot be used interchangeably.

3.7.11 THE RELATIONSHIP BETWEEN ADJUNCTIVE BEHAVIOURS AND OPERANT RESPONSES

Lejeune, Cornet, Ferreira and Wearden (1998) define adjunctive behaviours as: "consistent sequences of actions, usually described as stereotyped, which occur in periods between reinforcer deliveries or between measured responses such as lever presses" (p.352). They suggest that systematic study of the role that such behaviours may play in the "temporal regulation" of instrumental responses (such as lever presses) has been hindered by a number of problems. One problem is that researchers disagree about the origin and development of adjunctive behaviours that develop on FI or DRL schedules (*e.g.*, temporal or terminal activities, superstitious behaviours, analogous to displacement activities, by-products of temporal constraints imposed by schedules *etc*). A second major problem:

> "is that because adjunctive behaviors are usually measured by direct visual observation, acquiring information about adjunctive behaviors is extremely labor-intensive and effortful. Time- or event-sampling techniques, familiar to ethologists (Martin and Bateson, 1993), have been rarely if ever used in psychological studies" (Lejeune et al, 1998, p.352).

The theoretical significance of adjunctive behaviours and any relationship between such behaviours and operant responses is still to be determined. Lejeune et al (1998) discuss one major theory, which suggests that adjunctive behaviours serve as a "behavioral clock process" (p.353). They refer to Killeen and Fetterman's (1988) ***Behavioral Theory of Timing***, which posits that adjunctive behaviours serve as: "cues for the emission of responses measured on temporally constrained reinforcement schedules and other timing tasks" (Lejeune et al, 1998, p.353). In addition, animals are said to possess an internal "pacemaker", which results in their ability to time durations (scalar properties). Pulses are emitted from the pacemaker, which govern transitions from one adjunctive behaviour to another. Research has shown that pacemaker rate is sensitive to changes in reinforcement rate, but Lejeune et al (1998) stress that any resultant changes in adjunctive behaviours are typically "inferred rather than observed" (p.353). Lejeune et al (1998) stress that the adjunctive behaviours themselves (not pacemaker pulses) serve as discriminative stimuli for the operant response.

Lejeune et al (1998) used gerbils in a study of adjunctive behaviours during a differential reinforcement of response duration (DRRD) schedule with a parameter of time requirement (*t*). The operant response was that of staying on a small platform (perching response), and reinforced if the gerbils remained on the platform for a period of time greater than *t*. Adjunctive behaviours (per platform response) were systematically observed during the sessions (ranging from 137 to 200). Sessions were terminated after 30 minutes, 50 reinforcers or 250 platform responses (trials).

Some gerbils mounted the platform from the left (side of food tray location), progressively oriented their heads until they faced the food source ("like the hand of a clock starting with the head oriented at about 3 and progressing steplike to reach 9"), and then they dismounted (p.356). Other sequences involved mounting the platform and then rotating stepwise with the four feet and nose, and then dismounting. Lejeune et al (1998) used 12 behavioural categories that included immobility, grooming, jumplike vertical movement, rearing, sitting on hind legs, defecation, and scratching the platform with forepaws. Duration of behaviour was not measured.

Lejeune et al (1998) found 40 different adjunctive sequences (without taking outcome of trials into account) amongst their six subjects. Most of these sequences involved periods of standing still (immobility), and many included changes of head position interspersed by occasional bouts of grooming. However, this is probably not surprising, since balancing on a small platform is unlikely to lend itself to many movements. Although such a large number of adjunctive sequences were observed (& not just one or two stereotyped sequences), Lejeune et al (1998) point out that sequences need not be "absolutely invariant" from trial to trial (p.365). Lejeune et al (1998) varied the time requirement for reinforcement, and found that the gerbils tended to overestimate the time requirement, number of behaviours emitted varied little with time requirement, and rate of adjunctive behaviour increased with rate of reinforcement. Perhaps these adjunctive sequences should just be interpreted as being variants of the response topography. The reinforced operant requires that a certain amount of time is spent on the platform, which is likely to encourage immobility rather than large motor movements, which may result in gerbils overbalancing and moving off the platform.

Lejeune et al (1998) conclude that adjunctive behaviours do not mediate timed responses (or aid in timing), but rather that changes in adjunctive behaviours are arousal-based.

3.7.12 DOES ADJUNCTIVE BEHAVIOUR FUNCTION AS A COPING RESPONSE?

Ladewig et al (1993) maintain that inconsistencies in results to date make it clear that the relationship between stereotypic behaviours and the endocrine system is far too complex to fit a simplistic ***coping hypothesis***. The variety of stereotypic behaviours, differences in the way individuals perceive their environment, and the complexity of the endocrine system (peripheral physiological activities and higher brain activities) all complicate the issue. Some studies have shown that stereotypic behaviours reduce Hypothalamic-Pituitary-Adrenal and Autonomic Nervous System activity. However, other studies have found the reverse (Ladewig et al, 1993).

Cabib (1993) points out that most researchers define stereotypic behaviour as a response to stimuli (or changes in environmental conditions) that are arousing or stressful. However, she stresses that the two should not be perceived as being interchangeable. "Arousal" most accurately concerns the "first phase of the organism's response to environmental changes" (Cabib, 1993, p.129). Arousing stimuli need not be aversive or dangerous. Behavioural responses that allow the organism to cope with the environmental changes lead to the end of the arousal phase. However, if the organism is unable to cope (external or internal limitations) with these environmental changes, then the new phase of "stress" takes over (Cabib, 1993). Thus, arousing conditions need not be stressful, unless the organism is unable to cope behaviourally. Interestingly, Cabib (1993) suggests that rather than stereotypic behaviour serving as a coping strategy for stress:

> "displacement behaviours, although apparently irrelevant, may protect the organism from entering a stress phase in inescapable or otherwise uncontrollable situations... stereotyped alteration of behaviour may be a 'side-effect' induced by the physiological changes involved in adaptation to repeated or chronic stress conditions" (p.140).

3.7.13 MULTIMODAL DISTRIBUTIONS OF ACTIVITIES ON PERIODIC FOOD SCHEDULES (SCHEDULE ENTRAINED BEHAVIOUR)

Staddon and Simmelhag (1971) replicated Skinner's (1948) "superstition" experiment. They found that certain behaviours tended to occur immediately after food delivery (***interim behaviours***), when the likelihood of food delivery is low. Other behaviours (usually related to pecking or consummatory activities) tended to occur as the next reinforcer approached (***terminal activities***). On a fixed-time 12-second schedule, with pigeons as subjects, interim activities included side-stepping along the magazine wall, turning ¼-circles, pecking at the floor, and holding head in the magazine, whereas terminal activities included pecking directed at the magazine wall, and orientation towards the magazine wall.

Davey (1981) draws parallels between interim activities and adjunctive behaviours, since both tend to occur after food delivery or at times when food is unavailable. Similarly, he points out similarities between terminal activities and the consummatory activities directed at "a stimulus which was either paired with or highly predictive of the imminent delivery of a reinforcer" during autoshaping procedures (Davey, 1981, p.166).

Reid, Bacha and Moran (1993) state that stereotyped temporal patterns of behaviour typically occur on periodic food schedules (*e.g.*, fixed-time 60-second schedule), when the rat is in an operant environment that allows it to engage in a variety of behaviours (other than the operant response). These other behaviours appear "temporally entrained within the inter-reinforcement interval" or IRI (Reid et al, 1993, p.1). When a drinking tube and running wheel are available, rats tend to eat, drink, wheel-run, and then return to the feeder prior to the next food reinforcer.

Averaged over all IRI's, these activities typically peak at different times during the IRI. That is, the distributions of activity are multimodal. These multimodal distributions of behaviour have been observed in a variety of species, and in rats on a variety of interval schedules. Reid et al (1993) point out that the first behaviour engaged in after consumption of the food pellet is usually considered to be schedule-induced and excessive.

According to Reid et al (1993) models of schedule induction tend to be based on the assumption that intermittent schedules of food reinforcement "modulate the animal's motivational states across the inter-reinforcement interval" (p.1). They refer to Staddon's (1977) model, which proposes that a schedule-induced and excessive activity is the first to occur after food consumption, and represents the *interim* motivational state. This activity is followed by an activity such as wheel running, which is not considered to be schedule-induced or excessive, and represents the *facultative* motivational state. Prior to the next reinforcer, activities related to obtaining reinforcement occur (e.g., such as "operant behaviour or searching around the feeder"), representing the *terminal* motivational state (Reid et al, 1993, p.2). Reid et al (1993) maintain that terminal activities are analogous to Timberlake and his co-worker's "focal search" activity or searching for reinforcement (*e.g.*, Lucas, Timberlake & Gawley, 1988), which is the "dominant, highest priority activity in periodic schedules (Reid et al, 1993, p.2).

The temporal distribution of activities within the IRI may not be as stereotyped as many researchers believe. Reid et al (1993) point out that the temporal distributions of drinking and running actually overlap in some studies, and during some IRI's only one of the activities occurs. It is only when the results are averaged, that the multimodal distribution appears clear cut. Reid et al (1993) suggest that studies that allow subject's choice between activities are important, and should not be restricted to experiments of schedule-induced behaviour, since "these stereotyped patterns of activities have been observed even in the absence of schedule-induced behavior" (p.2).

In a series of experiments, Reid et al (1993) used an octagonal apparatus (66 cm from end to end), with four open areas each containing a response lever and access to a different activity (drinking from a tube, running in a wheel, & chewing an oak wooden block). Food pellets were delivered on a fixed-time 60-s schedule of reinforcement, but conditions of access to drinking tube, wheel and wood block varied according to the phase of the experiment. In the "free access" to all activities phase, drinking was the only behaviour considered to be schedule-induced, and occurred just after the food pellet was consumed. Chewing was rarely observed.

In one experiment, Reid et al (1993) imposed a fixed-ratio lever press requirement for access to drinking, which varied from FR0 to FR30. They found that the drink-run pattern did not occur in every IRI. These researchers suggest that the typical averaged multimodal distributions of drink-run occur as a result of variables such as inertia and bout-length that are unique to each activity, rather than "a modulating influence on the rat's motivational states" (Reid et al, 1993, p.13). That is, drinking occurs early in the IRI distribution, since licking can reach full speed quickly and bouts are fairly short. Running speed, on the other hand, takes some time to reach its maximum, rats pause within bouts of running and frequently change direction, and bouts last longer. They concluded that the schedule itself did not directly influence the sequence of drink and run activities.

In a second experiment, Reid et al (1993) varied the condition of access to each activity. If drinking and running occurred in different IRI's, then the time of onset was similar. In a third experiment, Reid et al (1993) used the FT 60-s schedule, and a FT 240-s schedule with a longer IRI. More instances of run-drink patterns occurred during schedules with longer IRI's. Since running bouts lasted longer, if running occurred first on schedules with shorter IRI's, then it was unlikely to allow enough time for drinking. If drinking occurred first, an activity of short duration, then time was still available to engage in running before the next reinforcement was delivered.

Reid et al (1993) found that drinking and running were only "slightly substitutable" for each other (p.23). They suggest that there may be a mechanism for the preference of drinking after the consumption of a food pellet. Reid et al (1993) state that:

> "the most frequent sequence of activities on periodic food schedules is a single period of drinking, running, or almost any other activity (schedule induced or not), beginning soon after consuming the pellet, followed by returning to the feeder in anticipation of the next pellet delivery" (p.25).

They suggest that intermittent schedules of food-reinforcement (imposing reward & temporal control conditions) determine the time engaged in behaviours that are reward-related (*e.g.*, consuming, working, or looking for food). The remaining time is then available for other activities. Thus, the temporal characteristics of the reward-related activities help determine the temporal organisation of other behaviours. Timberlake and coworkers' ***focal search*** (reward-related activities, terminal behaviours) comes under temporal control of periodic food schedules, and is most likely to occur early and late during the IRI, when the probability of finding food is high (Reid et al, 1993). Thus, Reid et al (1993) conclude that the temporal distribution of schedule-induced and non-induced activities is determined by the temporal distribution of ***focal search*** (& may occur within the remaining IRI).

3.8 CAN THE SKINNER BOX AND SCHEDULES OF REINFORCEMENT APPROXIMATE NATURAL ANIMAL ENVIRONMENTS?

> "Schedule research was born in the laboratory. It started with the finding that the schedule used to deliver food to rats influenced the speed and temporal pattern of their bar-pressing. Only later were parallels sought in the natural environment...Extrapolations from schedule research to ordinary life demand a leap of faith" (Zeiler, 1996, p.549).

In a discussion of the study of foraging within the psychological laboratory, Baum (1983) stresses the importance of conducting more "natural" experiments. That is, if studies of foraging in the laboratory are to have any relevance to behaviour in natural environments, then psychologists must address the "artificiality" of the typical experimental situation. Baum lists three main areas in which a typical operant behaviour experiment differs from nature: the small size of the Skinner box; the short time spent in the Skinner box; and the fact that schedules of reinforcement may bear little resemblance to the occurrence of food in natural environments.

3.8.1 THE SMALL SIZE OF THE SKINNER BOX

Certainly, the typical Skinner box is very small. As Baum (1983) points out, animals in their natural environments must search for food, and often travel great distances to find it. Within a few paces, a rat reaches the wall of the Skinner box. Locomotion is limited. Baum (1983) suggests that experimenters use larger experimental spaces or even work outdoors. In other words, provide a more naturalistic experimental environment.

3.8.2 THE SHORT LENGTH OF EXPERIMENTAL SESSIONS

Many experimental sessions are one-hour long, with the other twenty-three hours spent in the "home-cage". Free-ranging animals spend substantial portions of their day foraging for food, and are more active at certain times of the day. Baum (1983) warns that a one-hour sample in a laboratory situation may not be representative of foraging in that species. However, he points out that behaviour in a 24-hour experiment ("closed economy") differs little from behaviour in a one-hour session ("open economy"). Baum (1983) suggests that if researchers look at 24-hour behaviour in a more naturalistic environment (*i.e.*, not in a Skinner box), with opportunities for locomotion, a more realistic picture of how the animal exploits and manages its resources may emerge.

3.8.3 SCHEDULES OF REINFORCEMENT AS MODELS OF FORAGING

The third "artificiality" factor that Baum (1983) discusses, is the use of schedules of reinforcement. Is it possible for a schedule to model food distribution in natural environments? He suggests that foraging depletes food sources in nature. However, he neglects to mention that the use of ***extinction*** can in fact mimic the depletion of a food source. Baum (1983) also mentions that schedules of reinforcement remain invariant through time. Again, they need not. An experimentor could investigate a number of schedules, or run each animal on a variety of schedules. Operant behaviour and foraging share similarities on a "molar" level, since both involve "responding" and "eating". However, as Baum (1983) maintains, on a "molecular" level they differ vastly, since foraging involves many components, including search, capture, handling and eating.

A number of experiments have tried to use schedules to model the handling and search phases of foraging. Baum (1983) suggests that a ratio schedule could perhaps most closely model the "handling" aspect of foraging, since: "handling, whether it be subduing a mouse, opening a nut, or chewing up some foliage, represents a job to be done, with a beginning and end" (p.267). But, he adds that bar-pressing may not be analagous to manipulating a food item. The outcome of the "search" phase of foraging in natural environments is uncertain. Thus, "fixed" ratio or interval schedules are least "naturalistic".

Baum (1983) considers whether a variable-ratio or variable-interval schedule might be useful to model the "search" phase. There are at least two types of "search" strategies. Some animals lie in wait for their prey, and it (the "food") comes to them. Thus, no response is needed to find the food item. A variable-interval (or variable-time) schedule might be appropriate in this case. True "search" requires effort, and as: "with a ratio schedule, the more one searches the more one finds" (Baum, 1983, p.268). "Search" usually leads to depletion of the food-source, which a variable-ratio schedule fails to emulate, whereas a variable-interval schedule results in periods of "depletion" and "replenishment". That is, once a food-pellet has been obtained, the rat is less likely to obtain another (depletion), whereas, absence from the schedule is more likely to result in a food-pellet (replenishment).

Baum (1983) concludes that the schedule most likely to emulate a natural situation would be a combination of variable-ratio and variable-interval, an "adjusting" variable-ratio schedule. Again, Baum (1983) fails to mention the use of an ***extinction*** schedule following running on a schedule of reinforcement. Extinction represents the "true" depletion of a food source in an experimental environment. Thus, an investigation of a variety of schedules, followed by extinction could be valuable in investigating foraging in general.

3.8.4 BRIDGING THE GAP BETWEEN PSYCHOLOGICAL AND ECOLOGICAL RESEARCH

If schedules of reinforcement are to be used as models of foraging in the laboratory, then schedules must in some way be representative of "patches" of food/prey in natural environments. Baum (1983) suggests that a number of terms central to operant conditioning correspond to terms used by ecologists. For ecologists, a "patch" refers to the local distribution of food or "prey", and foraging/predation refers to the seeking and handling of prey/food. "Broadly speaking, "prey" corresponds to "reinforcement," "foraging" to "instrumental behavior," and "patch" to "programmed source of reinforcement"" (Baum, 1983, p.269). Merely to interchange terminology in such a way is likely to be too simplistic and problematic. It does, however, show that there might be parallels, and that it is possible to combine approaches.

Baum (1983) states that it is possible to physically model patches under laboratory conditions. Artificial patches can be created in "enclosed open areas". In other words, instead of using a schedule of reinforcement and Skinner box to simulate patches and foraging, a semi-naturalistic experimental "enclosure" is set up, with actual patches of food. Unlike the usual laboratory situation with only one subject observed in the experimental box, it is possible to observe a group of subjects in the more naturalistic "enclosure".

In an experiment with pigeons, Baum (1983) used a larger experimental area (8 feet wide x 8 feet high x 60 feet long) and observational techniques employed by behavioural ecologists to investigate foraging. An experimental patch was created, and a known quantity of hemp seed was randomly distributed throughout the patch (4 feet x 4 feet). The actual quantity of grain distributed by the experimentor varied unpredictably from day to day. Five subjects at a time were observed, from a larger flock of 20-25 pigeons. The observers recorded how many pigeons foraged at any given time, and for how long, and at the end of each session the amount of grain left was recorded. Baum (1983) found that pigeons stopped foraging if they were satiated, or if a "criterion of scarcity" was met. The experiment raised many questions about group size, number of patches, and predictability of amount of food. However, it demonstrated that it is possible to conduct an "ecological" experiment of foraging behaviour, with quite strict experimental control (weather was an intervening variable), on a group of subjects in a larger semi-naturalistic environment.

Baum and his coworkers have continued to develop operant simulations of foraging in the laboratory. Aparicio and Baum (1997) state that:

> "Operant behavior may be viewed as foraging, and foraging may be studied as operant behavior (Shettleworth, 1988). Foraging and operant behavior both involve locomotion, and both are modified by their consequences" (p.177).

Operant techniques, which allow "relatively precise tests", have been used to test models of prey selection, and optimal models of foraging (Aparicio & Baum, 1997, p.177). Schedules of reinforcement allow researchers to model a variety of environments, in which patches of food can become depleted. The forager (subject) must decide when to move to a new patch. Variables that determine "giving-up" include the quality of the patch and the travel cost of moving to another patch.

Aparicio and Baum (1997) point out that a number or researchers have modified operant conditioning chambers to include factors such as locomotion or "travel" into their foraging simulations. Such modifications have been used to overcome criticisms that suggest operant foraging models, which omit travel requirements are unrealistic. That is, a rat that bar-presses for food on a schedule of reinforcement that simulates patch utilisation (residence time), depletion (giving-up time) and travel between patches is likely to expend less energy than a rat that must physically travel between patches or sources of food. However, prior to Aparicio and Baum's (1997) study, no researchers had actually directly compared bar-press "travel" (travel simulated with an operant response) to locomotion or actual travel, within the same experimental situation. Earlier work by Baum (1982) with pigeons showed that key pecking was qualitatively similar in its effects to travelling between patches in a choice situation (running around barriers that separated the patches).

Aparicio and Baum (1997) investigated operant conditions that modelled a variety of foraging conditions that a rodent might face (*e.g.*, hunting under bushes for fallen seeds). Their modified operant conditioning chamber was a large rectangular wooden box, divided length-wise by wire mesh. A one-way trip from the left to the right lever was 260cm. The patches of food contained one, two or eight reinforcers. The amount of searching (represented by lever-pressing) needed to obtain prey (a reinforcer) varied randomly. (The actual experimental conditions represented by different requirements of right and left lever pressing & travel between levers- direct or over hurdles- are complex & will not be discussed in detail here.) These researchers found that rats typically obtained all the prey items available, before leaving the patch. Importantly, lever-press and locomotion travel produced equivalent effects on residence and giving-up times. That is, they are functionally equivalent.

Aparicio and Baum (1997) suggest that interval schedules control travel time, and random-ratio schedules can be used to vary lever-press travel time. Locomotion with hurdles (which involves more energetic climbing) did increase residence and giving-up times. These researchers concluded that rats probably use different foraging strategies under different environmental conditions. The determinants of patch leaving include travel time to next patch and inter-reinforcement interval.

Twenty-five "open peer commentaries" were published along with Fantino and Abarca's (1985) groundbreaking paper, which presented an interdisciplinary approach to "foraging within the framework of the delay-reduction hypothesis" (p.315). The ***delay-reduction hypothesis***, which derives from studies of choice (operant conditioning experiments using modifications of the concurrent-chains procedure), states that: "the effectiveness of a stimulus as a reinforcer may be predicted most accurately by calculating the decrease in time to food presentation correlated with the onset of the stimulus, relative to the length of time to food presentation measured from the onset of the preceding stimulus" (Fantino & Abarca, 1985, p.315). The number of commentaries, as well as the varied and largely supportive comments contained within them, indicate that many biologists (*e.g.*, Gass, 1985) and psychologists (*e.g.*, Davison, 1985) of the time were eager to advance and embrace "the interaction between operant psychology and behavioural ecology" (Caraco, 1985, p.333). Dinsmoor (1985) and Brown (1985) emphasised the need to include Pavlovian principles or mechanisms in any integrative approach. Gass (1985), a biologist, eager to speed up the process of adapting the behavioural approach (as proposed by Fantino & Abarca, 1985) to foraging in more complex and less controlled environments, lamented: "I work in that other discipline, where present methods are often inadequate to discriminate between hypotheses, and there is great potential in the experimental rigor of psychology if it can be applied effectively to ecologically relevant problems" (p.337).

3.9 SCHEDULES OF REINFORCEMENT IN SEMI-NATURALISTIC AND NATURAL ANIMAL ENVIRONMENTS

As Davey (1989) points out:

> "the Skinner-box is not exactly a true analog of the animal's natural feeding habitat. If, in the wild, a particular food source did deliver food periodically, then at times when the food was unavailable from this source, animals would presumably leave and search elsewhere - returning only at the time when food

> was due to become available again. However, the Skinner-box does not provide alternative food sources, nor does it permit the animal to leave to investigate alternative food prospects elsewhere" (p.73).

Davey (1989) warns that it is difficult to extrapolate from an animal's performance on simple schedules in a Skinner box to the behaviour of an animal in its natural environment. "The Skinner-box provides only one source of food; an animal's natural environment usually has many. Thus, Skinner-box schedules which either directly or indirectly program for reinforcement intermittently generally prohibit the animal from investigating other sources of food during periods of nonreinforcement, and thus may well give false impressions of how a free-ranging animal might act in such circumstances" (Davey, 1989, p.75).

Not all researchers recognise the existence of a dichotomy between natural and laboratory environments. In fact, Davison (1985) stresses that "it is a matter of external validity that a laboratory experiment gives us information about natural foraging – but only if a *dichotomy* of natural versus unnatural is first accepted. I fail to see this dichotomy. The laboratory and the "real world" differ only as points on a multidimensional plane of behavior-affecting variables and their values" (p.335). Thus, instead of creating a dichotomy between the Skinner box and the "wild" situation, it would be useful to investigate environments along a continuum from a modified open-field style Skinner box, to a zoo environment, and then ultimately a "wild" situation.

3.9.1 SCHEDULES OF REINFORCEMENT IN MORE NATURALISTIC OPEN-FIELD STYLE SKINNER BOXES

Under natural conditions, a rat's food would be "patchily" distributed in both space and time. The "patch" of food would have to be found, sampled, exploited, and then left when it was depleted (Davey, 1989). ***Optimal foraging strategies*** might account for the behavioural patterns observed during schedules of intermittent food reinforcement in a laboratory situation. A more naturalistic open-field style Skinner box (such as the one used in Litchfield's 1987 study) provides an opportunity to assess behaviour centred at a food source, as well as exploratory and other behaviours away from this source.

Schedules of intermittent food reinforcement might be considered to mimic a "patchy" resource (in time). That is, food is only available under certain conditions, and one would expect the rat to explore the experimental box in search of alternate food sources. If stimulus objects are provided, rats should investigate these, as well as the outer perimeters of the experimental box. The "fixed" schedules are perhaps the least "patchy" of the five schedules investigated (with food arrival being more predictable), whereas, the "variable" schedules are the most "patchy" (with food arrival being least predictable). DRL schedules might be considered to encourage leaving the food patch, since low rates of bar pressing are required. Whether the schedule is variable or fixed, ratio or interval, a rat would continue to return to the manipulandum and food-trough area, since this is the only known source of food available.

The "extinction" schedule, which follows each of the intermittent reinforcement schedules, may mimic the situation where a food patch has become depleted. It is now less "risky" for the rat to leave the food-trough area and engage in other behaviours. In fact, it could more "risky" to stay (especially, in a "real-life" situation). Exploratory behaviour directed towards stimulus objects and other areas of the experimental box might bring the rat into contact with other potential sources of food. Thus, "patch-depletion" may account for increases in exploratory behaviour, since a new food patch must be found to meet the rat's food/energy requirements.

3.9.2 BEHAVIOURS (OTHER THAN INSTRUMENTAL RESPONSES) OBSERVED IN MORE NATURALISTIC OPEN-FIELD STYLE SKINNER BOXES

A number of researchers (Forster, 1992; Holme, 1990; Litchfield, 1987) have shown that larger and more naturalistic open-field Skinner boxes provide the opportunity to investigate a range of behaviours, in addition to the operant response (which is just as readily conditioned). The increased size allows rats to engage in more ambulation and exploration, as well as escape-related behaviours (*e.g.*, propping & scrabbling against the walls). Soft substrates (*e.g.*, sawdust) allow rats to engage in pica, digging or burying/sawdust pushing behaviour. This section will focus on two unusual behaviours that have been observed in rats run in a larger more naturalistic Skinner box, namely: ***jump at lid*** and ***sawdust pushing/burying behaviour*** (Litchfield, 1987).

3.9.2.1 JUMPING AT THE LID

Rats run on a ***fixed-ratio*** schedule of reinforcement (FR30) have been found to jump at the lid of an open-field style Skinner box (Litchfield, 1987). That is, they have been observed to leap at the perspex lid of the box, with all four paws off the ground. The rats either hunched down and pushed off with the back legs, or propped themselves against the wall, before propelling themselves off the wall and into the air. Such leaps also included somersault-like twists in the air, touching the lid momentarily with the paws, and then a landing on all four paws (Litchfield, 1987).

It is difficult to ascertain whether other researchers have observed this ***jumping at the lid*** behaviour, since behavioural definitions are often insufficiently detailed. For example, Heynen, Sainsbury and Montoya (1989) state that the black-hooded rats, Richardson's ground squirrels and thirteen-lined ground squirrels all attempted to "jump out of the box", but no further information about the topography of the response is provided (p.185). This jumping behaviour and rapid digging were classified together as "fleeing" behaviours.

Callard, Bursten and Price (2000) describe a repetitive, "backflipping" behaviour in captive-bred black rats (*Rattus rattus*). This behaviour resembled a "backwards somersault or backflip", which appeared to be "triggered by weaning and maintained by a heightened state of arousal in a relatively impoverished environment with limited opportunities for perceptual and locomotor stimulation" (Callard, Bursten & Price, 2000, p.139). These researchers found that the behaviour developed rapidly after weaning, occurred mostly during the dark phase of the light/dark laboratory cycle (>90%), and differed considerably between litters or families (*i.e.*, possible maternal or genetic effects). Interestingly, if the cage height was increased, a delay in the development of the behaviour, as well as differences in the topography of the behaviour, occurred. The provision of a wooden nest box (*i.e.*, cage enrichment) greatly reduced the level of performance.

Rensch and Ducker (1959) describe a mongoose somersault "game" in which the animals run up to a wall, jump against it, and somersault. Somersaults and sudden vertical jumps may provide vestibular reinforcement, since these movements stimulate the "balancing mechanism contained in the labyrinth of the inner ear" (Aldis, 1975, p.57). Body twisting and jumping are "locomotor-rotational" movements, which may be a simple form of play (not observed in brown rats according to Wilson, 1973). "(S)poradic hopping, jerking and jumping" or "popcorn" behaviour has been observed in young rodents when they first become mobile (Hole & Einon, 1984, p.98). Leaping and "hyperexcitable" behaviours have been observed in young rats, sexually aroused and isolation-reared males, and adult rats exposed to "intense auditory and visual stimulation" (Hole & Einon, 1984, p.98). Hole and Einon suggest that these behaviours may occur as a result of high stimulation levels. Furthermore, they maintain that the explosive leaps, sudden catapults or aerial somersaults that have been observed in rodents may be ***anti-predator*** or ***escape behaviours***. Therefore, the ***jump at lid*** category may have adaptive significance, and should not be considered bizarre.

3.9.2.2 BURYING OR SAWDUST-PUSHING BEHAVIOUR

Early studies of sawdust-pushing behaviour

Brief mentions of sawdust-pushing behaviour can be traced back to abstracts of conference papers given by Hudson (1939; 1940a; 1940b). He classifies this behaviour as an unlearned avoidance response, along with cautious approaches towards, and withdrawals from either aversive or novel stimuli. These early reports indicate that more than one type of stimulus can elicit the sawdust-pushing response. Hudson found that both shock (1939) and introduction of an unfamiliar object into the living cage (1940a; 1940b) could elicit the same behaviour.

Hudson's (1950) procedure involved administering a single shock to each rat's mouth as it ate from a metal food holder, mounted on a square of black-and-white horizontally striped bakelite. This pattern was removed after the single learning trial and later (days, weeks or months) returned with the baited food holder for the five-minute "extinction" trials. Avoidance behaviours directed towards this object (pattern) were then recorded. The five-minute test trials continued daily until no avoidance responses were observed on two consecutive days (*i.e.*, criterion for extinction of avoidance responses).

Pushing of wood shavings appeared in 95% of Hudson's adult rats during the first test trials, and was considered a "useful measure of avoidance" (1950, p.106). The topography of the response varied, although one form dominated throughout the experiments. Hudson (1950) describes the behaviour as being:

> "usually accomplished by a movement of the forepaws which sends a shower of shavings in the direction of the object of avoidance" and "many animals proceeded to cover the pattern by piling the shavings from the floor of the cage against it, and having partially or fully accomplished this, would occasionally approach close enough to snatch food from the holder" (p.106).

Digging was also often followed by this forepaw pushing of shavings. A topographical variant involved use of the hind feet to "shower" the shavings at the pattern (Davis, Moore, Cowen, Thurston, & Maggio, 1982, observed this response topography in Mongolian gerbils). Hudson (1950) discusses a third topography in which the mouth is used to collect and carry materials, which are then packed against the pattern. In this instance wood shavings were not the only materials employed by the rats. Wood chips, faeces, and a wire loop (removed after much effort from the side of the cage) were also added to the stack of shavings by the pattern. Calhoun (1962) reports that rats use forepaws, nose and teeth to seal burrow entrances with dirt and rocks. Silverman (1978) observed rats plugging a hole with faeces to prevent cigarette smoke from entering.

Hudson (1950) states that both frequency and intensity of sawdust-pushing behaviour decreased over trials until all that remained was a "brief tremor of the forepaws" (p.107). Another avoidance behaviour recorded was approach to, and withdrawal from the striped pattern. Being food-deprived (8-48 hours) the rats were attracted to the baited holder, yet simultaneously repelled by the unfamiliar pattern (an approach-avoidance conflict situation). Stretched approaches followed by quick withdrawals were the norm for early trials, gradually giving way to trials in which rats snatched food from the holder. During later trials, rats spent most of the time eating.

Burying behaviour in response to aversive stimuli

Since these early experiments, studies of defensive burying by rats have typically used a prod that delivers shock, and the subsequent amount of burying directed at this prod is used as an index of fear and/or anxiety (Williams & Scott, 1989). However, sawdust-pushing may not only represent a form of defensive behaviour. In some cases it may be a form of nondirected burrowing behaviour or a nest-maintenance response (Williams & Scott, 1989). Shock is not the only aversive stimulus to elicit defensive burying in rats. Flashbulbs discharging, Tabasco sauce delivered through a tube, gusts of air and mouse traps have all elicited this behaviour in laboratory experiments (Heynen, Sainsbury & Montoya, 1989; Terlecki, Pinel & Treit, 1979). Traps or flashbulbs have also been buried before they hve gone off (*i.e.*, unconditioned defensive burying), which Terlecki et al (1979) suggest is "part of the neophobic reaction to the appearance of an unfamiliar trap or flashbulb in the familiar test environment" (p.349). Interestingly, prod burying (after shock) is suppressed in the presence of conspecific and predatory (cat) odours (Willimas & Scott, 1989).

Along with defensive burying, there are three other *species-specific defense reactions* (SSDRs) that are observed in rats, namely: freezing, fleeing or fighting/attacking (Heynen, Sainsbury & Montoya, 1989; Pinel & Treit, 1978). Williams and Scott (1989) suggest that different types of ethological stressors produce different patterns of SSDRs. That is, some elicit burying, others elicit freezing or attack.

The burying behaviour exhibited in California ground squirrels is very similar (topographically), and has been observed in response to snakes (Owings & Coss, 1977). Williams and Scott (1989) compared the SSDRs of black-hooded (Long-Evans) rats with Richardson's ground squirrels and thirteen-lined ground squirrels. They found some interesting differences in burying behaviour between the rats and the ground squirrels. After being shocked, eight of the ten rats used alternating forelimb movements to spray corncob bedding at the prod. The ground squirrels engaged in far less burying behaviour, but sprayed the bedding towards the prod even before they were shocked. Eight of the ten Richardson's ground squirrels sprayed bedding at the prod as they approached it, and subsequently often attacked the prod (biting & scratching). The rats did not attack the prod. After shock, both species of ground squirrels pushed the bedding towards the prod, but with "simultaneous forelimb pushing movements" (not alternating), and the Richardson's ground squirrels also kicked bedding at the prod with their hind paws (Williams & Scott, 1989, p.188). Less than half of the thirteen-lined ground squirrels engaged in any burying behaviour.

Burying behaviour in response to nonaversive stimuli

Poling, Cleary and Monaghan (1981) point out that rats also bury normal palatable food or marbles, which are nonaversive stimuli, evoking approach rather than avoidance behaviour. These researchers found that the topography of the burying response was the same for nonaversive stimuli. That is, both the snout and forepaws were used to shovel the wood shavings and wood chips towards the stimulus objects until they were buried. Whereas the burying of aversive stimuli may be an SSDR, the burying of nonaversive stimuli may be related to hoarding, since wild rats burrow, dig and hoard food in their natural environments (Poling et al, 1981). Wild Norway rats (of low status) certainly plug up the entrance holes that lead to underground nests, to prevent entry, if they are exposed to territorial threats by high status rats (Calhoun, 1962). The biological significance of the burying behaviour observed in laboratory situations still remains unclear.

Burying behaviour as a by-product of conditioning

Litchfield (1987) observed burying behaviour in four of the twenty Hooded Wistar rats used. It occurred as a by-product of the conditioning phase of the experiment, and was elicited by an unknown stimulus. The rats had consumed the pellets available during the ***familiarisation*** session, and burying did not appear until ***magazine training*** had commenced. The four rats showed some fear of the stimulus buzzer/light which accompanied reinforcement during the ***pairing trials***, but it is difficult to ascertain whether the burying behaviour occurred as a result of this fear.

Topographically the behaviour involved the rat pushing sawdust forwards with alternating forepaws in the direction of the food-trough, until the sawdust filled the trough. The snout was not used at any stage (*i.e.*, different from the topography described in the literature). The behaviour was always directed at the same area, and did not cease until the food-trough had been filled. If the sawdust was removed from the trough and flattened out, the rat began the process again. The only apparent variation was in how vigorously the behaviour was performed and how quickly it was completed. Since it proved impossible to train these rats whilst sawdust was present in the box, the sawdust was removed. Once this was done, conditioning proceeded rapidly, with no excessive fear of the buzzer/light in evidence. The behaviour did not reappear during later experimental sessions, when sawdust was again available. Thus, it is unclear what elicited the burying behaviour. The rats may have been plugging up the only "entrance" to the box, and the only possible aversive stimuli may have been the white-noise (on all the time) or buzzer/light that accompanied reinforcement.

3.9.3 SCHEDULES OF REINFORCEMENT AND DEVELOPMENT OF ABERRANT BEHAVIOURS IN ZOO AND "WILD" ENVIRONMENTS

It is only possible to speculate upon the possible schedules of reinforcement that might be encountered in zoo or natural ("wild") environments. Zoo and sanctuary environments range from barren cages to large and naturalistic open-range enclosures (see Chapter 4). "Wild" environments also range from small fenced reserves to large tracts of land. If animals are provisioned in these natural environments (*e.g.* chimpanzees at Gombe, Goodall, 1986; bonobos at Wamba, Kano, 1992; free-ranging barbary macaques on Gibraltar; O'Leary, 1996), then a feeding schedule is arguably being imposed, just as it is in zoo environments. Provisioning of "wild" animals can lead to the development of aberrant behaviours, particularly increased aggression (Goodall, 1986). Barnard (1985) points out that "(a)t least one natural analogue of VI schedules has been found in renewing food accumulations along the banks of the river Thames" (p.331), which has an effect upon the behaviour of pied wagtails (Davies & Houston, 1981).

Animals in zoos are often exposed to a noncontingent intermittent schedule of food reinforcement (Carlstead, 1998). That is, the animals are fed at a particular time, irrespective of what the animals are doing at the time. Zoo carnivores, in particular, have traditionally been fed once every twenty-four hours, in a predictable manner that requires little effort to obtain food (*i.e.*, they are presented with a piece of meat). Not surprisingly, aberrant behavioural patterns (stereotypic behaviours), similar to the adjunctive behaviours observed in laboratories have been observed. Periodic response-independent reinforcement gives rise to stereotyped patterns of species-typical behaviour (Davey, 1989). The range of aberrant behaviours observed in primates housed in zoo environments is even greater. This will be discussed in some detail in Chapter 5. The responses that are observed in zoo environments or natural environments in which animals are provisioned, may result from Pavlovian processes (*e.g.*, autoshaping) and/or schedule contingencies (*i.e.*, as a result of Pavlovian &/or instrumental conditioning). That is, there may be a complex interplay between Pavlovian and instrumental learning (taken into account by the ***Behaviour Systems Approach***, which will be discussed in Chapter 4).

> "In their natural environment animals are rarely in an "emergency" deprivation state and their behavior is motivated by a range of factors related to their environmental niche and their lifestyle rather than any state of psychological deprivation. Understanding the factors which motivate an animal to feed in its natural environment helps us to understand some of the conditions under which stimuli become reinforcing" (Davey, 1989, p.235).

A ***concurrent schedule of reinforcement*** may most resemble the situation in natural environments. That is, the animal may have more than one source of reinforcement available at any given time, in which case it must "make a choice about which reinforcer to respond to" (Davey, 1989, p.112). The availability of food in the natural environment also varies considerably throughout the year (*i.e.*, fruits only ripe for a short period of time & fluctuations in prey density). Average hunting success rates in cats appear to share similaities with schedules of reinforcement (*i.e.*, for many species the hunting success rate for various prey items has been calculated as a percentage, which could easily be translated into a ratio, Kitchener, 1991). Certainly, animals exhibit peak feeding times in natural envionments, and activity budgets have been determined for many species. Ecological approaches to the study of behaviour will be discussed in the next chapter.

3.10 CHAPTER SUMMARY

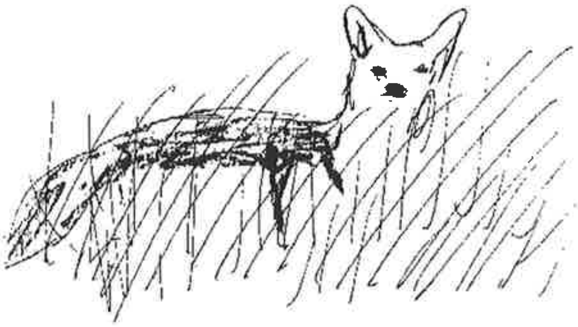
Since the 1980s, schedules of reinforcement have largely become tools used to investigate other phenomena. For example, researchers have used them to model general foraging strategies, but have not always manipulated the key variables in an ecologically relevant way. Researchers have also developed more naturalistic open-field style Skinner boxes, which allow more extensive investigations of behaviours (other than the operant response) that occur during schedules of reinforcement. Rats will engage in exploratory behaviour during schedules of reinforcement, if the opportunity is available. Importantly, the gap between psychological and ecological research is rapidly diminishing.

Falk's (1971) discovery of polydipsia and other adjunctive behaviours during schedules of intermittent food reinforcement opened up a whole new field of interest, with respect to schedules of reinforcement. Certain schedules coupled with the appropriate environmental conditions increase the probability of a particular aberrant (or "normal") behaviour occurring. Researchers have attempted to draw similarities between adjunctive behaviours and displacement activities, or also stereotypic behaviours. However, it appears that despite the similarities, they are different categories that cannot be used interchangeably.

Although it is only possible to speculate upon the existence of schedules of reinforcement in zoo or natural ("wild") environments, it is possible that they exist, particularly in zoos where animals are fed at fixed times, or in natural environments where animals are provisioned. These human-imposed feeding strategies, may also lead to the development of aberrant behaviours, which will be discussed in detail in Chapter 5.

CHAPTER 4

LINKING LABORATORY, ZOO AND FIELD RESEARCH: A COMPARATIVE AND INTEGRATIVE APPROACH



4.1 ANIMAL ENVIRONMENTS: FROM THE "WILD" TO CAPTIVITY

Beck and Castro (1994) question the commonly held view that animal environments are dichotomous: "contrasting naturalistic with nonnaturalistic, free-ranging with enclosed, indoor with outdoor, and wild with captive" (p.259). Instead, there are many types of environments, lying on a continuum from the "wild" to small cages. The "wild" is often a National Park, which in many cases is no longer pristine, nor immune to increased human penetration (Figure 4.1), whether poacher, researcher or tourist (Figure 4.2). Beck and Castro (1994) describe the Poco das Antas Biological Reserve in Brazil (5,000 hectares), which constitutes the "wild" for Golden Lion Tamarins. Set in a heavily populated area, with citrus plantations and cattle ranches developing around it, these researchers state, that: "(N)o surviving tamarin lives out of earshot of chainsaw and bulldozer.....The drone of cars, trucks, trains, and planes rivals that heard around any urban zoo" (pp. 260 & 261).

Part of this species' conservation program involved an attempt to trap and anaethetise all wild Golden Lion Tamarins. They were then checked for internal and external parasites, tatooed, administered with antibiotics. Some individuals were fitted with radio-collars, X-rayed, or had blood and faecal samples taken. The Reserve itself has gates, trails, signs and tours for education programs and tourists. As Beck and Castro (1994) point out, all of these protective measures, used to ensure the survival of this primate and its remaining natural habitat, are the very tools employed by zoos. This leads the researchers to wonder whether this "wild" environment is naturalistic or non-naturalistic, and whether the tamarins are free ranging and wild, or enclosed and captive? Whilst this example of a "wild" environment may not be representative of all natural habitats, similar trends and problems are being experienced at other National Parks around the world. Further, in "pockets" of the "wild" that are not given National Park status, and are thus afforded little, if any protection, the situation may be worse. Along with the great apes, it is likely that many animal populations will be increasingly restricted to reserves and national parks (Wrangham, 1998). Agricultural encroachment and other human land use have already resulted in reserves that are biologically isolated (Figure 4.3), with no genetic interchange possible, and high rates of extinction predicted (*e.g.*, Gombe Stream National Park).

4.2 LABORATORY RESEARCH

The main benefit of a laboratory test environment is that the experimental conditions can be more strictly controlled, and effects of confounding factors minimised (Martin & Bateson, 1993). Well-designed experiments in laboratory situations allow greater prediction and control of behaviour. That is, internal consistency or internal validity is high. The complete history of the animal is usually known, and thus factors such as housing and rearing conditions (social or singly housed, cage size, access to food & water) and previous exposure to testing or experimental environments can be taken into consideration (or manipulated).

The main problem with laboratory-based research is that it may provide results that cannot be generalised to other situations outside the laboratory. That is, external validity may be low. The laboratory environment may be so "sterile" and conditions so controlled, that it is too far removed from "real life" and natural determinants of behaviour. However, Timberlake (1990) points out, that: "behavior in even the most restricted laboratory environments is related to evolutionary determinants" (Timberlake, 1993, p.679). He argues that animals have the same evolved behavioural repertoire irrespective of the type of environment they find themselves in. Further, Timberlake (1993) maintains that even traditional laboratory researchers (*e.g.*, Skinner, 1938) modify their experimental methods and apparatus to suit a particular species and its behaviour (*e.g.*, lever for rats to press & key for pigeons to peck at).

It is almost impossible to provide a complete simulation of a natural environment in the laboratory. As Glickman and Caldwell (1994) point out, the challenge for laboratory researchers is to identify the "salient elements", or conditions necessary (in housing & experimental setting) to "provide sufficient support for the emergence of biologically significant results" (p.197). These researchers state that captive settings rarely introduce the "risk" elements of natural habitats (*e.g.*, predators or disease carriers), or daily or seasonal fluctuations in climatic

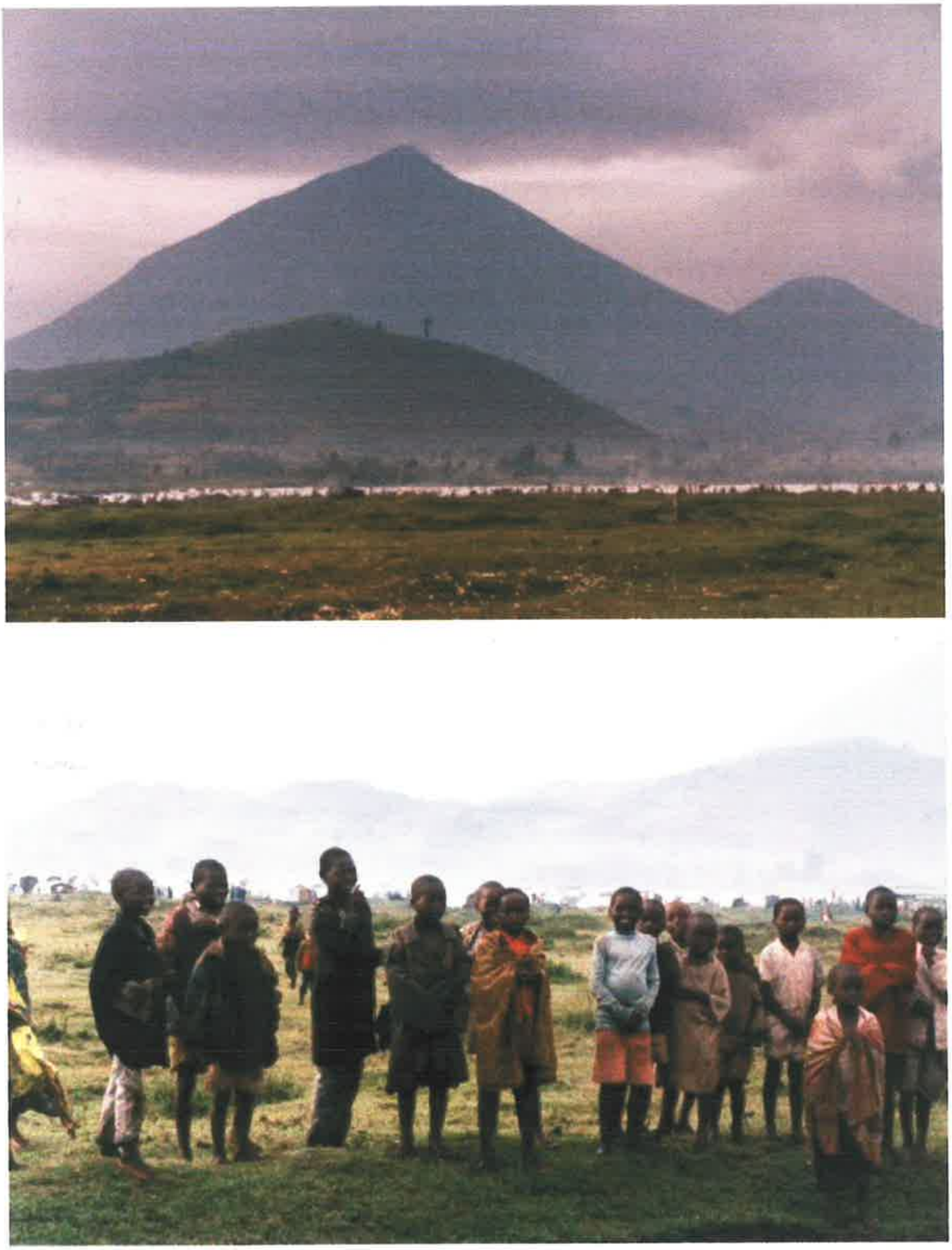


Figure 4.1. The Nyakabande refugee camp close to Mgahinga Gorilla National Park in Uganda is a stark reminder that mountain gorillas live in an area of Africa that is beset by human civil unrest (photo taken in January 1997).

Figure 4.2. Top- tourists who are eager to glimpse a kill or take that special photo may encourage tour operators to move vehicles up as close as possible to the animals. Bottom- drivers and tourists are drawn to clusters of vehicles, which may indicate the presence of a big cat or special event, like the lion up this tree (Masaai Mara in Kenya in 1994).

conditions. Instead of sticking within traditional laboratory limits, Glickman and Caldwell (1994) maintain that housing and experimental conditions should be based upon naturalistic data concerning the species' needs (*e.g.*, food, water, shelter, social requirements) and environmental features (*e.g.*, temperature, topography, lighting).

Janson (1994) emphasises that studies conducted in the laboratory "can be important in sharpening the inferences from traditional adaptationist field studies" (p.278). He summarises the advantages of laboratory research into five key points. Behaviour that is rarely seen in the field can be studied in detail. Hypotheses that have been derived from fieldwork can be tested. Developmental and genetic effects on behaviour can be studied under standardised conditions. Laboratory studies can also "yield data to allow conversion of fitness correlates to actual fitness differences" and "reveal latent behavioral capacities not demonstrated in nature" (Janson, 1994, pp. 278 & 279). Janson (1994) stresses that although field researchers may not be interested in laboratory studies, they should not underestimate the possible contributions afforded by such research.

4.3 RESEARCH IN ZOOS AND SANCTUARIES

Zoos provide the opportunity to study numerous species in captive settings that allow greater experimental control than "wild" environments, but also provide more naturalistic conditions (in most cases) than a laboratory environment. The range of possible species that can be studied is diverse. Experimental techniques and settings can be quite readily standardised and controlled. As Kleiman (1992) states: "a zoo cannot be surpassed for comparative studies of homologous behaviors (i.e., the evolution of behavioral characters from an array of closely related species)" (p.301).

Information gleaned from research conducted in captivity can be useful for field researchers. Law, MacDonald and Reid (1997) point out that many wild felids are rarely observed, and many of their social or reproductive behaviours may never be seen. Observations of behaviour, recordings of vocalisations and plaster casts of paw prints obtained from captive felids (*e.g.*, margays, jaguars & clouded leopards) are helping field researchers better identify and understand wild conspecifics (Law et al, 1997).

Zoos around the world vary with respect to the way in which animals are housed and displayed. Thus interesting opportunities exist for behavioural comparisons of one species housed under a variety of zoo conditions (*e.g.*, indoors or outdoors, large enclosures or smaller cages). For example, chimpanzees are group housed in a large outdoor enclosure at Taronga Zoo, as a family group in a large outdoor enclosure at Adelaide Zoo, and as a pair in a large outdoor cage at Rockhampton "Zoo" (personal observation). In 1997, Uganda chimpanzees were housed (as groups, pairs or singly) in outdoor enclosures (large cages) at Uganda Wildlife Education Centre. At this centre, vervet monkeys range freely, and one female vervet regularly engaged in mutual grooming (through the bars of the enclosure) with a female chimpanzee (Figure 4.4). Zoos can also be "open-range" in nature, which provides the opportunity to observe animals that are able to range over large enclosed (fenced) areas (Figure 4.5).

Sanctuaries provide another type of environment in which to study animal behaviour. These environments can be very large and naturalistic, such as Ngamba Island in Uganda. This 100-acre forest island sanctuary is currently home to about 20-orphaned chimpanzees (personal observation). The Monkey Sanctuary in Cornwall provides woolly monkeys with complex enclosures that are linked together by runways (Tudge, 1991).

4.4 RESEARCH IN OTHER CAPTIVE ENVIRONMENTS

Traditional laboratory and zoo environments are obviously not the only captive situations in which animals are housed or studied. Some behavioural research is conducted on farms with animals that are kept as pets, *e.g.*, horses in paddocks and stables (Waring, 1983). Other researchers observe farm animals that are kept for commercial purposes, *e.g.*, red deer hinds in large paddocks (Pollard, Grant, & Littlejohn, 1998); pigs in tether-stalls (Pedersen, Barnett, Hemsworth, Newman, & Schirmer, 1998); and laying hens in litter-floored pens (Lambe & Scott, 1998). Some researchers focus on behaviour and stress in dogs (*e.g.*, Sonderegger & Turner, 1996) and cats (*e.g.*, Kessler & Turner, 1997) kept temporarily in kennels or catteries, or circus elephants housed temporarily in paddocks (*e.g.*, Schmid, 1995).

For a period of time (until it was closed), marmoset monkeys were housed and studied by Menzel and co-workers in a large greenhouse with small trees growing in a dirt floor at the State University of New York (O'Leary, 1994). Glickman and Caldwell (1994) studied the behaviour of woodrats in large indoor rooms (8 foot x 8 foot), with floors covered in wood shavings, twigs and branches. Researchers conducting companion animal studies observe behaviour in a number of settings, *e.g.*, hospitals, nursing homes, and home environments (Podberscek, 1997).

These are just a few of the many variants of captive environments in which animals are housed and studied. Thus there is a large range lying on a continuum from fairly restricted (with greater experimental control like a laboratory environment) to very naturalistic (with less experimental

Figure 4.3. Signs of agricultural encroachment and other human land use are evident at many of the national parks and reserves in Uganda (top- agricultural activities take place right up to the boundary of Mgahinga Gorilla National Park, and bottom- pockets of forest alongside tea plantations near Kibale National Park)

Figure 4.4. Female vervet monkey grooming a female chimpanzee through the bars of an enclosure at the Uganda Widlife Education Center (December 1996)

Figure 4.5. Orphaned chimpanzees relocated from Burundi were able to range over a half-acre area at Sweetwaters Rhino and Chimpanzee Sanctuary in Kenya (photo taken by Debby Cox)

control like a "wild" environment). As a result, they vary with respect to internal validity and external or ecological validity, just like laboratory or field experiments.

4.5 FIELD RESEARCH

Martin and Bateson (1993) cover the benefits of field research in some detail. In the field it is usually possible to observe a wider range of the animal's behavioural repertoire. Factors that affect an animal's behaviour in captivity may not do so in natural habitats. The study of free-ranging individuals that can interact with their own and other species, within their natural environment (usually) allows researchers to understand more fully the conditions to which each behaviour is adapted. Social and ecological determinants of behaviour may be determined, as researchers relate observed behavioural patterns to the social and ecological conditions in which they typically occur. If a particular behaviour occurs in one situation and not in another, clues as to its function and proximate causation may be obtained. Martin and Bateson (1993) suggest that fieldwork provides:

> "the raw material from which research questions and hypotheses can be formulated. Moreover, it provides an understanding of how an animal's behaviour is adapted to the environment in which it normally lives, in the same way that its anatomical or physiological characteristics are adapted" (p.12).

Many of the problems associated with field research are logistical in nature. As Martin and Bateson (1993) maintain, field workers must often compromise between what is "ideal" and what is "practicable", since conditions in the field often make it difficult (or even impossible) to collect systematic observations of behaviour. The focal animal(s) may disappear from view, may not be found at all, or may not be sufficiently habituated to human observers. The weather may prevent observations from being made, or researchers may be faced with physical or emotional traumas that create hardships that are difficult to overcome (illness, danger, loneliness *etc.*).

Importantly, it may take years of time spent in the field to obtain enough systematic observations for meaningful analysis and interpretation. As Martin and Bateson (1993) assert, it cannot be assumed that behavioural observations collected in one type of habitat are representative for other populations of the same species in other habitats. Grooming and tool-use in chimpanzees provides a relevant example. Not all chimpanzee communities have the same behavioural and cultural traditions (McGrew, 1992). Chimpanzees at Kibale National Park (Uganda) and at Mahale Mountains National Park (Tanzania) engage in hand-clasp grooming (Figure 4.6), but other chimpanzee communities do not. Chimpanzees at Gombe Stream National Park (Tanzania) fish for termites, those at Tai National Park (Ivory Coast) crack open nuts with a hammer and anvil technique, whilst chimpanzees at Kibale National Park do neither. They do however use

Figure 4.6. Chimpanzees engaged in ***hand-clasp grooming*** at Kibale National Park in Uganda (photo taken in 1995)

subtle leaf signals (*e.g.*, leaf clipping or leaf grooming) to show sexual interest. Vocalisations also appear to show dialectical differences, possibly even within the same forest, *e.g.*, between chimpanzees of the Ngogo and Kanyawara study communities within Kibale National Park (Richard Wrangham, personal communication).

Janson (1994) points out that field studies often provide a "wealth of unsolved behavioral questions" (p.278). He suggests that controlled experiments in captive environments can then be conducted to try and answer these questions. Captive studies, on the other hand, may discover inter- or intra-species behavioural differences, which may be best interpreted by field studies. That is, the results obtained from field studies can provide important insights when researchers are attempting to understand behavioural variation obtained in captive environments, since usually "it is not possible in captivity to assess accurately the intensity of natural selection experienced by animals in the wild" (Janson, 1994, p.278).

4.6 FIELD EXPERIMENTS

In the field, researchers can either conduct unobtrusive observational studies of "natural variation" in behaviour, or they can conduct field experiments that examine behavioural responses to changes in particular variables or to events that rarely occur in the "wild" (Davies, 1992). Field experiments can be particularly useful in long-lived species, where in order to investigate the long-term consequences of behaviour, individuals must be followed and studied throughout their lives (decades in many cases). Field experiments can test functional hypotheses as well as providing insight into how behavioural patterns are controlled (Martin & Bateson, 1993). As Davies (1992) points out, field experiments (with adequate controls) can eliminate the possibility that one or more confounding variables ("correlated with the feature under study") may be the cause or effect of an event. However, the experimental manipulation itself may "disrupt features other than those under investigation" (Davies, 1992, p.20), and interfere with "the natural character of behaviour" (Martin & Bateson, 1993, p.26).

Davies (1992) in his study of Dunnocks conducted a number of field experiments (*e.g.*, removal of individuals & feeding experiments) in order to study their mating systems, how males and females compete for habitat and mates, influence of food on territory size, and so on. His experiments with different coloured model cuckoo eggs show a complete lack of discrimination in Dunnock hosts. Davies (1992) maintains that the opportunity to investigate responses to stimuli that do not occur in the "wild" is a major advantage of field experiments.

The study of vervet monkey alarm calls by Seyfarth, Cheney, and co-workers, arguably provides the quintessential example of field experiments. Vervets appeared to make different alarm calls for different predators (leopards, eagles, or snakes). In addition, each type of alarm call elicited different escape responses from other monkeys. In 1980, a series of playback experiments allowed Seyfarth, Cheney and Marler to test alternative explanations for monkey responses to different alarm calls (Cheney & Seyfarth, 1990).

Previously recorded leopard, eagle or snake alarm calls (made by individual's in the subjects' group) were used in the playback experiments (Cheney & Seyfarth, 1990). The researchers waited until the area was clear of predators and a number of vervets were visible. Then filming of the vervets commenced, followed after 10 seconds by an alarm call presented from a concealed speaker. For all three types of alarm call (snake, leopard & eagle) the monkeys looked in the direction of the speaker and visually scanned the area. However, the response to each type of call was very different. Leopard alarm calls typically resulted in monkeys on the ground running into trees. If an eagle alarm call was heard, monkeys on the ground responded by looking upwards or running into bushes. If monkeys were in tress, they also looked up and sometimes ran out of trees and into bushes. Snake alarm calls resulted in monkeys looking down from trees, or if they were on the ground they stood bipedally and looked around them on the ground. The results of the field experiments allowed the researchers to show that "different predators evoke both acoustically distinct alarm calls and different escape responses" (Cheney & Seyfarth, 1990, p.109).

Field experiments have resulted in significant advances in our understanding of animal communication, and behavioural traditions. Early experiments by Kortland using stuffed leopards allowed him to investigate chimpanzee anti-predator behaviours. Recent experimental work by Matsuzawa (1996) with chimpanzees in captivity and the wild has allowed a more complete picture of chimpanzee intelligence to emerge. His work will be discussed in the following section.

4.7 USE OF EXPERIMENTAL METHODS ACROSS ENVIRONMENTS

Whilst the use of well-designed and conducted field experiments may seem the ideal situation, Martin and Bateson (1993) state that fieldwork alone may not be enough, and it may be necessary to use the laboratory where it is possible to control conditions. Wyers (1994) points out that the:

> "Continuum of research methods ranging from laboratory study to field research includes naturalistic settings as intermediate way stations, comprising anything from abstract representations of critical natural elements to realistic renderings of what is known about a particular animal's lifestyle. As such, laboratory settings blend into naturalistic ones" (p.24).

Wyers (1994) stresses that behavioural experiments conducted in laboratory settings are "naturalistic in intent and import" and "cannot be done without taking biological functions into account" (p.24). However, he is careful to point out that ecological validity (or generalisability of findings to nature) is only possible if the research setting represents an animal's "morphological, physiological and psychological needs" (p.25). Naturalistic experimental settings (*e.g.*, large indoor or outdoor enclosures) provide greater experimental control than the "wild", but also provide greater ecological validity than traditional experimental laboratory settings. In addition, findings may lead to improvements in captive environments.

Wyers (1994) posits that in order truly to understand animal behaviour, behavioural observations should be conducted in as wide a variety of research settings as possible. Further, the most complete view of the whole animal is possible if general observations are a "counterpart" of experimentation. Wyers (1994) asserts that what:

> "we can do is observe behavior from as narrow or as broad a physicalistic perspective as is required, sometimes "zooming in" for a close-up and at other times "zooming out" for a view of wider scope" (p.32).

Matsuzawa (1996) has conducted both laboratory and field experiments to investigate chimpanzee intelligence. Not only has he used two very different experimental settings (a laboratory in Japan and forest in Bossou, West Africa), but he has also combined the use of "cognitive" methods (to study symbol-referent relationships) and systematic "behavioural" observations (to study tool-object relationships). Further, he has used both humans and chimpanzees as subjects. Matsuzawa (1996) maintains that such a synthesis of settings and methods allows a "new bridge" to be formed between traditionally separate areas of research. He refers to his approach as "Comparative Cognitive Science". This researcher advocates the use of unified objective scales that measure the performance of different species. That is, the same test apparatus and same experimental procedure should be used.

Matsuzawa and his co-workers have used computer-controlled apparatus in the laboratory to investigate and compare chimpanzee and human colour perception, form perception, complex pattern recognition, face recognition, and the concept of number (Matsuzawa, 1996). The laboratory experiments used individual subjects who worked with the computer system in an isolated social setting. The field experiments investigated chimpanzee use of stone tools (hammer & anvil) to crack open nuts in a social context. Direct comparisons were made between young chimpanzees and human children, and Matsuzawa (1996) found that successful use of stone tools first occurs at the age of three years. He also investigated the behaviour of a neighbouring chimpanzee community.

In one field experiment, an outdoor laboratory (with a buried water container) was set up to allow researchers to observe and video-record the use of leaves to drink water. The stone tool use experiments also involved setting up an outdoor laboratory. To observe nut cracking directly was too difficult. The location of the palm trees was close to a village (the chimpanzees were too "timid" when in this area), and the foliage around the trees reduced visibility (Matsuzawa, 1994). Stones and nuts were taken to the top of a hill in the centre of the chimpanzee community's home range. The number of stones and nuts, and location and arrangement of these items were varied by the researchers according to the experimental requirements. Observers watched and filmed from behind a screen of grass (20 metres away). Thus Matsuzawa (1996) and his co-workers were able to create experimental situations in a natural environment that allowed maximal control of conditions and ensured optimal filming and observation opportunities.

Janson (1994) posits that semi-naturalistic environments (in captivity) can bridge the gap between field and laboratory studies. Such environments provide researchers with the opportunity to exert experimental control and easily observe behaviour, whilst providing conditions that are sufficiently complex to study species-typical behaviours. Most laboratory settings are too small and simplistic to provide animals with the opportunity to search for food (not just exploit a known food source). Yet foraging (searching & consuming) for unknown sources of food can take up to 75% (or more) of an animal's waking day (Janson, 1994). Field studies, on the other hand, are usually unable to distinguish "direct causal relationships from indirect correlated responses" (Janson, 1994, p.274). Well-designed experiments conducted in semi-naturalistic settings could allow behavioural ecologists (& others) to determine more readily and accurately the ecological determinants of various behavioural patterns.

4.8 THE FOUR "WHYS" OR DETERMINANTS OF BEHAVIOUR

As Tinbergen (1963) recognised, the study of behaviour raises four main types of problem (Martin & Bateson, 1993). His classification is still widely used and accepted today. Martin and Bateson (1993) maintain that historically, comparative and experimental psychologists have tended to focus on questions about the proximate causes of behaviour ("how" questions), whereas ethologists have concentrated on how behaviour is controlled, what it is for, and how it evolved ("why" questions). These different approaches to the study of behaviour will be discussed in the next section. Table 4.1 presents the four determinants of behaviour, as originally posited by Tinbergen (1963).

Table 4.1
The four "whys", "problems" or determinants of behaviour (incorporating points made by Krebs & Davies, 1991; Martin & Bateson, 1993; Tinbergen, 1963).

SURVIVAL VALUE (FUNCTION)	**PHYLOGENY (EVOLUTION)**	**CONTROL (CAUSATION)**	**ONTOGENY (DEVELOPMENT)**
Ultimate Causes		***Proximate Causes***	
Concerned with: ♦ How a particular behavioural pattern contributes to survival and reproductive success ♦ non-adaptive mechanisms may also operate	**Concerned with:** ♦ Evolutionary history of behaviour in a population or lineage	**Concerned with:** ♦ "immediate" causal mechanisms of a behavioural pattern (internal & external)	**Concerned with:** ♦ developmental history of behaviour of individuals as a result of genetic and environmental factors
Related to questions about : ♦ populations ♦ What is it for?	**Related to questions about :** ♦ populations ♦ How did it evolve?	**Related to questions about :** ♦ individual organisms ♦ How does it work?	**Related to questions about :** ♦ individual organisms ♦ How did it develop?

Martin and Bateson (1993) provide a brief and clear summary of the four "problems". Researchers concerned with ***control*** (proximate causation) examine which stimuli elicit a particular pattern of behaviour. Further, they are interested in the mechanisms (neurobiological, psychological, or physiological) that control an animal's behaviour (in the short term). The study of ***ontogeny*** is the "behavioural equivalent of embryology" (Martin & Bateson, 1993, p.8). Researchers are interested in the development or "assembly" of behavioural patterns during the lifetime of an individual. Survival value or ***functional*** questions are concerned with the current use of a behavioural pattern. That is, researchers investigate how engaging in a particular rbehaviour can aid an animal's survival (& reproduction). Researchers concerned with ***phylogeny*** are interested in how behaviour was "moulded" during the evolutionary history of a species.

Tinbergen's (1951; 1963) four problems or questions are "logically" distinct, but researchers need not confine themselves to addressing just one type of question. Questions about the function of a particular behaviour may lead to insights about how to study proximate causation or underlying mechanisms (Martin & Bateson, 1993). Krebs and Davies (1993) provide the example below to illustrate four different (all correct) answers or explanations to the same question. These "reflect four distinct levels of enquiry about the same phenomenon" (Martin & Bateson, 1993, p.8):

Question: "Why do starlings (*Sturnus vulgaris*) sing in spring?

- ***Explanation 1 (control or proximate causation)***: Increasing day-length triggers changes in starling hormone levels (external factor), or air flows through the syrinx which sets up membrane vibrations (internal factor).
- ***Explanation 2 (ontogeny or development)***: Starlings sing because they have learned songs from their parents and neighbours.
- ***Explanation 3 (survival value or function)***: Starlings sing in order to attract mates for breeding.
- ***Explanation 4 (phylogeny or evolution)***: Starling songs have evolved from avian ancestors. Primitive living birds make simple sounds, so the complex songs of starlings probably evolved from simpler ancestral calls.

Krebs and Davies (1993) maintain that researchers most frequently confuse functional or "ultimate" factors (survival value) with causal or "proximate" factors. Martin and Bateson (1993), on the other hand, suggest that evolutionary and functional questions (both "ultimate") are frequently "muddled".

Timberlake (1993) suggests that Tinbergen's (1951; 1963) questions have provided "historical coherence" to the field of animal behaviour. The diverse nature of the four questions "explicitly encourage a balance of approaches and causal levels" (Timberlake, 1993, p.678). Whilst, the four questions remain an integral part of animal behaviour research, Timberlake (1993) stresses that:

> "Tinbergen's questions by themselves do not provide a unifying picture of the fit between animal and environment. The clarity of the ethologist's original picture has been lost in the ensuing forty years" (p.678).

Typically, the analysis of behaviour and learning within psychology has focussed on causal factors and excluded an analysis of function, or the biological explanations (Zeiler, 1992). This will be discussed in greater detail in the following sections.

4.9 ETHOLOGICAL AND PSYCHOLOGICAL APPROACHES TO THE STUDY OF BEHAVIOUR

Just as there are a variety of environments in which to study behaviour, there are a variety of research methods that can be employed. Historically, psychologists and ethologists have used different methods, and had different interests in the study of behaviour (Barker, 1997). Table 4.2 contrasts the two approaches (very general comparison). Recently, behavioural biologists (ethologists/behavioural ecologists/socio-biologists) and psychologists have been transferring ideas and methods (Barker, 1997). For example, behavioural ecologists interested in how animals forage for food have been using experimental methods developed by psychologists. Similarly, psychologists have been using observational methods developed by biologists to study the behaviour of children (human ethology). As mentioned previously, psychologists are also focussing on the adaptive functions of behaviour, or how behaviours facilitate survival (Barker, 1997).

Thus, researchers today may combine the use of both experimental and observational methods, and must take the possible adaptive significance of behaviour into account (Litchfield, 1987). Ecological factors (*e.g.*, food abundance & distribution) influence behaviours in natural environments, and must be taken into account when discussing survival value. As Davies (1992) asserts:

> "Ecological conditions set the stage on which individuals play out their behavioural strategies" (p.5).

Tinbergen suggested in 1963 that many sciences concerned with the study of behaviour were beginning to "fuse" into one "coherent science", the "*Biology of behaviour*" (p.430). He points out that Konrad Lorenz (perhaps the "father" of ethology) recognised that "behaviour is part and parcel of the adaptive equipment of animals" and could be "studied in fundamentally the same way as other biological phenomena" (p.430). Tinbergen (1963) classified himself as "both a naturalist and an experimenter at heart", maintaining that "one of my primary interests has always been to find out, if possible by experimentation, how animal behaviour contributes to survival" (p.417). Davies (1992) stresses that Tinbergen "taught us the power of simple manipulations and championed the use of the field as a natural laboratory for the ethologist" (p.21). Considering how influential Tinbergen's 1963 article was (on biologists in particular- see Krebs & Davies, 1993), it is somewhat surprising to see that over thirty years later the need for this "fusion" of disciplines and methodologies is still being discussed.

Table 4.2

Contrasting the psychological and ethological approaches to the study of behaviour (based on Table 2.1 in Barker, 1997, p.71).

TRADITIONAL PSYCHOLOGICAL APPROACHES (comparative and experimental)	**TRADITIONAL ETHOLOGICAL APPROACHES**
FOCUS AND INTEREST	**FOCUS AND INTEREST**
◆ Focus on individual differences within a species/ across species ◆ Interest in general processes in vertebrates ◆ Ultimate focus is human species	◆ Focus on species-typical behaviour across species ◆ Interest in species-specific behaviours ◆ Focus on non-human animal behaviour
METHOD OF STUDY	**METHOD OF STUDY**
◆ Study domestic animals under laboratory conditions ◆ Intervention and manipulation (by humans) of animal behaviour ◆ Stress experimental design and quantitative methods	◆ Study "wild" animals within natural ecological niche ◆ Unobtrusive observations of animal in its natural environment ◆ Stress biological/adaptive functions of behaviour
RESULTS AND APPLICATIONS	**RESULTS AND APPLICATIONS**
◆ Use of animal models ◆ Extrapolation to human behaviour ◆ Tests of general theories	◆ Animals do not "model" behaviour ◆ Little or no interest in extrapolation to human conditions or testing "general" models

Timberlake (1993) discusses Tinbergen's Four Questions, and then presents his own analysis of the main methods of comparing behaviour. He provides four categories based on the concern with the dimensions of genetic and ecological relatedness. Timberlake (1993) maintains that comparative psychologists have tended to focus on ***Protoevolutionary comparisons*** (Classifications, Trends & Grades; Scaling Functions & Allometry; & Universal Laws) and ***Microevolutionary comparisons*** (Genetics & Development; Within-Species Strategies; & Micro-Model Systems). Ethologists, on the other hand, focused on ***Phylogenetic comparisons*** (Homologies; Series; & Animal Models) and ***Ecological comparisons*** (Convergence & Divergence). However, recently, these distinctions have become blurred and some empirical research methods have "cut across all categories" (Timberlake, 1993, p.682).

Martin and Bateson (1993) stress that purely observational behavioural research is no less "scientific" than experimental research. Scientific research aims to generate and test quantitative hypotheses. Both experimental and observational research can "generate empirical data that distinguish between competing hypotheses" (Martin & Bateson, 1993, p.11).

In summary, comparative psychologists in the past have been associated with laboratory research. They have used laboratory-bred animals, "arbitrary" stimuli, "automatic recording of arbitrary response elements", and statistical analysis (Timberlake, 1993, p.679). At the opposite extreme, ethologists in the past were associated with field research. They observed animals in uncontrolled natural conditions, and focused on complex patterns of behaviour and "impressionistic reporting" (Timberlake, 1993, p.679). Timberlake (1993) maintains that these traditional:

> "stereotypes, always of doubtful accuracy, are inappropriate now that laboratory and field approaches have become increasingly difficult to distinguish…However, differences remain in how frequently individual investigators use the full range of research options" (p.679).

Timberlake (1993) presents a balanced and integrative view of suitable research environments. Instead of adhering to a single approach, he suggests that researchers pursue a variety of approaches. Sometimes fieldwork could precede laboratory research (dealing with external validity first), and at other times laboratory analysis of phenomena could precede fieldwork (dealing with internal validity first). There is no "right" or "wrong" environment or species for research purposes. Importantly, researchers should take both the environment and the animal into account, and analyse the "fit between animal and environment" by studying different species in a variety of environments (Timberlake, 1993, p. 679).

4.10 BEHAVIOURAL ECOLOGY: THE STUDY OF BEHAVIOUR AND BEHAVIOURAL ADAPTATION

Davies (1992) acknowledges Niko Tinbergen as the pioneer of "modern field studies of behavioural design", studying the function of behaviours just as an anatomist might study a bone or other structure, making "measurements to elucidate its function" (p.6). Early ecologists were primarily interested in species-specific behaviour patterns, or how behaviours were advantageous to individuals of a particular species. Davies (1992) states that behavioural ecologists today are particularly interested in understanding individual differences within a population or species (more like the comparative psychological focus mentioned in Table 1). He stresses that the study of individual differences in behaviour is important, because "Individual differences are the raw material for natural selection" (p.7). The study of these differences can help determine the costs and benefits of behavioural traits and why changes in populations occur over time. Individual differences can also indicate that there may not be just a "single 'best' design" for a particular behavioural pattern or strategy in a species (Davies, 1992, p.7).

Recently behavioural ecologists have also started to focus on "conflicts of interest" within populations (*e.g.*, between rival males, males & females, or parents & offspring). Davies (1992) points out that this change in focus or approach has implications on how behavioural adaptation is interpreted. In the 1960s and 1970s, researchers focussed on how behavioural traits influenced the success of an individual within a population (individual fitness), rather than the evolution of behavioural traits that were advantageous to the species as a whole. Today behavioural ecologists are interested in "what selection is expected to produce when there are conflicts of interest" within a population (Davies, 1992, p.7).

Over the last few years advances in the area of DNA fingerprinting have allowed researchers to monitor the "adaptiveness" of behavioural patterns or strategies. That is, the ability to measure the maternity or paternity of animals provides a means of assessing whether the behaviour of an individual promotes its own reproductive success (Davies, 1992). DNA fingerprinting can be conducted on samples of blood (*e.g.*, Dunnocks or other birds, Davies, 1992), or on non-invasively collected hair samples (*e.g.*, chimpanzees at Kibale National Park, Uganda, personal observation), or fecal samples (*e.g.*, western lowland gorillas, Bradley, Doran, Boesch & Vigilant, 2000). Davies (1992) maintains that the method of DNA fingerprinting is so powerful that it can determine paternity in species "where close relatives were sharing matings" (p.123).

4.11 OBSERVER EFFECTS AND ETHICAL ISSUES

Irrespective of the environment in which an animal's behaviour is being investigated, an observer must always be aware that his/her presence may be influencing the subject. In the laboratory the observer can remain hidden behind a screen (although the subject may still be able to hear or smell the observer), or be out of the experimental room altogether, whilst the animal is being filmed on video. In the field it is often impossible to study or observe an individual (or group) until the animal has become habituated to the presence of the observer(s). This habituation process can take months, or even years. However, it should be noted that: "the impression that well-habituated subjects are not affected by the observer's presence is difficult to verify and should be treated with some scepticism" (Martin & Bateson, 1986, p.17). In the zoo the observer may be just one of the many daily visitors. However, since the observer is likely to spend long periods of time observing the animal(s), s/he cannot expect to remain unnoticed. Thus, as in the field, the observer should allow the subjects to become habituated to his/her presence.

As Martin and Bateson (1993) point out, the general public and scientists have shown marked changes in their attitudes towards animals in research. Animal Ethics Committees and scientists must consider whether studies using animal subjects are worthwhile (in terms of contributions to human understanding, education, economy, the environment) and minimise the number of animals needed and potential suffering or stress (physical & psychological well-being). Martin

Figure 4.7. Animal skins and parts can be seen and bought in a variety of places in Uganda. Stalls selling body parts for traditional medicine can be found in Kampala (top). Traditional dancers may be seen wearing black-and-white colobus skins around their waists (bottom) at Mweya Lodge in Queen Elizabeth National Park (photos taken in December 1996).

Figure 4.8. Habituated chimpanzees (top- Kibale National Park, Uganda) and mountain gorillas (centre & bottom- Mgahinga Gorilla National Park, Uganda) may be visited by thousands of tourists, researchers, guides, rangers and trackers every year.

and Bateson (1993) stress that ethical issues concerning animal research do not only apply to laboratory-based experiments, but also to observational and field studies.

The observation of animals in natural environments can be disruptive or stressful for the animals, particularly if animals are captured, marked or tagged (for identification), or measured. Cuthill (1991) criticises field ecologists and behavioural ecologists for often failing to recognise the ethical issues that surround field experiments. He poses the question of how much tampering with nature is justifiable. Apart from the effects of tagging and marking individuals, Cuthill (1991) considers the ethical issues linked to a number of experimental techniques used in the field. These manipulations include the use of stuffed predators, non-trivial handling (taking tissue or blood samples, capture/recapture, attachment of radio transmitters), playback of alarm calls, food provisioning, removal or displacement of individuals, brood manipulation and phenotype manipulation.

Habituating "wild" animals to the presence of humans (*e.g.*, researchers & tourists) brings its own ethical dilemmas. By allowing humans closer, the animals may be at increased risk from poachers and human illnesses or disease (Figure 4.7). This is a particularly serious issue for endangered species, such as the mountain gorilla. Approximately 650 individuals remain, and of these, 184 have been or are being habituated for tourism and research purposes. These habituated gorillas may receive up to 35,000 visitors (tourists) per year (Figure 4.8). In addition, every year, up to 1,600 and 900 researchers, guides, rangers and trackers spend time with each gorilla research and tourist group respectively (International Gorilla Conservation Programme, 1998).

Results obtained from observations of animal behaviour in the laboratory and natural environments can be applied to animal welfare issues. As Martin and Bateson (1993) state:

> "applied ethology uses the results of behavioural studies to improve conditions and solve problems of pets, farm animals and zoo animals. Studies of animals can be useful in wildlife management and preservation of the environment" (p.16).

Such applied research is not limited to the discipline of ethology, but is also carried out by psychologists. Accurate behavioural information is important for improving captive environments. Knowledge about an animal's behavioural repertoire, activity budgets, ranging patterns and other ecological information aid in the design of appropriate enclosures that encourage behavioural diversity and psychological well-being (this will be discussed in detail in the following chapter). Accurate ecological and behavioural information is vital for the conservation of endangered species and their natural environments. Conservation management plans based around Population and Habitat Viability Assessments rely on computer simulations (*e.g.*, the VORTEX programme used by the Conservation Breeding Specialist Group of the IUCN) of possible catastrophes and the likelihood of a particular population's survival. That is, the computer software simulates the effects of deterministic forces as well as environmental, genetic and demographic stochastic events on wild populations (Edroma, Rosen & Miller, 1997). Accurate scenarios and calculations are only possible with accurate and specific behavioural and ecological information.

4.12 LOW SUBJECT NUMBERS IN ANIMAL BEHAVIOUR RESEARCH

In recent years, in response to ethical and financial considerations, scientists studying animal behaviour (particularly those that conduct experiments) have had to reduce the number of animals used "without sacrificing scientific goals" or rigour (Still, 1982, p.873). In order to test a statistical hypothesis, experimenters attempt to minimise type I errors (reject null hypothesis when it is true) and type II errors (fail to reject null hypothesis when it is false). As Still (1982) points out, researchers aim to minimise the probability of a type I error, whilst maximising the power of a statistical test (1 - probability of type II error). Typically, researchers have tended to increase the number of subjects (*N*) used in an experiment, in order to increase the power. However, Still (1982) stresses that if a test is already powerful, then an increase in subject numbers is wasteful. Further, power can be increased by other means, including greater precision (accurate measurement & control of extraneous variables), use of more powerful tests (parametric rather than non-parametric, where possible), better experimental design (repeated measures rather than independent groups), and using a larger level of significance (0.05 instead of 0.001).

Still (1982) maintains that the sample size can be chosen on the basis of previous experiments and pilot studies. If the " a priori probability of the phenomenon is very high" (*e.g.*, rats freezing & "stretching" after electric shock) it is unnecessary to aim for high power using large sample sizes, since the scientific community can be just as "convinced" with low subject numbers (Still, 1982, p.876). Still (1982) also points out that visual inspection of data from two or three subjects (*e.g.*, in physiological or operant conditioning experiments) is "usually enough to confirm that the pattern is sufficiently similar for generalization", or to make inferences about populations (p.877). If experimenters try to generalise from low subject numbers, they should not base inference upon the strict requirement of random sampling, but instead upon random assignment of subjects to treatments or groups. Still (1982) stresses that scientific interest rather than statistical criteria should "determine what observations are of interest" (p.879). Thus, studies of individual animals or a group of social animals can be important and of scientific interest.

Although Still (1982) makes a number of valid points, he does not make any mention of power analysis. Many researchers disregard statistical power analysis. As a result, there is still "no increase in the probability of obtaining a significant result" (Cohen, 1992, p.155). That is, most studies fail to estimate power or the necessary sample size needed to obtain the population effect size posited. "Statistical power analysis exploits the relationships among the four variables involved in statistical inference: sample size (*N*), significance criterion (α), population effect size (ES), and statistical power" (Cohen, 1992, p.156).

Cohen (1988, 1992) proposes the convention of using a power of 0.80 (*i.e.*, the probability of a Type II error is 0.20), since a lower value would increase the risk of a Type II error, and a larger value would result in a sample size demand "that is likely to exceed the investigator's resources" (p.156). Unfortunately (for animal researchers in particular), to detect a medium difference (population effect size) between two independent sample means at a significance criterion of 0.05 ($\alpha = 0.05$), a sample size of 64 subjects is needed per group ($N = 64$). Other statistical tests may require even greater sample sizes to increase the probability of obtaining a significant result.

Whilst ethical and financial considerations have forced laboratory scientists to reduce the number of animals used in experiments, zoo researchers have often had no choice but to use single subject (or small *N*) research designs. Nevertheless, researchers must be aware of the existence of statistical power analysis, and realize the implications and limitations of not being able to use adequate sample sizes. Saudargas and Drummer (1996) maintain that small subject research designs are now widely used and are a viable option for basic and applied research conducted in zoos. According to these researchers, these experimental designs use repeated measures, have high internal validity, and can clearly establish functional relationships between variables.

Saudargas and Drummer (1996) state that experiments using small subject numbers in zoos include studies of the behavioural effects of enrichment techniques (*e.g.*, addition of novel objects, changes in feeding routines & enclosure modifications) and behavioural management procedures (*e.g.*, restraint for veterinary procedures). These researchers stress that a vital component of the success of single subject (small *N*) research is a stable behavioural baseline prior to the introduction of the experimental condition. Saudargas and Drummer (1996) maintain that zoo researchers should aim to systematically replicate their research at other zoos wherever possible, in order to strengthen external validity and generality of findings. They conclude that data should not only be analysed by visual inspection, but also by parametric and nonparametric statistical tests (*e.g.*, ANOVA & *t* tests), if a relatively large number of data points exist. Thus, researchers of animal behaviour in captive environments are faced with low subject numbers, but careful consideration of experimental design and analysis of data can ensure that external validity is enhanced and that important research questions can be addressed and answered.

4.13 IS AN INTEGRATIVE AND HOLISTIC APPROACH TO THE STUDY OF ANIMAL BEHAVIOUR POSSIBLE?

For some time, psychologists have been aware of the need to take the adaptive significance, or biological and evolutionary perspectives of behaviour into account. The ecology of an animal is inexorably linked to its behaviour. How a particular behaviour pattern develops in an animal's natural environment and whether it aids survival (individual & species) is something that should be taken into consideration. However, psychology is not the only discipline to study behaviour in a less than complete fashion. As Barker (1997) points out, biological or ecological approaches to the study of behaviour have failed to take the importance of learning and memory into account. Conservation biologists have tended to ignore behavioural research altogether (& the place of learning). Yet, the behavioural patterns of a particular species, or group of animals, are likely to have an impact on their subsequent survival or demise.

The survival of threatened or endangered species will ultimately depend on an understanding and recognition of all aspects of a species' behaviour in captivity and its natural environment. Further, the interactions between animals and humans must also be investigated, particularly in areas where humans and free-ranging animals come into conflict. Clearly, a more interdisciplinary approach to the study of behaviour is required. It must recognise the importance of processes within animals, the ecological and environmental determinants of behaviour, and how behaviour patterns are linked to survival (or possible extinction). To espouse the use of an integrative approach is easy. Actually to put such an approach into practice is somewhat more complicated. It requires changes to all aspects of behavioural research, from the initial planning stages, to the collection of data, and finally to the interpretation and application of findings.

Timberlake (1993) presents evidence that an integrative approach to the study of behaviour is possible. A number of his suggestions have been discussed elsewhere in this chapter. As already mentioned, researchers are already combining experimental and observational methods of data collection, in a variety of settings, and with a variety of species. Thus, researchers from a number of disciplines are studying behaviour in the laboratory, naturalistic captive enclosures (indoor & outdoor) and in the field. They are able to use computer-controlled apparatus in the laboratory, as well as video cameras or closed circuit television to conduct behavioural observations. In the field they are able to set up outdoor laboratories (*e.g.*, Matsuzawa, 1996), use video or sound recording equipment, *e.g.*, playback experiments (Cheney & Seyfarth, 1990), or just conduct unobtrusive behavioural observations. Researchers such as Timberlake (1993) espouse an integrative approach that combines the best of available methods, environments, and technological advancements. However, to be truly integrative, an appropriate theoretical framework is necessary for the interpretation of findings.

An integrative framework that is animal-based rather than apparatus- or procedure-based is recommended for behavioural ecologists, psychologists interested in ecological determinants of learning, behaviour and motivation, and researchers in other areas (Timberlake, 1993). The ***Behaviour Systems Approach*** provides an integrative framework. According to Timberlake (1993), this approach provides an appropriate "framework for integrating the answers to Tinbergen's questions and the results of different methods of comparing behavior" (p.696). It takes sensory-motor capabilities, motivational states, and social systems into account. In addition, developmental factors, neurophysiological underpinnings of behaviour, and environmental factors are considered.

Importantly, as Timberlake (1993) points out, the ***Behaviour Systems Approach*** can be used to deal with areas such as animal cognition and animal welfare- areas that have been avoided by traditional behavioural researchers. Cognitive learning abilities such as memory, timing and navigation have ecological relevance. Researchers again should focus on ecological and evolutionary aspects, and not just deal with general principles, definitions and experimental procedures. The ***Behaviour Systems Approach*** can also be applied to the reduction of stereotypical behaviours in zoo animals, or other research that focuses on psychological well-being or animal welfare.

Timberlake (1993) concludes that a flexible and heuristic integrative approach, which encourages collaborative inter-disciplinary research:

> "treats behavior (including perception) as a bidirectional link between animal and environment in both local and ultimate senses. Locally, behavior creates environments as much as local environments create behavior. This point is particularly salient in highly social species. In an ultimate sense, behavior is the ambassador of environments to the genes as well as the representation of the genes in environments" (p.700).

4.14 INTEGRATIVE AND HOLISTIC APPROACHES TO THE STUDY OF HUMAN BEHAVIOUR

The attempt to bridge the gap between psychological and ecological research within the area of animal behaviour is a relatively recent phenomenon. Yet, the areas of *behavioural ecology* and *ecological psychology* have existed for many years within the more general area of environmental psychology (Wicker, 1979; Willems, 1977). These researchers have been concerned with the ecological study of human behaviour. This section will briefly investigate the way in which psychologists interested in human behaviour have applied ecological principles to their study of the relationship between behaviour, environments and adaptation. Environmental psychologists have tackled applied ("real-world") problems of environmental design for humans for decades. Despite the striking parallels in the problems and shortcomings encountered within the study of behaviour in humans and animals, many psychologists choose to focus on either humans or animals, and may be unaware of developments in their "counterpart" area. The study of human behaviour is mentioned here to illustrate that a multi-disciplinary, integrative and holistic approach can be applicable to the study of human and/or animal behaviour.

Psychologists were already using the term *ecology* in the 1940s. Wicker (1979) traces the ecological viewpoint in psychology back to Kurt Lewin (1944) and his paper on "psychological ecology". However, this early research was based on human subjects' ***perceptions*** of their environments rather than on environmental features. By 1949, two of his associates (Barker & Wright) were arguing that ecology should become a branch of psychology. Wicker (1979) points out that these researchers were trying to broaden the environments in which psychologists typically studied human behaviour. Instead of concentrating on human behaviour under experimental laboratory conditions, Barker and Wright suggested that an ecological approach would investigate human behaviour in "everyday" naturalistic environments and employ careful observational techniques. In subsequent research, Barker and Wright conducted day-long observations of children to investigate the relationship between their surroundings and behaviour. One of these published day-long records of behaviour was 435 pages long (Wicker, 1979).

Wicker (1979) defines ecological psychology as: "*the study of the interdependent relationships between the goal-directed actions of persons and the behavior settings in which these actions occur*" (p.16). Ecological psychologists recognise the fact that environments are comprised of a series of ecological units or self-regulating systems, or environments within environments, and that the human behaviour is linked to the environment.

Two important suggestions that Wicker (1979, p.189) makes for future research in ecological psychology are:

(1) that "there are many different research strategies that are appropriate for pursuing questions of interest to ecological psychologists" ; and

(2) that "it is desirable for ecological psychologists selectively to borrow concepts and methods from other areas of psychology and from other disciplines".

4.15 BEHAVIOUR, ECOLOGY, EVOLUTION AND CONSERVATION: AN INTEGRATIVE APPROACH

As Martin and Bateson (1986) point out:

> "empirical data that distinguish between competing hypotheses can be obtained by observing natural variation as well as by performing controlled experiments. Thus, for many purposes, it is unnecessary to draw a rigid distinction between observational and experimental research" (p.16).

The ***ethoexperimental approach*** to the study of behaviour, which emerged in the late 1980s, suggests that researchers continue to investigate behaviour in the laboratory, but that they apply ethological "considerations" to create laboratory environments that are more "meaningful" to the species under study, and develop more exhaustive descriptions of behaviour, or ethograms (Brain, 1989). Brain (1989) maintains that the use of semi-naturalistic experimental environments allow rats to dig and construct tunnels and interact with conspecifics, which "radically changes the behavior of the laboratory rat making it much more like its colonially aggressive feral counterpart" (p.25).

Wyers (1994) suggests that to understand animals scientifically, it is necessary to observe and measure their behaviour: "in as wide an array of research settings as possible" (p.32). Instead of viewing general observation as a "supplement" to experimentation, it should be considered a "counterpart". Further, behaviour can be investigated in a very focused way, or as part of a wider scope. Wyers (1994) alludes to the problem that although most people are concerned with the welfare and well-being of captive animals, often the requirements and procedures used for housing and maintenance are purely arbitrary and not based on research data. "Cosmetic changes that look good to humans, but do not benefit captive animals, are a disservice to science and to the animals themselves" (Wyers, 1994, p.33).

Timberlake (1993) points out that there are no "absolute rules" for conducting successful scientific research, and referring to the work of Maynard-Smith (1982) he states that in:

> "practice most adept scientists appear to be more like game theorists, using conditional rather than absolute rules – deduction *and* induction, observation *and* manipulation, strong inference *and* demonstration, one species *and* many" (p.680).

Thus, the key to good integrative behavioural research is to remain flexible, make use of individual strengths, and incorporate a variety of approaches.

Timberlake (1993) provides three interesting suggestions for an integrative research approach. Firstly, researchers should step back and return to a "naïve" or "ignorant" state. That is, they should test "obvious" interpretations, ask simple questions (*e.g.*, why does the form of a response vary over time?), and query traditional methods and models. Secondly, Timberlake (1993) maintains that researchers should take the animal's view or perspective. That is, they should be "theromorphic" (which is very different from "anthropomorphic"), or animal-centered rather than human-centered in their approach. Such an approach involves asking a variety of experimental and observational questions about an animal and its behaviour, based upon knowledge of a species' sensory, cognitive and motor abilities and motivation and decision rules. Such an approach allows the "integration of intuition and experimental results", which is essential in designing experiments and interpreting behavioural results. Thirdly, researchers should be wary of taking an approach that is too simplistic (*e.g.*, simple causal models based on manipulation of just one or two variables). Instead, scientists should take a more heuristic "systems approach", since "animals are sets of functional systems that operate within and influence the context of environment, physiology, behavior, social relations, and evolution" (Timberlake, 1993, p.681).

Psychologists along with most scientists have aimed to develop general laws or principles. Timberlake (1993) points out that instead of attempting to emulate physics, many behavioural researchers would have been better off emulating chemistry. Many comparative psychologists have focused on universal laws of classical and operant conditioning (learning). Recently, behavioural ecologists have focused on a universal law based on the principle of optimality. However, Timberlake (1993) asserts that the:

> "fit of billiard ball and environment is not the same as the fit of an animal and its environment. Something like a dynamic "periodic table" relating animals, environments, and behavior is necessary before more accurate general laws are possible" (p.685).

Zeiler (1992), like Timberlake (1993), addresses the problems that arise when psychologists take a Newtonian physical science perspective rather than a biological perspective. Unlike the causal laws of physics (mechanisms), which are based on fixed and invariant properties of inanimate matter within "(v)acuums and frictionless states", the functional approach to behaviour recognises the effects of behaviour "on the behaver and on the social and physical environment" (Zeiler, 1992, p.418). However, biologists or behavioural ecologists too have neglected aspects of behaviour. They have concentrated on the evolutionary significance or function of behaviour but largely ignored the immediate function of behaviour (Zeiler, 1992).

The physical science approach to the study of behaviour may focus exclusively on present and past environmental conditions that accompany or apparently elicit a particular pattern of behaviour. Yet, as Zeiler (1999b) emphasizes, to truly understand behaviour as a biological activity within an evolutionary framework, the animals themselves and what they "bring with them in their dealings with the environment" must be considered (p.289). He stresses that:

> "The importance of the animal is highlighted in the theory of evolution by natural selection, where animals inherit processes that have enabled their species to adapt to the environment. A biological approach to behavior treats the environment as the poser of adaptive problems that the animal solves with its internal resources. Environments occasion behavior; they do not produce it by themselves" (Zeiler, 1999b, p.289).

Whilst some psychologists may have confused function with goal-directedness or causation with function, some behavioural biologists have also confused short-term effects with evolutionary effects. Zeiler (1992) stresses that the ***immediate function*** of behaviour concerns the ***current*** accomplishments or consequences of behaviour that may increase an individual's chance of reproductive success or inclusive fitness. ***Evolutionary function***, on the other hand, concerns ***future*** effects or fitness enhancement that "involves a genetic effect on numerous later generations" (Zeiler, 1992, p.419).

4.15.1 THE ECOLOGICAL APPROACH TO LEARNING

> "Ecology and psychology have much in common...Both have been highly quantitative descriptive sciences. Both have been ad hoc sciences. Basic conceptual principles of ecology - the food chain, the niche, the ecosystem - are inherently descriptive terms that themselves demand explanation. Principles of psychology – reinforcement, stimulus control, levels of processing – are equally descriptive and nonexplanatory. Both fields have had their theories, but both have been without first principles. Evolutionary theory provides both with an integrating conceptual framework and a relation to the rest of science" (Zeiler, 1992, p.425).

An ecological analysis of the study of learning has helped researchers understand a number of learning mechanisms (*e.g.*, autoshaping or sign-tracking) or unexpected findings (*e.g.*, animal misbehaviour or instinctive drift) that have not been adequately dealt with by traditional learning theory (Davey, 1989). The performance aspects of learning can only be understood if information concerning a species' behavioural repertoire (or specific behaviour systems), natural habitat, and importantly the environmental or ecological stimuli that release an animal's responses are known (Davey, 1989).

Davey (1989) suggests that autoshaping (or sign-tracking) occurs when:

> "a localizable conditioned stimulus acts as a signal for forthcoming food, many species of animal will eventually "learn" to approach the conditioned stimulus and direct species-specific feeding-related behaviors toward it" (pp.16-17).

This researcher maintains that early studies of autoshaping failed to take the different prey capture strategies into account when they attempted to explain the biological significance of this learning mechanism. Once the range of species studied was increased, Davey (1989) maintains that it became clear that an animal would only emit an autoshaped (learned) response if the conditioned stimulus were ecologically significant and relevant to the feeding strategy used. An extensive knowledge of life histories and feeding habitats of species in natural environments is essential. Davey (1989) points out that cats often locate their prey via auditory cues, and thus can autoshape to a localised auditory conditioned stimulus that signals food. Rats, on the other hand, do not use such auditory cues, and as a result do not autoshape to such a conditioned stimulus.

As already mentioned in Chapter 3, early studies of instrumental conditioning also failed to take ecological factors into account. Any behavioural pattern observed in the laboratory, or indeed any "temporal control seen in the laboratory reflects processes that may have influenced survival and fitness in the history of the species" (Zeiler & Powell, 1994, p.8). Thus, ecological accounts of "timing" effects observed in the laboratory, must consider which behaviourrs in natural environments demonstrate similar patterns of temporal control. However, as Zeiler and Powell (1994) point out, a particular temporal pattern may reflect very different "temporal control" processes (*e.g.*, avoiding predators, coordinating movements with prey, or regular feeding of offspring).

Zeiler and Powell (1994) suggest that a "starting point in understanding the post-reinforcement pause is to determine what waiting to respond accomplishes for hungry animals" (p.8). However, common timing principles may not underlie the various consequences of operant responding observed in the laboratory (*e.g.*, lack of responding when food is unavailable, gradual increases/decreases in response rate, or withholding responses on DRL schedules), since each consequence may implicate a different "evolved system" (Zeiler & Powell, 1994, p.8). Zeiler and Powell (1994) conclude that the "development of rigorous experimental techniques for analyzing the effects of a particular kind of behavior may be critical to understanding the mechanisms that control it from moment to moment" (p.8).

Zeiler (1999b) warns that an ecological approach to understanding temporal patterns and operant behaviour is likely to cast doubt upon the notion of an "internal clock", since "(c)oncern with time is distinctly human, and the necessary internal devices for meeting such demands are either non-existent or are grossly inadequate" (p.291). Unlike human societies, which often require accurate timekeeping in order to function properly, animals in natural environments do not depend on clocks to function and survive. Instead "other stimuli are available to indicate when to eat, when to sleep, when to wake up, when to mate, when to avoid predators, or when to tend to offspring" (Zeiler, 1999b, p.290). Zeiler (1999b) suggests that the sensitivity to time that is reflected in experimental situations can be attributed to the flexible and powerful "general processes of memory" (p.291).

4.15.2 THE IMMEDIATE FUNCTION OF BEHAVIOUR: OPTIMALITY THEORY AND BEHAVIOUR-SYSTEMS THEORY

Recently, two main theoretical approaches based on the immediate function of behaviour have emerged, namely ***optimality theory*** and Timberlake's (1983) ***behaviour-systems approach*** (Zeiler, 1992).

Zeiler (1992) discusses a number of problems that plague ***optimality theories***, including discrepancies between optimality predictions and observed behaviour. As its name suggests, an ***optimality theory*** (such as optimal foraging theory) predicts that an organism will behave in the best possible way to ensure ***optimal*** or ideal performance or achievement. Theories of operant behaviour also often predict, that: "behavior maximizes benefits" (Zeiler, 1992, p.420). However, as Zeiler (1992) points out, natural selection actually "works on what it has, not on ideals" (p.420). That is, natural selection does not need to maximise returns or ***optimise***, instead it should ***satisfice*** or "do well enough to get by" (Zeiler, 1992, p.420). Zeiler (1992) suggests that ***satisficing models*** do exist, but are faced with the challenge of having to quantify "doing well enough" (p.420). This researcher states that the tests employed by behavioural biologists involve ***immediate*** function, but the concept of optimality is used to "relate behavior to evolutionary function" (p.420). Not surprisingly, behavioural evolution is difficult (or even impossible) to test.

Importantly, Zeiler (1992) stresses that behaviour is generated by antecedent causal conditions (causation) and <u>not</u> by outcomes (function). Therefore, behaviour may in fact "not perfectly implement function" (Zeiler, 1992, p.421). An organism's <u>current</u> behaviour pattern is determined by causal mechanisms (evolved over evolutionary time), which only need to work "well enough on average to be selected", and not accomplish a function perfectly or optimally (Zeiler, 1992, p.421). Thus "(a)s long as natural selection can only use what it is given, optimization is likely to be rare" (Zeiler, 1992, p.421).

Zeiler (1987) suggests that a distinction exists between optimality in "particular immediate local conditions" and "in the long term" (p.38). That is, an animal may appear to behave in a non-optimal way during an experiment, but the behavioural pattern observed may be advantageous "in the larger context of adaptation to changing environments" (Zeiler, 1987, p.38). In fact, as Zeiler (1987) points out, for an animal to remain flexible enough to alter its behaviour as new contingencies arise, it should not be "locked in" to any particular "preference rule", even if this results in departures from a predictable and optimal performance (p.38).

Timberlake's (1983) ***behaviour-systems approach*** provides a way of viewing behaviour in terms of immediate function (Zeiler, 1992). Feeding, reproduction, defense and body care are just some of the functional systems of behaviour that "any animal brings to an environment" (Timberlake, 1990, p.34). Figure 4.9 provides a schematic representation of a behaviour system (feeding in the rat), which is a sequential-hierarchical model comprised of four levels of control, namely: system, subsystem, mode and perceptual-motor module (Timberlake, 1990). Every part of each behaviour system is "integrated, linked and differentiated by its fit with the environment. Thus, learning can be remarkably varied and complex, and can include changes in integration, differentiation, tuning, instigation, elicitation, and linkage within and across entities and levels in a system" (Timberlake, 1990, p.36).

Timberlake (1990) stresses that the ***behaviour systems approach*** to learning recognizes that all learning (whether in the laboratory or natural environment) is a "product of the combination of appetitive structure and environment. Pavlovian and operant conditioning, like song learning, occur because of the contact of the environmental circumstances with the appetitive structure of the organism" (p.36). Silva and Timberlake (1999) emphasise that the "behaviour systems approach incorporates information based on the animal's ecology" (p.185). This approach has been used to interpret "appetitive strings of behavior", and has combined naturalistic ethological observations with experimental findings. Essentially, the approach incorporates species-typical foraging patterns.

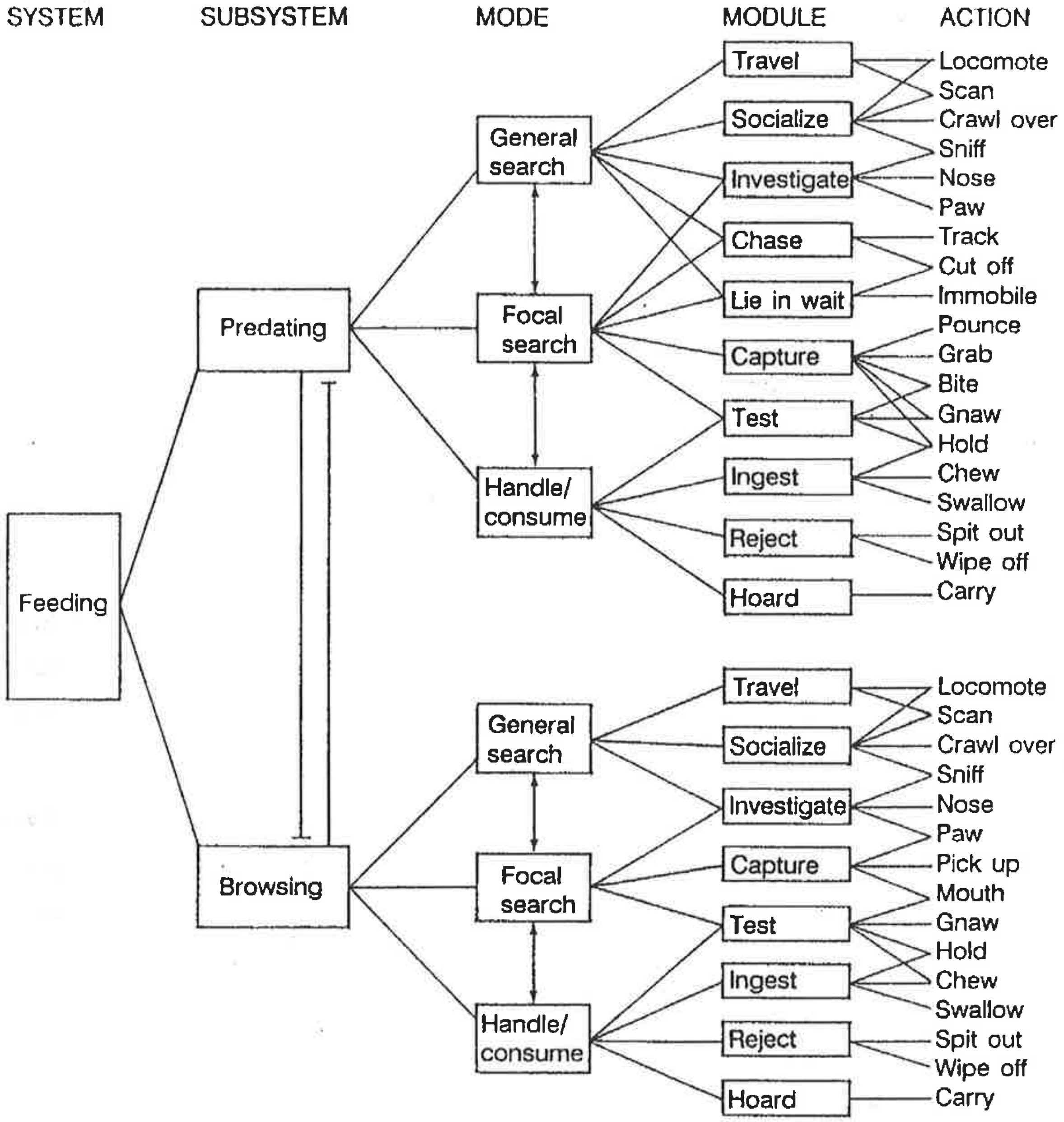


Figure 4.9. Timberlake's (1990) schematic representation of the feeding system of the rat (Figure 1 in Timberlake, 1990, p.35)

If an animal is searching for food, Silva and Timberlake (1999) suggest that a sequence of search modes is followed. Each of these search modes "in conjunction with external stimuli, controls a particular repertoire of preorganized food-related responses" (Silva & Timberlake, 1999, p.184). These search modes have been observed in laboratory studies of rats. If rats are periodically presented with food, then their behaviour shows predictable changes during the interfood interval IFI). Immediately after food, rats typically search near the feeder, which represents the ***postfood focal search*** mode. This search mode is followed by the ***general search*** mode, which usually occurs during the middle of the IFI, and is characterized by the rat moving around the experimental apparatus. As the next food delivery approaches, the rat typically returns to the food site (& begins "nosing in the feeder"), which represents the ***focal search*** mode. Upon delivery of food, during the ***handling/consuming*** mode, the rat chews and ingests the food (Silva & Timberlake, 1999).

Lucas, Timberlake and Gawley (1988) investigated the behaviour of four rats in a 24-hour baseline environment. During this phase of the experiment, the rats had free access to water, food, and a running wheel. During the experimental sessions, the rats were provided with food at minimum intervals of 16, 32, 64, 128, 256 and 512 seconds. The rats were exposed to each interfood interval for a minimum of 12 days. Lucas et al (1988) found that the rats anticipated the delivery of food. That is, prior to food, they displayed ***focal search*** behaviours (nosing & pawing in/around the food tray). After food delivery the rats engaged in ***area-restricted search*** (near & in the food tray). Rearing, drinking, locomotor activity, chewing, wheel running, and returning to the nest all took place after ***area-restricted search***. Timberlake (1990) states that both "rearing and drinking (the most consistent adjunctive behaviors) appear to be transition behaviors occurring between post-food focal search and more general search or withdrawal" (p.43). By comparing the baseline behaviour after each meal with the behaviour after each food pellet, Lucas et al (1988) found that they were strikingly similar for the moderate and long inter-pellet intervals. "In other words, with respect to the pattern of drinking following food, it appears that rats treat each pellet as though it were the end of a meal" (Timberlake, 1990, p.44).

More recently, Williams and Fantino (1996) have investigated the effect of response-dependent ***prechoice*** on foraging-related choice. Typically, the rate-maximising version of ***Optimal Foraging Theory*** (with its roots in Behavioural Ecology) has been associated with a more ***molar*** view of "a forager's choice for one prey item over another" (although response-dependent prechoice factors have not been tested as such), whereas early "operant analogues of foraging" have taken a more ***local-contextual*** approach (Williams & Fantino, 1996, pp.638 & 639). That is, operant approaches to foraging have tended to focus on a foraging cycle that is comprised of three main phases: searching, handling and consumption of prey. In reality, there is a prechoice period, which falls between consumption of a prey item and the search for the next prey item. In a series of three experiments using different modifications of the concurrent-chains procedure, Williams and Fantino (1996) investigated the effect of presence or absence of a Fixed-Interval 200-s prechoice period on the choice behaviour of pigeons. Interestingly, these researchers found that "prechoice delays may not influence choice" (p.639). They conclude that the "local-contextual view of rate maximization…appears to be adequate", although "as we systematically reintroduce increasingly complex aspects of the forager's world into our operant simulations, we may begin to identify increasingly molar contingencies that may influence the decision-making strategies used by the optimal forager" (Williams & Fantino, 1996, p.639).

> "Operant analogues of foraging provide tests of the generality and external validity of behavior-analytic principles of choice while simultaneously testing predictions based on behavioral ecology's theories of optimal foraging" (Williams & Fantino, 1994, p.465).

The more holistic ecological approach to the study of behaviour, particularly the optimal or non-optimal choices that animals make in laboratory or natural environments, is not only applicable to an interdisciplinary partnership between psychology and the biological sciences. Indeed, Fantino (1998) has expanded his more holistic approach to the investigation of human choice (optimal & nonoptimal) and decision-making. That is, a partnership between the behavior-analytic approach and traditional cognitive psychology (human information processing), or a "behavioral cognitive revolution" might provide a more general and powerful approach to the study of human (& animal) behaviour (Fantino, 1998, p.362).

4.15.3 CLOSED AND OPEN FEEDING ECONOMIES

Recent ecological approaches to the study of behaviour during intermittent schedules of reinforcement have taken the feeding or deprivation level of the animal into account (Fantino & Abarca, 1985; La Fiette & Fantino, 1988; Zeiler, 1991; 1999a). That is, schedule effects may in part be dependent upon whether the experimental arrangements conform to a ***closed*** or ***open economy***. Zeiler (1999a) points out that researchers have differed slightly in their interpretation of what the distinction between the two economies is (the presence/absence of supplemental feeding is one commonly used distinction). An ***open economy*** might maintain an animal at 80% of its free-feeding weight. That is, it would be food-deprived, but provided with supplemental feeds if necessary (after the experimental sessions). A ***closed economy*** would use animals that were not food-deprived, and would obtain all their food during the experimental sessions (Zeiler, 1999a). Most of the traditional theories of behaviour provide explanations for behaviour in an ***open economy***, or "textbook-characteristic schedule effects" (Zeiler, 1999a, p.180). However, Zeiler (1999a) has shown that ***closed economy*** schedule effects are also orderly and replicable, although they may be "reversed".

> "The pressing need for food and the consequences of failure to get it quickly dominate behavior in the open economy. In the closed economy, the activity may not be totally determined by feeding but may be influenced by the inability to meet other needs while working in the experiment" (Zeiler, 1991, p.24).

A ***closed economy*** may most resemble a natural environment that provides ample food, whereas an ***open economy*** resembles an environment with little available food. This highlights the fact that traditional operant experiments have failed to model a realistic natural environment, since an animal that is chronically food-deprived and operates at a less than optimal body-weight might not survive in the "wild". That is, food-deprived animals are unable to conserve or maintain their weight at their free-feeding level. If animals are not food-deprived during experimental sessions (*i.e.*, a ***closed economy***), they have been found to "adjust their food intake to the frequency of encountering a food source" (Zeiler, 1999a, p.184), and consequently maintain or conserve their body weight. As Zeiler (1999a) points out, in the natural environment, an animal would be unlikely to survive a lengthy drought if it did not migrate out of its home range and seek alternative sources of food, or find a way to conserve energy (reduce metabolic demands). Zeiler (1999a) concludes that: "any general theory of operant behavior must deal with how feeding economies influence behavior. The disparate effects of the two economies suggest different systems involving unique processes" (p.185).

Hunters can obtain food by using two very different strategies, namely, by actively searching or waiting for prey (Zeiler, 1993). In the laboratory situation, Zeiler (1993) suggests that the choice between these strategies depends on the "ecological-motivational factors", although a "bias for active search over waiting" has tended to be observed in adult pigeons (p.433). Two factors that are likely to affect foraging patterns are the animal's level of food-deprivation and the availability of food (Zeiler, 1993).

Zeiler (1993) maintains that food availability is low and restricted in the ***open economy***, and consequently natural selection may favour animals, which actively search for food, since they should be more likely to find food and survive. On the other hand, when food is readily available in the ***closed economy***, animals are less likely to search for food, since there is "no pressing survival need to find a more fruitful feeding patch" (Zeiler, 1991, p.18). Interestingly, Zeiler (1993) found that neither hunting/feeding strategy (active searching or waiting) was preferred (both used interchangeably), if pigeons were not food-deprived and "able to eat freely at each feeding opportunity" (p.443). Indeed, under these conditions, the pigeons demonstrated an optimal performance. Importantly, Zeiler (1993) reminds researchers, that:

> "food deprivation and limited food availability may cause animals to leave their present environment. In nature they would leave. In the laboratory they cannot"

Thus, researchers must always consider what a free-ranging animal might do in any given situation (in order to survive), but also remember that many experimental situations do not allow the animal to leave a depleted patch, which creates a scenario, which "does not correspond with what evolved for nonlaboratory settings" (Zeiler, 1991, p.18). Furthermore, researchers must view behavioural patterns as adaptive (facilitate survive) and not as mere effects that have been evoked by "either a fixed internal process or an inflexible environment" (Zeiler, 1991, p.18), although internal processes and the environment clearly influence essential behaviours, such as foraging. La Fiette and Fantino (1988) point out that many studies which attempt to contrast the effects of ***closed*** and ***open economies***, merely compare their own results from a ***closed economy*** situation "against the literature on open economy findings" (p.467). La Fiette and Fantino (1988), on the other hand, investigated the multiple-schedule performance of pigeons in ***open*** and ***closed economies*** within the same experiment. This allowed them confidently to conclude, that: "the results were differentially affected by economic context" (p.467).

4.16 A COMPARATIVE AND INTEGRATIVE APPROACH TO THE STUDY OF EXPLORATORY BEHAVIOUR ACROSS ENVIRONMENTS

Forster (1995a) found that both prior and concurrent learning increased object-directed exploration in laboratory rats tested in an open field. She found relationships between learning and exploration, and novelty and exploration. In her first experiment, 36 rats were divided into three groups: bar, no-bar and control. The bar and no-bar groups (food-deprived) were trained to bar press for food. Following this, all rats were placed on extinction, and their exploratory behaviour was observed over three 15-minute sessions. The no-bar and control groups did not have a food-trough or manipulandum present during these sessions. For all groups there was a reduction in exploratory behaviour over sessions (habituation effect), but the amount of exploration in the bar group was much higher in every session. Forster (1995a) suggests that exploratory behaviour increases when a learned response undergoes extinction (but the bar must be present in the box).

In a second experiment, Forster (1995a) found that if objects were present during four 15-minute conditioning sessions (continuous reinforcement), then food-deprived rats trained to bar press explored objects more than those in the control groups (no bar present), irrespective of whether the objects were novel (new set of three objects for every session) or familiar (same set of three objects for every session). During the subsequent four 15-minute extinction sessions, a sharp increase in object-directed behaviours occurred if objects were familiar, in the group conditioned to bar press (*i.e.*, the previous reliable food source was now exhausted). Over extinction sessions, the effects of novelty became more noticeable. Those rats exposed to novel objects in every session engaged in far more exploration. That is, novelty sustained the rats' interest in objects.

Forster (1995a) likens the conditioning phase to "a situation in which an animal is behaving successfully in its environment, in the sense that it has found an adequate food supply" (p.150). Since the rat was continually reinforced for bar pressing, the novelty or familiarity of the objects in its immediate environment were not "relevant". By contrast, novelty plays an important role in an environment, in which the food supply is exhausted (*i.e.*, extinction). In this situation, an animal would be expected to explore novel objects rather than familiar ones, in order to increase its chances of finding food.

Interestingly, if rats were tested in an experimental chamber in which food was signaled by the appearance of a moving ball bearing (based on a study by Timberlake, Wahl & King, 1982), and objects were available for exploration, novelty alone was equally or more effective in enhancing exploration than the simple learning procedure (Forster, 1992). However, it should be noted, that the experimental group did engage in more object-directed exploratory behaviour, but not in more general activity (in the form of ball bearing contacts). In a further study, a new set of objects (two with movable parts, two without movable parts) was used for each session. Forster (1992) found that rats directed most attention towards the most movable and noisy object, namely swinging chains suspended from a bar. With continued novelty, there were no declines in exploratory behaviour over sessions, during conditioning or extinction (with an increase during the first extinction session).

In laboratory studies with common marmosets, Forster (1995b) again discovered that "novel objects remained a constant interest throughout the experiment", whereas "activities associated with learning tended to decline over time" (p.501). She found that exploratory behaviour (directed towards the objects) was particularly high when testing was carried out in the home cage (surrounded by other marmosets- all singly housed), rather than in an isolated experimental cage. The learning tasks used involved training the marmosets to jump onto a small lever, which triggered a banana feeder (in the home cage experiment), or jumping onto a wire grid to obtain a yoghurt reward, which triggered the opening of a door (to view a marmoset in a neighbouring cage, in the isolated experimental cage experiment). Forster (1995b) suggests that learning increased general activity (walking, running, jumping, climbing around the cage & chewing the perch), but not necessarily object-directed behaviour. She points out that the term "investigation" may be more appropriate for novel object exploration, whereas "exploration" may refer to undirected general activities.

Forster (1995a; 1995b) emphasizes that these findings can be applied to the enrichment of laboratory and zoo environments. That is, exploratory behaviour can be "produced by either the implementation of learning programs, or by the maintenance of novelty in an animal's surroundings (especially when food is not available)" (Forster, 1995a, p.150). She suggests that researchers should combine the use of "work therapy" (e.g., Markowitz) and use of novel objects (e.g., Paquette & Prescott, 1988) to enhance captive environments. This would not only increase the animals' well being, but it would also increase opportunities for etho-experimental approaches to the study of behaviour.

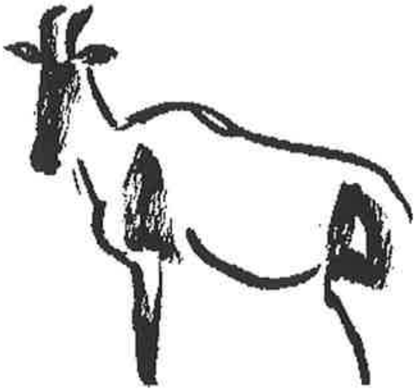
Series of experiments such as these, allow researchers to investigate the effects of novelty and learning across environments. Although Forster (1992) only observed marmosets and rats in laboratory environments (open-field & home cage), she laid the groundwork for extension into zoo environments. That is, researchers could clearly examine these effects in a zoo enclosure.

4.17 CHAPTER SUMMARY

This chapter examined the advantages and disadvantages of studying behaviour in captive or "wild' environments, before moving on to an analysis of ethological and psychological approaches to the study of behaviour. Not surprisingly, researchers today are opting for a more integrative approach to the study of learning and behaviour. Timberlake's (1983; 1990) ***behaviour systems approach*** provides a way of viewing behaviour in terms of immediate function (Zeiler, 1992), whilst combining naturalistic ethological observations with experimental findings. Importantly, all researchers must consider the ecological implications of their findings (Fantino & Abarca, 1985). Finally, it is suggested that a comparative and integrative approach to the study of exploratory behaviour across environments is both possible and desirable.

CHAPTER 5

PRACTICAL APPLICATIONS OF LABORATORY BASED RESEARCH ON EXPLORATORY BEHAVIOUR



5.1 BEHAVIOURAL ENRICHMENT IN ZOOS

Environmental-, habitat-, or behavioural-enrichment, are terms that have been used in connection with "the lives of both domesticated and zoo animals" (Robinson, 1998, p.156). Most zoos aim to simultaneously promote "natural" behaviours (educational & interesting), and eliminate "unnatural" or aberrant behaviours. This chapter investigates a number of issues related to captivity and psychological well-being (& normal *vs* abnormal behaviour).

Researchers may assume that behavioural enrichment for captive animals involves providing an enclosure, which replicates the natural environment. However, as Brain (1980) points out, there "is no such thing as the optimal or "typical" environment for any species" (p.25). That is, the populations that have been studied in the wild may not be representative of the species, studies may not have been conducted over a long enough period of time, or may only reflect "a limited range of the capacity of the species" (Brain, 1989, p.25). For example, Jane Goodall has now been studying the chimpanzees of Gombe Stream National Park for 40 years, but these chimpanzees do not always behave in the same way as chimpanzees at other sites. Findings from many other field studies have shown great variability in many aspects of chimpanzee behaviour (McGrew, 1992).

Robinson (1998) states that it is:

> "still the essence of ethology to discover, and then define, the world in which species live; it is the role of us responsible for the care of animals in zoos to

> provide the animals with their world, or as much of it as possible, given the tensions between public perception and reality. For this we need to strengthen ethological studies so that we can identify the components of habitat that animals attend to…studies of the reactions between species and their physical environment are in a minority compared to studies of intraspecific or social behaviour" (p.155).

5.2 CAPTIVITY AND PSYCHOLOGICAL WELL-BEING

Beck and Castro (1994) assert that "the wild": "is far more stressful, and captivity (under good but not extravagant conditions) is far less stressful, than the more radical animal welfarists would have us believe" (p.269). In natural environments food is often sparsely distributed (in time & space), predators stalk, climatic conditions may be wet and cold, insects and parasites may "feed" on the animal, and neighbouring conspecifics and unseen territorial boundaries create "a slightly different type of psychological cage" (Beck & Castro, 1994, p.268). Captive animals may be larger, heavier, have shorter inter-birth intervals, and have a greater life expectancy. If captive animals are appropriately housed, with respect to their social groupings (whether in a social group, monogamous pair, or singly), then other problems such as hyper-aggression or self-mutilation can be alleviated.

Captivity is certainly a "safer" environment for golden lion tamarins. Only 32 (& 22 wild-born offspring) of the original 79 tamarins reintroduced into the "wild" in Brazil (since 1984) remain (Beck & Castro, 1994). The deaths or disappearances of these individuals have been attributed to various factors, including: "(V)iral disease, exposure, intraspecific conflict, toxic fruits, predators, and theft by humans" (Beck & Castro, 1994, p.269). These researchers suggest that if the reverse had been done, that is, 79 tamarins brought from the "wild" into captivity, then far more would still be alive. Beck and Castro (1994) conclude that captivity and good management reduces stress, enhances tamarin wellbeing, and that health and reproduction are not necessarily promoted in naturalistic environments. In fact, if captive primates are to be successfully reintroduced into the "wild", then their captive environments should be more naturalistic, by providing "more stress and less well being" (Beck & Castro, 1994, p.270).

Markowitz (1997) points out that "zoos are simultaneously condemned for failing to provide natural habitats and are expected to treat each animal as if it were a pet" (p.2). Indeed, captive environments may be selecting for "docility and tameness" (Figure 5.1) rather than the "wariness" of wild individuals (Markowitz, 1997, p.2). Predators are unable to hunt live prey, and selection pressures and dangers that ensure the survival of only hardy individuals are absent.

Figure 5.1. Despite signs stating that animals must not be fed or touched, humans the world over seem to feel the need to interact closely with primates (top- golden lion tamarin at Adelaide Zoo, centre- monkeys in China and at Mugga Lane Zoo in Canberra, bottom- lowland gorilla at London Zoo)

Figure 5.2. A composite photo of a tiger pacing (in a figure 8 pattern) in front of the viewing window at Taronga Zoo

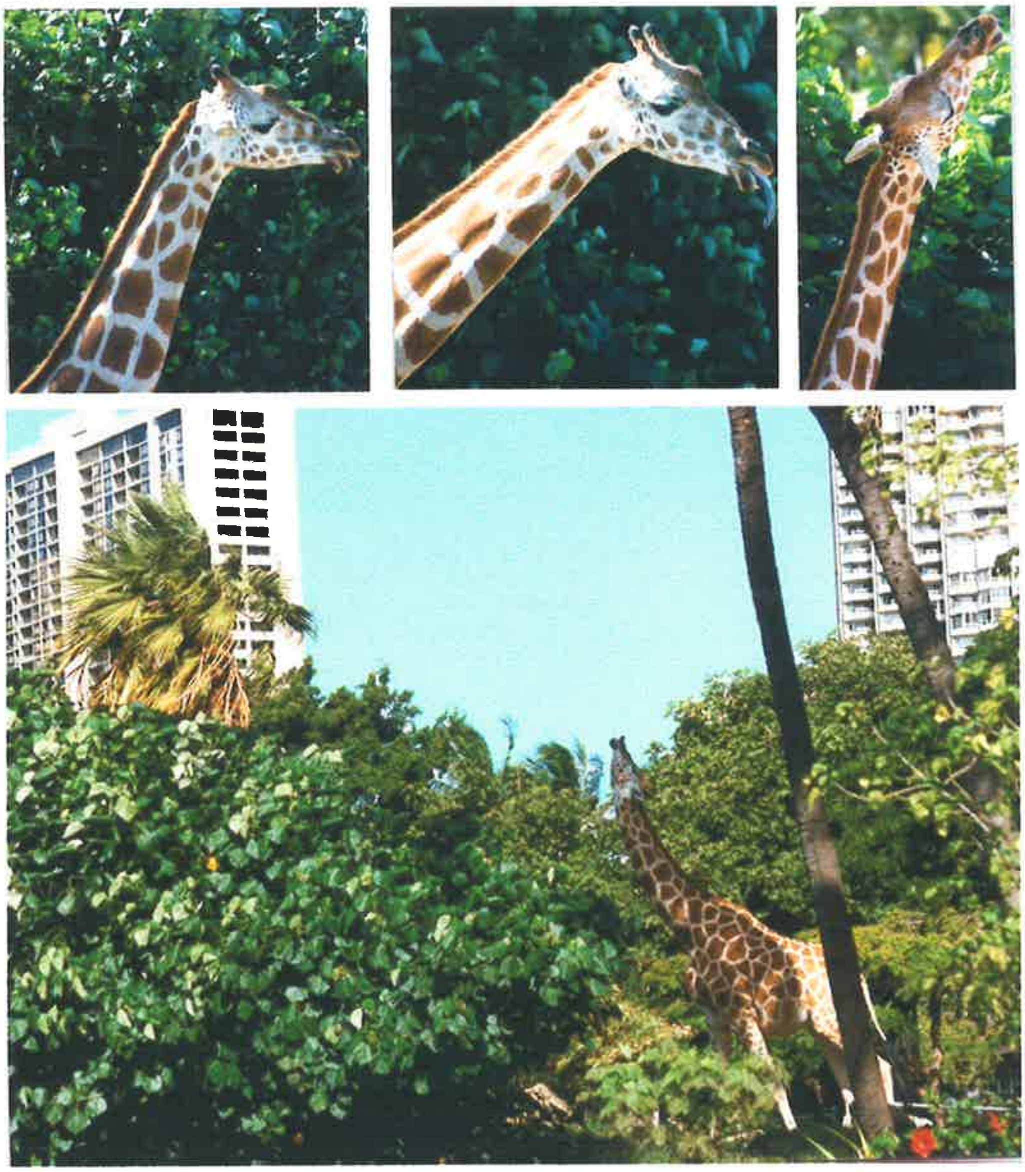


Figure 5.3. Giraffe pacing and head-tossing at Honolulu Zoo (December 1991)

The "species-typicality" of an animal's behaviour is an indicator of an animal's well-being or "quality of life". However, truly to conserve species-typical behaviours in captivity, methods would have to be used that conflict with "vocal protectors of animal welfare" (Markowitz, 1997, p.2).

To conserve species-typical behaviour and morphology, Markowitz (1997) asserts that special reserves, which select for hardy individuals (suitable for reintroduction & conservation programmes) are needed, that provide the full range of contingencies encountered in the "wild". Concurrently, zoos should help visitors come to the understanding that truly natural habitats cannot be produced within the typical zoo environment. However, enrichment programmes should be established to encourage species-typical behaviour, thus increasing appreciation of a species and educating visitors. Markowitz (1997) laments that landscaping budgets (for "natural-appearing facades") continue to exceed behavioural enrichment budgets.

Markowitz (1997) emphasizes that even:

> "if the foraging animal is "hunting" for treats that keepers have stuffed in holes drilled in trees, even if the "prey" that an animal "captures" is mechanical or acoustical rather than live, and even if the "termite mound" exploration with twigs is rewarded with fruit salad rather than termites, surely seeing animals at work in ways that are apparently attractive and rewarding to them is critically important to the animals and to the visitor experience" (p.2).

In zoos, animals have their physical needs met. They have time to relax and play, meals are always on time, enclosures are always clean, there is shelter from the rain and cold, and vets take care of illnesses. However, predictability of the daily routine, the all too familiar surroundings, and access to food that is readily available and quickly consumed, can lead to animals that are bored, or unstimulated.

In the "wild", many animals may spend up to or even over half their day foraging for food, *e.g.*, chimpanzees, ungulates, and bush-babies (Tudge, 1991). They have to "work" for their food, and use a variety of skills to obtain it. Searching for food and shelter, as well as being on the look out for possible predators, requires every one of a wild animal's five senses. Survival in the wild involves an animal's brain constantly processing a barrage of sensory information (visual, auditory, tactile & olfactory) coming in from its surroundings. Life in the wild is not simple. As Jane Goodall puts it, wild chimpanzees:

> "use – and need – all their mental skills during normal day-to-day life in their complex society. They are always having to make choices – where to go, or with whom to travel…Indeed, the study of chimpanzees in the wild suggests that their

> intellectual abilities evolved, over the millennia, to help them cope with daily life" (1990, p.19).

Wild or free-ranging carnivores exert a great deal of time and effort in hunting and foraging for food. As Ings, Waran and Young (1997) point out, feeding carnivores provides one of the greatest "animal welfare challenges" to zoos (p.343). On the one hand, feeding live vertebrate prey to carnivores raises ethical issues (& is illegal in many countries). On the other hand, the lack of opportunity to hunt may result in reduced animal welfare (*e.g.*, abnormal behaviours) for carnivores (Ings et al, 1997).

Between meals, there is ample free time for zoo animals. Therefore, special care needs to be taken to ensure that they have enough interesting and stimulating things to do. In other words, the animal's psychological well being, as well as its physical well being, must be considered (Tudge, 1991). Like their wild counterparts, zoo animals require mental and physical challenges to keep their brains and bodies healthy. Perhaps the biggest challenges facing the great apes in particular are physical survival for those in the wild and mental survival or staying "sane" in captivity. The notion of keeping captive primates healthy psychologically (or "contented"), as well as physically is not new. As early as 1925, Robert Yerkes states:

> "It would be difficult to exaggerate the importance of knowledge, on the part of those who desire or need to have captive primates, of suitable ways of keeping them healthy and contented and of breeding them in captivity" (p.203).

Konrad Lorenz already referred to the term "psychological well-being" in his popular 1952 book, *King Solomon's Ring*. When discussing anthropoid apes, Lorenz suggests:

> "they are the only captive animals which can derive serious bodily harm from their mental suffering. Anthropoid apes can become literally bored to death, particularly when they are kept alone in too small cages" (p.73).

Recognising the importance of psychological, as well as physical well being, Lorenz (1952) goes on to issue a harsh condemnation of zoos that did not take both factors into account. He states:

> "to keep anthropoid apes in solitary confinement and in such small cages as are still to be found in many zoos is an act of cruelty which should be punishable by law" (1952, p.73-74).

Shepherdson (1989a) points out that psychological well-being is essentially a welfare issue concerned with the "happiness" or "contentedness" of captive animals. Of course, this is impossible to determine, but we can compare the behaviour of a species in zoos, with the behaviour of the same species in the wild. If the behaviour in the zoo is very different from that observed in the wild, in either the type of activity, or the amount of activity, then something needs to be done to reduce, or eliminate, such aberrant behaviours. Using species-typical behaviour in the wild as a model for comparison is not the only way of assessing the psychological well being of zoo chimpanzees. Symptoms of poor psychological health may include poor physical health, distress (detected by both behavioural & physiological measures), and poor coping skills (Bloomsmith, 1991).

5.3 STEREOTYPY AND ABERRANT BEHAVIOURS

Erwin and Deni (1979) provide an extensive list and discussion of "abnormal" behaviours or "behavioural pathologies" that may be observed in captive primates. They divide these "abnormal" behaviours into two broad categories: qualitative and quantitative (p.6). The former set encompasses behaviours that are only observed in captivity, whilst the latter category includes behaviours that occur more or less in captivity than they would in natural environments. Although Erwin and Deni (1979) restrict their discussion and examples to primates, many of the "abnormal" behaviours can be observed in a variety of animal species, housed in a variety of captive environments. However, merely constructing a list, or fitting observed behaviours into these categories is too simplistic. It would not address the underlying problem of how to assess the extent or nature of "abnormal" behaviour. How does one define what is "abnormal" or indeed "normal" for any given species? (The term "aberrant" is preferred for the purposes of this discussion, since the behaviours may in fact serve an adaptive function, & the term "abnormal" may be construed as having negative overtones).

Stereotypic behaviours include: "pacing, head flicking, weaving, bar gnawing, crib biting, wind sucking, spot pecking and many other normal behaviours which are performed for an excessive length of time or in inappropriate contexts" (Shepherdson, 1989b, p.100). As Shepherdson (1989b) points out, stereotypic behaviours may be very visible or even prominent in zoo enclosures, leading to visitor perceptions of animals that are "bored" or even "mad" (Figures 5.2 & 5.3). Thus: "stereotypic behaviour presents a problem for zoos" (Shepherdson, 1989b, p.100).

The form of a particular stereotypic behaviour may be defined fairly easily. However, a clear and exhaustive general definition of stereotypic behaviour is not so readily available. Stevenson (1983) presents a definition by another researcher, but then alludes to its possible inadequacy by stating that: "Odberg (1978) goes to some lengths to try and decide what is meant by the term" (p.184). Similarly, Shepherdson (1989) refers the reader to a definition by Dantzer and Mormede (1983) as being "fairly representative", but then criticises the definition by suggesting that it: "leaves a lot to be desired" (p.100).

Table 5.1
Erwin and Deni's (1979) information about qualitative and quantitative "abnormal" behaviours in captive non-human primates, presented here in tabulated format (pp.6-14). Additional "abnormal" behaviours from a number of sources are provided in the right-hand column.

QUALITATIVE "ABNORMAL" BEHAVIOURS (occur only in captivity)	**QUANTITATIVE "ABNORMAL" BEHAVIOURS (occur more or less in captivity than in natural environments)**	**ADDITIONAL "ABNORMAL" BEHAVIOURS**
(1) bizarre postures ♦ floating limb ♦ self-biting ♦ self-clasping and self-grasping ♦ saluting / eye-poking	(1) activity patterns ♦ apathy or depression ♦ inactivity or hyperactivity ♦ temporal distortion	(1) O'Neill (1989) ♦ self-orality ♦ lack of play ♦ lack of exploration or responses to complex stimuli
(2) stereotyped motor acts ♦ stereotyped pacing ♦ bouncing in place ♦ somersaulting ♦ rocking ♦ head-tossing or weaving	(2) appetitive disorders ♦ hyperphagia ♦ hypophagia ♦ polydipsia ♦ refusal to eat or drink	(2) Bloomsmith (1989) ♦ Repeated regurgitation ♦ Over-grooming ♦ Self-mutilation ♦ Head-banging
(3) appetitive disorders ♦ coprophagia ♦ paint eating and pica	(3) agonistic disorders ♦ hyperaggressivity	(3) Fouts, Abshire, Bodamer, & Fouts (1989) ♦ Inappropriate or lack of maternal behaviour in females ♦ Unresponsive or inappropriate responses to social stimulation
(4) sexual disorders ♦ inappropriate orientation ♦ homosexual behaviour ♦ sexual dysfunction ♦ autoerotic stimulation		

Tudge (1991) stresses that a distinction must be made between stereotypic behaviours that may represent a possible form of exercise (*e.g.*, pacing), and those that may be considered: "truly neurotic and self-destructive" (p.216). Regular feeding schedules may elicit pacing prior to arrival of food, and such behaviour: "can be reasonably construed as nothing worse than anticipation" (Tudge, 1991, p.216). Lawrence and Rushen (1993) emphasise that stereotypic behaviours are not only observed in zoos, but in any captive or "confined" setting including laboratories, farms (Figure 5.4), and backyards (with pets or companion animals).

As well as being able to recognize what stereotypic behaviour is, it is important for researchers to be able to determine how severe a particular stereotypy is. Stereotypic behaviour can be indicative of a welfare problem. For improved captive management, the ability to assess the degree of stereotypy is obviously essential (Shepherdson, 1989b). Shepherdson (1989b) provides a set of five guidelines for zoo workers and researchers to use as a means of determining the severity of stereotypy in the zoo situation (pp.102-103). These guidelines are provided in Table 5.2.

Table 5.2
Shepherdson's (1989b) set of five guidelines for the assessment of degree and severity of stereotypic behaviours exhibited in zoo environments, presented here in tabulated format (pp.102-103).

MORE SEVERE PROBLEM	**LESS SEVERE PROBLEM**
(1) behaviour is more "abnormal" ♦ *e.g.*, head twisting	(1) behaviour itself is not "abnormal" ♦ *e.g.*, pacing
(2) a high proportion of the animal's day is spent engaged in stereotypic behaviour(s) ♦ *e.g.*, >10% of waking day is spent engaged in stereotypic behaviour(s)	(2) a low proportion of the animal's day is spent engaged in stereotypic behaviour(s) ♦ *e.g.*, <10% of waking day is spent engaged in stereotypic behaviour(s)
(3) animal is not easily distracted from the behaviour; and the animal is less aware of its surroundings when engaged in stereotypic behaviour	(3) animal is easily distracted from the stereotypic behaviour; and the animal is more aware of its surroundings when engaged in stereotypic behaviour
(4) no reason for the behaviour is obvious ♦ *i.e.*, "spontaneous" stereotypy	(4) reason for the behaviour is obvious ♦ *i.e.*, "responsive" stereotypy ♦ *e.g.*, occurs just before feeding next to the entrance of the enclosure
(5) stereotypic behaviour occurs at the expense of other normal behaviour; and/or there is reduced behavioural diversity	(5) can still observe normal behaviour and behavioural diversity still exists

It is unclear what function stereotypic behaviour may serve. Chamove (1989) points out that when an animal engages in stereotypic behaviour, it may be alleviating stress by lowering adreno-cortical levels. That is: "animals use abnormal behaviour to improve their condition" (Chamove, 1989, p.167). However, even if stereotypic behaviour is an adaptation to captive environments, Chamove (1989) stresses that it would be fallacious to conclude that such behaviour is "somehow beneficial and therefore good" (p.167).

Figure 5.4. Stereotypic behaviours can be observed in any captive setting (top- wind sucking in a stallion at an Adelaide horse property, and bottom- excessive tongue manipulation or paint-licking in a giraffe at Cheyenne Mountain Zoo in Colorado in December 1991)

5.3.1 BEHAVIOURAL MEASURES AS INDICATORS OF WELFARE PROBLEMS

In order to assess the welfare (or state) of an animal, a range of measures should be used. Broom & Johnson (1993) suggest that in practice: "measurements of poor welfare are more common than those of good welfare, since poor welfare is associated with more obvious behavioural, physiological and pathological signs" (p.87). These researchers maintain that behavioural responses are often the most obvious indicators of an animal's difficulty in coping with a particular situation or problem. Some behavioural measures of good welfare include animals displaying a wide range of "normal" behaviours (especially "preferred" behaviours) and behavioural indicators of pleasure (Broom & Johnson, 1993, p.85). However, as Broom and Johnson (1993) point out, recognising pleasure in animals is difficult, and sometimes misinterpreted. For example, tail wagging by dogs may indicate submission rather than pleasure.

Some behaviours are clearly pathological (*e.g.*, self-mutilation), but it is not always easy to distinguish between pathological behaviour and adaptive attempts to cope, particularly if an animal has been stressed for a long period of time (*i.e.*, weeks/months/years rather than minutes/hours/days). Broom and Johnson's (1993) book, *Stress and Animal Welfare*, provides a comprehensive analysis of all the indicators available at the current time, which can be used to assess problems in housing and handling animals, which in turn lead to physiological and behavioural problems or pathologies in those animals.

5.3.1.1 INDICATORS OF SHORT-TERM PROBLEMS FOR ANIMALS

A number of physiological changes may occur in animals that are subjected to short-term stress, including: levels of plasma cortisol, β-endorphin, epinephrine, heart rate (tachycardia & bradycardia), respiratory rate, core body temperature, and reproductive hormones (*e.g.*, prolactin & luteinizing hormone). However, Broom and Johnson (1993) point out that it is not always possible or advisable to measure physiological changes (especially since handling itself can be stressful), whereas many behavioural responses are easily quantified, and can be made unobtrusively (*i.e.* non-invasive observations). For example, researchers can readily determine the frequency of distress calls, or the duration of kicking at a localised pain source.

Simple behavioural measures, however, must be carefully interpreted, since individual differences may be great. For example, measures of activity levels, on their own, may not be reliable as welfare indicators, since one animal may show a passive withdrawal response when confined with an aggressive individual, whereas another animal may exhibit an active avoidance response (Broom & Johnson, 1993). Therefore, Broom and Johnson (1993) suggest that a single measure should be used as a first indicator of poor welfare, but a combination of measures should be used to fully assess the conditions. Nevertheless, behavioural responses often are the most obvious indicators of difficulties in coping with a situation or problem.

Broom and Johnson (1993) state that an animal's first reaction to environmental change is often an orienting response (directing the senses towards the stimulus), which may be followed (or preceded) by startle responses (indicating behavioural disturbance), such as sudden movements, freezing, vocalising, fleeing, or cessation of resting, feeding or grooming. The responses depend on both the species and the individual. These startle responses may be followed by either fight/defensive or flight reactions. Most researchers can readily identify flight behaviours, but Broom and Johnson (1993) maintain that defensive behaviours may be difficult to identify, since they range from growling in predators to tonic immobility in prey. An index of disturbance can be obtained by measuring the intensity, duration and frequency of these responses. One of the simplest indicators of behavioural disturbance is cessation of normal behaviour, which can be quantified by measuring the delay in resumption of the normal behaviour. Sudden disturbances (*e.g.*, a loud noise or human activity or approach) can result in "mass hysteria" effects in social groups of animals, as a result of social facilitation. That is, one animal may respond with a flight response and alarm calls, which elicits similar responses in other members of the group (Broom & Johnson, 1993).

Behavioural responses are particularly important as indicators of pain, although again, the responses to short-term pain can vary greatly between and within species. Broom and Johnson (1993) refer to a number of responses that are characteristic indicators of pain across species. These include: avoiding the use of a painful limb, licking a painful area of the body, changes in posture during abdominal pain, vigorous responses if a painful area is touched, and rubbing the mouth or refusal to eat if the mouth is sore (for more examples see Broom & Johnson, 1993).

Although the responses to short-term problems obviously may not appear as problematical as responses to long-term problems, nevertheless, they can affect an individual's fitness. Physiological responses can result in cardiac damage, postponement of breeding, and increases in parasite loads. Behavioural responses can lead to increases in vulnerability to predation (Broom & Johnson, 1993).

5.3.1.2 INDICATORS OF LONG-TERM PROBLEMS FOR ANIMALS

If an animal is exposed to a problem situation for a long period of time (weeks, months or years), the physiological changes and behavioural responses can be numerous. Variables that interfere with reproduction and survival clearly reduce individual fitness, and provide clear evidence of stress (Broom & Johnson, 1993). Animals may not reproduce if food is inadequate, or if they are unsettled or disturbed by their environment (*e.g.*, housed in an inappropriate social group, exposed to excessive noise, inappropriate temperatures *etc*). In addition, inadequate early experiences can lead to inappropriate sexual behaviour or poor (or absent) mothering skills. Life expectancy may be reduced by sub-optimal living conditions.

Other physiological/physical indicators of poor welfare include loss of weight in adults and lack of weight gain (or growth) in juveniles, permanent increases in basal blood pressure, variations in hormone levels, immunosuppression (using measures of white cell numbers, antibody production & T-lymphocyte function, which may indicate increases in susceptibility to infection or tumour production), changes in the incidence of diseases, and elevated levels of endogenous opioids (Broom & Johnson, 1993).

As with the short-term problems, some of the best indicators of long-term problems are provided by behavioural measures. In some cases the behaviour is adaptive, since it allows the animal to cope with an environmental difficulty. However, as Broom and Johnson (1993) point out, the behaviour itself may be "making the situation worse for itself or for other animals; this is a behavioural pathology" (p.131). Pathological responses indicate an inability to cope or adapt. However, both types of behavioural responses indicate poor welfare (Broom & Johnson, 1993).

Behavioural responses to lack of resource(s) or inability to carry out behaviour(s)

If animals are housed in enclosures with slippery floors, normal movements (*e.g.*, walking & lying down) may not be possible, or the sequence of movements may be altered (*e.g.*, cows lying down rump first). If they are housed in environments that prevent exercise, locomotion or flying may be impaired. When unable to carry out normal sequences of behaviour, animals may modify their behaviour (*e.g.*, sitting like a dog if lying down is not possible) or exhibit "grossly modified attempts to show these movements", such as excessive grooming of areas that can be reached or bizarre sequences made up of elements of sexual displays (Broom & Johnson, 1993, p.134).

Broom and Johnson (1993) stress that low food availability can result in stereotypic behaviours based on parts of the feeding repertoire (*e.g.*, sham-chewing, bar-biting & drinker-pressing in confined sows), or other responses related to finding food (*e.g.*, prey-catching movements in carnivores or digging & sifting through dirt). Some "abnormal" feeding behaviours (*e.g.*, pica) may occur as a result of dietary deficiencies (*e.g.*, phosphorus). Eating of hair and faeces "must be considered an indication of a welfare problem" (Broom & Johnson, 1993, p.134).

Social animals that are reared or housed in isolation show a variety of abnormal behaviours (*e.g.*, poor parental behaviour, inappropriate sexual behaviours, aggression etc). Lack of social stimulation, and inability to engage in the search for conspecifics, are important contributing factors (Broom & Johnson, 1993). According to Broom and Johnson (1993), some behaviours are essential (grooming/preening, exploration/curiosity, social interactions, manipulation of certain materials, & suckling in young mammals), and if animals are unable to engage in these behaviours, behavioural and physiological abnormalities are shown. For example, piglets that are weaned too soon may "belly-nose" other piglets or suck on navels or penises (Broom & Johnson, 1993). Pigs, hens and calves may engage in stereotypic behaviours (*e.g.*, excessive licking in cows & tail biting in pigs) if they are not provided with soil, straw or other manipulable materials (Broom & Johnson, 1993).

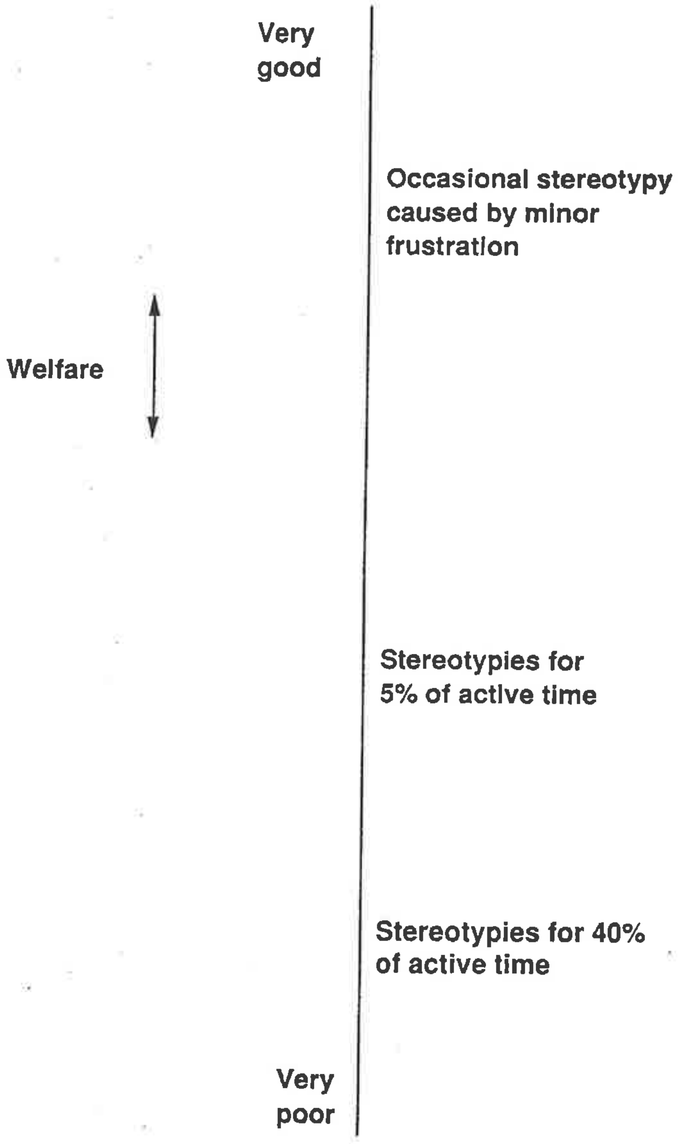


Figure 5.5a. The significance for animal welfare of different measurements of stereotypies (taken from Figure 4.4, Broom & Johnson, 1993, p.79).

Behavioural responses to frustration and lack of control

The three most common responses to frustration or lack of control (unpredictability) are aggression, stereotypies and apathy or unresponsiveness. As Broom and Johnson (1993) state, aggression may indicate poor welfare of the aggressor, but it also clearly affects the welfare of the target animal(s). Stereotypic behaviours will not be discussed here, since they have been covered in some detail elsewhere. Figure 5.5a provides a visual representation of the welfare continuum (very good – very poor). This indicates that 5% of active time spent engaged in stereotypies is cause for concern (compared to the 10% criterion suggested by Shepherdson, 1989b), whilst 40% of active time spent engaged in such activities clearly indicates very poor welfare. Animals housed in inadequate conditions are often apathetic or inactive. Broom and Johnson (1993) maintain that the "reduced activity, apparent unawareness, and lack of interest in the surrounding world" observed in these animals is strikingly similar to the behaviour observed in depressed people who have trouble coping with life. Usually apathetic animals remain responsive to the arrival of food, but may show little response to the person bringing the food (unless they approach very closely). Clearly, it is maladaptive for an individual not to respond to events in the environment. Broom and Johnson (1993) suggest that unresponsive animals may use endogenous opioids (self-narcotization) to cope, but the behaviour should nonetheless be considered abnormal. These researchers stress that:

> "Unwillingness to explore is often shown by people who are unresponsive to stimuli presented to them. Quantitative measures of responsiveness and explorative curiosity could be more widely used when assessing welfare" (Broom & Johnson, 1993, p.141).

Behavioural responses to lack of stimulation or over-stimulation

Impoverished captive environments may be characterised by a degree of sensory deprivation, lack of novelty and absence of opportunities to explore. As Broom and Johnson (1993) point out: "a profound lack of stimulation is something to which no vertebrate animal is likely to be able to adapt", since life in the natural environment is so complex (p.142). Initially an animal's behavioural response to "boredom" may be to attempt to increase the level of sensory input. However, the longer-term behavioural effects of stimulus deprivation are stereotypies or inactivity/apathy. Over-stimulation can also result in reduced exploratory behaviour and stereotypic behaviours, since animals may withdraw from the "confusing part of the environment" and concentrate on "activities with predictable consequences" (Broom & Johnson, 1993, p.142). The similarity of responses to over- or under- stimulation, indicate that behavioural abnormalities may arise as a direct result of "lack of control of its environment" (Broom & Johnson, 1993, p.142).

Figure 5.5b. Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are still being hand-reared at a number of zoos around the world (top- chimpanzee at Lincoln Park Zoo in Chicago, & bottom- bonobo at San Diego Wild Animal Park in December 1991)

Finally, localised stimulation or irritation may lead to animal's repeatedly rubbing a part of their body. For example, animals may rub the anus with limbs or on objects, if they are infested with threadworms, lice or fungal infections. Injuries may also elicit behavioural responses that are not damaging in the short-term, but may lead to tissue damage (even self-mutilation) and other physical and behavioural problems (see Broom & Johnson, 1993, for more examples).

5.3.2 ABERRANT BEHAVIOURS IN CAPTIVE CHIMPANZEES

Some of the aberrant behaviours that have been observed in captive chimpanzees are: rocking in the same spot; stereotypic or repetitive pacing, or other motor behaviours; coprophagy or ingestion and manipulation of faeces; sexual disorders; inactivity; increased aggression; and eating disorders (see Erwin & Deni, 1979, for more information). Fortunately, something can be done to reduce or eliminate such "problem" behaviours. Behavioural or environmental enrichment provides the key.

It is not enough for a zoo just to provide chimpanzees with a larger, more naturalistic enclosure (although, of course this should be encouraged!), since over time, after thorough exploration by the chimpanzees, the enclosure becomes familiar and less stimulating. Obviously, zoos cannot continuously change or modify their existing enclosures. Fortunately, there are inexpensive alternatives (*e.g.*, introduction of novel objects) that can reduce the predictability of the chimpanzees' environment (Shepherdson, 1989a). Behavioural enrichment addresses all these issues.

As with human children, the first few years of life are important for normal chimpanzee development. If an infant chimpanzee is removed from its mother, and reared by humans (*e.g.*, in a nursery) for the first few years of life, this can lead to a variety of behavioural problems, including an inability to breed or stereotypic motor behaviours, such as, rocking (Maple, 1979). Early social experience with other chimpanzees appears to be essential for a normal and socially competent chimpanzee to develop.

> "The mother-infant bond is essential to normal psychological development of an infant chimpanzee. In addition, relationships with other chimpanzees during infancy lead to the acquisition of normal social and parental skills. Therefore every effort must be made to raise infants in multi-mother groups that also include compatible adult males" (Committee for Conservation and Care of Chimpanzees, 1989).

Typically, a hand or nursery-reared infant chimpanzee or bonobo is bottle-fed, wears nappies, sleeps in a crib or cot, and when it is older plays with toys – just like a human infant (Figure

5.5b). If the infant is being hand-reared away from a social group, the other young females in the group are unable to observe mothers raising their offspring, thereby unable to learn maternal behaviours. Within a couple of generations, a social group may not contain any experienced mothers, leading to the necessity of removing infant chimpanzees for hand-rearing, since the mothers are unable to rear their own infants.

Maple (1979) gives various possible reasons for why behavioural problems may develop in chimpanzees (& other Great Apes) that have been hand-reared or nursery-reared. Lack of social experience with other chimpanzees, development of a preference for human caregivers, and a lack of motion stimulation that is usually provided by the mother chimpanzee's movements while the infant clings on, may all lead to behavioural problems.

5.4.4 ABERRANT BEHAVIOURS IN CARACALS

Carlstead (1998) states that if zoo carnivores (such as caracals) are housed in traditional enclosures (barren) and fed according to traditional methods (every 24-hours), then the 24-hour temporal pattern of stereotypic behaviour observed is similar to the adjunctive behaviours (terminal & interim activities) seen in laboratory animals run on noncontingent, intermittent schedules of food-reinforcement (as mentioned in Chapter 3).

Stereotypic pacing is the most common form of aberrant behaviour observed in captive felids (caracals & other species). However, the exact pattern of pacing may vary. Some animals may trot or run, others may pace in a figure-8 pattern, and some may even pace out an exact number of steps before turning around (Carlstead, 1998). In a study of stereotypic pacing in four species of cat (jaguars, pumas, leopards & servals) housed in outdoor enclosures at the National Zoo (Washington, D.C.), Carlstead (1998) found that pacing mainly occurred before and during food presentation by the keepers (the pumas & servals also showed a peak in pacing during the late afternoon).

Thus pacing may be a food-anticipatory stereotypy, not unlike schedule-induced terminal activities observed in laboratories. Other non-food-related stereotypies between feeds may be akin to interim activities observed in the laboratory. Carlstead (1998) stresses, that zoo managers must be aware of the behavioural effects of such feeding schedules (*i.e.*, food is presented in a very predictable way & is not contingent on the animal's behaviour). She also points out that there may be seasonal variations in the time devoted to stereotypic and other behaviours, as well as species and individual differences.

Post-feeding stereotypic running has been observed in fennec foxes, which may be related to the motivation to cache food. In the wild, fennec foxes may cache large kills, and if they are housed in enclosures that do not provide sufficient space or substrate, stereotypic behaviours may develop (Carlstead, 1998). Therefore, researchers in zoos must be aware of behaviour in the wild, and determine whether the enclosure provides the elements needed to engage in the full range of behaviours. If not, then stereotypies may develop, and simple solutions may be overlooked.

5.4 AIMS OF BEHAVIOURAL ENRICHMENT

Chamove (1989) provides a lengthy discussion of the goals of various enrichment studies in his review of environmental enrichment. He maintains that enrichment studies have two short-term goals, namely to increase "desirable" behaviour whilst decreasing "undesirable" behaviour. In addition, there are two longer-term goals: allowing captive animals to engage in behaviours observed in their wild counterparts; and to prepare animals for subsequent release to the wild. Enrichment studies also have a variety of specific goals. These include the reduction of stress in captive animals, allowing animals to have greater control over their captive environments, increasing the complexity and reducing the predictability of captive environments, and increasing stimulation, thereby, increasing the range of behaviours in captive animals (Chamove, 1989). Chamove (1989) proposes a unifying concept for the various goals and techniques of enrichment, which is to increase the "psychological space" of enclosures.

5.4.1 SHORT-TERM GOALS: INCREASING "DESIRABLE" BEHAVIOURS AND DECREASING "UNDESIRABLE" BEHAVIOURS

The short-term aims of behavioural enrichment focus on increasing "desirable" behaviours (*e.g.*, foraging, play, exploratory behaviour, & affiliative behaviour), whilst simultaneously decreasing "undesirable" behaviour (*e.g.*, coprophagy, regurgitation, self-mutilation, & stereotypic behaviours). Chamove (1989) uses the terms desirable and undesirable rather than normal and abnormal. This reflects the fact that "normality" is only one of three possible ways of approaching or assessing what can be considered "desirable" in captive animals. His discussion of the assessment of the "desirability" of behaviour indicates that the setting of achievable goals in the area of behavioural enrichment is far from simple. The enrichment goal chosen for a particular study depends on the approach taken.

Chamove (1989) maintains that there are three mutually exclusive approaches to assessing the ***desirability*** of behaviour. These may overlap and lead to similar solutions in any given situation. Each of these approaches will be discussed in turn. The **first approach** is based on the concept of "normality". The ***form and frequency of behaviour in the wild*** is considered "normal", and behaviour: "which approximates that found in the wild is held to be desirable" (Chamove, 1989, p.163). However, as Chamove (1989) points out, there is no single "norm" for behaviour patterns in the wild for a particular species, since environmental variables such as weather conditions, season, habitat, and group size may lead to variations in behaviour. The use of the "wild is normal" approach exclusively may be restrictive in terms of what can be employed for behavioural enrichment in captivity. For example, animals in the wild do not use mechanical puzzles, get taught human sign language, or spend time in certain areas (*e.g.*, callitrichids are rarely on the ground). However, the use of mechanical devices, inter-species communication, or encouraging use of all areas of an enclosure can lead to more normal levels of other behaviours, even if the activity itself is not "normal" by wild standards (Chamove, 1989).

Another approach to assessing what is "desirable" behaviour is based upon whether the behaviours displayed by captive animals are ***"acceptable" to zoo staff and zoo visitors***. Not surprisingly, zoo visitors dislike observing "abnormal" behaviours such as coprophagy, or regurgitation / re-ingestion of food. However, as Chamove (1989) states, zoo visitors may also dislike observing normal behaviours such as mating. In addition, zoo visitors prefer animals that are active (even though the animals may be inactive at those times in the wild) and visible (even though some species are particularly elusive or hidden by foliage in the wild). Chamove (1989) stresses that if captive animals are hidden from view, and this conflicts with visitor expectations, then problems may be overcome by education and information. Activity can be encouraged in primates by simply scattering or hiding food, or by providing extra browse. Zoo visitors are thus provided with more active animals engaging in natural foraging behaviour (Chamove, 1989).

Chamove (1989) posits a **third approach** to assessing "desirability" of behaviour, which is based on ***theoretical perspectives***. A theoretical objective may be set, such as exercise or calorie expenditure, occupation of animals or increased problem solving opportunities, or facilitation and increase of normal behaviour patterns. When setting goals, the theoretical approach takes feeding strategies and activity budgets of animals in their natural environments into account. This approach is perhaps less concerned with factors such as visitor and staff perceptions. Chamove (1989) provides examples of theoretical aims. Problem solving skills can be enhanced if an animal's food is buried in wood-chips. Laboratory primates can be provided with the opportunity to use a variety of skills by including swimming and fishing pools in their enclosures (Gilbert & Wrenshall, 1989; King & Norwood, 1989).

Chamove and Anderson (1989) provide a **fourth approach** for assessing the desirability of behaviour, which is based on ***practical considerations***. Enrichment studies may be influenced by a zoo's need to reduce costs, food or resource wastage, or improve animal management and husbandry (*e.g.*, reducing aggression & self-injury in animals). "Multiple species" enclosures maximize use of enclosure space, whilst minimizing food wastage. "Ground living rodents, birds or fish eat fallen fruit in bird, bat, or primate exhibits in Edinburgh, Milwaukee, Sydney, Copenhagen, Stockholm, and San Diego Zoos" (Chamove & Anderson, 1989, p.188).

5.4.2 LONG-TERM AIMS: IMPROVING QUALITY OF LIFE AND TRAINING ANIMALS FOR THE "WILD"

For researchers in a zoo situation, it is unlikely that goals based solely on theoretical perspectives would be set. An awareness of the four main approaches to assessing "desirability" of behaviour can lead to the setting of realistic goals that incorporate facets of all four approaches. For example:

> "management practices aimed at reducing stereotyped movements, say by increasing food variety (a practical measure), may lead to behavior that is more like that seen in the wild (normality approach), increases the similarity of the activity profile to that observed in the wild (theoretical approach), and probably also increases public acceptability along with improving the animals' physical health (practical)" (Chamove & Anderson, 1989, pp.188-189).

With respect to the broader long-term goal(s) of enrichment, Chamove (1989) stresses that this goal: "should be to allow and encourage animals to show behaviour patterns which are within the normal range of their wild counterparts" (p.163). He distances himself from the second broad long-term aim of ensuring that captive animals are "produced" which could successfully reproduce and survive in the wild, by referring to these researchers as "others".

Tudge (1991) suggests that the first aim is to ***improve the quality of life*** for captive animals (welfare aspect). Not surprisingly, this aim has been the main focus of research on behavioural enrichment. He emphasizes that the second aim is vital for successful reintroduction of captive animals to the wild. In fact, Tudge (1991) asserts that: "the ultimate aim must be to return animals to the wild" (p.233). In order to achieve successful reintroduction, animals:

> "in zoos must be encouraged to retain enough of their natural behaviour to make it possible for them to go back to the wilderness; or enough at least of their native wit to enable them to relearn the necessary skills" (Tudge, 1991, p.193).

The two aims can clearly be linked, since setting a goal of maintaining natural behaviour patterns (*e.g.*, foraging & problem solving skills) can ensure that animals retain behaviours vital to survival in wild environments. Further, the opportunity to engage in a diversity of natural behaviours, ensures that "quality of life" is enhanced for the time spent in captive environments.

5.5 MECHANICAL DEVICES FOR BEHAVIOURAL ENRICHMENT

Behavioural enrichment studies usually fall into one of two categories, namely, mechanical or "naturalistic" (Tudge, 1991). The fundamental differences and the emergence of a combined approach will be discussed in a subsequent section. Tudge (1991) maintains that the mechanical approach with its use of apparatus to challenge and "occupy" animals can be traced back to Yerkes (1925). This American primatologist states: "The greatest possibility for improvement in our provision for captive primates lies in the invention and installation of apparatus which can be used for play or work" (Tudge, 1991, p.211). In the same year, Köhler was providing chimpanzees with objects to "work" and "play" with. Mental and physical challenges were presented in experiments investigating ape "mentality" or problem solving strategies. Tudge (1991) emphasizes that Yerkes (as a laboratory scientist) was not restricted by the appearance of apparatus (*e.g.*, cardboard boxes, machines, or a gymnasium), which must be taken into consideration in zoos. His prime concern was with the ape's mental wellbeing, and the maintenance of natural behaviour patterns for him to study (Tudge, 1991).

In recent times, the mechanical approach has been associated with Hal Markowitz and his work at Portland Zoo (Oregon) in the 1970's (Tudge, 1991). Other zoos that have used the mechanical approach include Washington Park Zoo (*e.g.*, Mellen, Stevens & Markowitz, 1981), the Panaewa Zoo, and Brookfield Zoo in Chicago (Forthman Quick, 1984).

5.5.1 "HUNTING" ARTIFICIAL ZEBRAS AS BEHAVIOURAL ENRICHMENT FOR AFRICAN HUNTING DOGS

In the early 1990s, Duisberg Zoo began testing a "run-and-fun-lift" for their group of nine African (Cape) Hunting Dogs, as a means of providing a more "species-specific" method of feeding. A number of zoos in Europe (*e.g.*, Neuwied Zoo, Salzburg Zoo & a game park at Herberstein in Austria) provide cheetahs with the opportunity to chase or "hunt" moving artificial prey (Gewalt, 1992). These large felids usually hunt alone, and the actual hunt is fast but lasts for only a few minutes. African wild dogs, on the other hand, hunt as a pack and for longer periods (sometimes for longer than half an hour). Based on the "electric-hare" system used in Greyhound-racing, the zoo was aiming for a piece of equipment that would carry the "prey" around the enclosure for several laps, before being "killed" by the hunting dogs.

Thus, Gewalt (1992) designed an artificial metal zebra, suspended (1-1.5m above the ground) from a cable. This prey along with about 5 kg of meat (horse or beef ribs) suspended from a slide moves between 20 and 50 km per hour along a track. The dogs chase the zebra (& meat) for several laps around the enclosure (152m circuit) before the zebra slowly comes to a halt. Any remaining pieces of meat are "attacked" and pulled down by the dogs.

Gewalt (1992) provides no data or behavioural evidence for the success of this enrichment device. However, he states that even after using it daily for a year, the dogs continue to chase the zebra and jump for the meat at the end of the chase (even though they could just sit & wait for the zebra). Thus, the artificial prey provides the dogs with the ability to hunt and the zoo visitors with the opportunity to observe a pack of African wild dogs in action.

5.5.2 SERVALS LEAPING FOR "BIRDIE"

In their natural environments servals hunt: "small mammals and birds through tall grass, often making spectacular leaps to capture flushed birds. Unfortunately, this dramatic capture pattern is rarely, if ever, seen by zoo visitors" (Mellen et al, 1981, pp.196-197). At Washington Park Zoo Mellen, Stevens and Markowitz (1981) designed a piece of apparatus that would provide the three captive-bred servals (one male & two females) with an "opportunity to use their special leaping abilities" (p.197). As well as allowing the animals to engage in this leaping behaviour, it was designed to enhance the zoo visitor's perception of this cat species, and its natural behaviour patterns. This study continued on from a series of earlier studies. Schmukal (1974) reported that these three "generally inactive" servals: "would stalk and jump at a rope or other object suspended from the ceiling of their enclosure" (Mellen et al, 1981, p.197).

Schmukal's (1974) study ran for over twelve months, providing the baseline for future work with these cats. Although no figures are given, Markowitz (1982) states that two main behavioural patterns emerged. The servals were completely inactive for long periods, or when active, the behaviour typically took the form of stereotypic pacing. The servals were housed in a glass-fronted concrete and steel cage, and keepers fed them by pushing food through a feeding slot.

After the baseline study, the researchers changed the feeding routine by "simultaneously dropping three pieces of food from overhead into three different areas of the exhibit", instead of feeding them in a single location (Markowitz, 1982, p.176). This change allowed potential aggression or sexual dimorphism to be monitored, before introducing major changes or enrichment techniques. Markowitz (1982) describes these early findings as "startlingly systematic" (p.176). Food was consumed according to an "absolutely rigid hierarchy" with the male always eating the first pieces of meat. One of the females (always the same one) ate next. Only after these two cats were "largely satiated" was the last female allowed access to food. Markowitz (1982) points out that the two females were similar in age and size.

Markowitz (1982) does not mention whether the more dominant servals, which had access to food first, typically ate at one of the three "drop" locations, or whether they moved from one to the next. It is unclear how the dominant serval (or two) was able to defend the three separate feeding sites simultaneously. Was a hiss or threat enough to intimidate the subordinates? Aggressive behaviour was not considered to be a "significant worry" based on the observations carried out over a "lengthy period" (Markowitz, 1982, p.176).

The enrichment technique chosen allowed the servals to engage in active "prey-chase" behaviour, with "flying meatballs" constituting the prey. Each meatball consisted of ZuPreem (a prepared red meat product for carnivores) inside a sausage casing. Allowing the servals to hunt for live birds or small ground mammals had been rejected on "political and humane" grounds (Markowitz, 1982, p.176). Initially Markowitz (1982) and his co-workers had planned to lower the meatball to only a few feet off the ground, since previous research as well as published photos had suggested that servals were capable of leaping further horizontally than vertically. However, "on the initial trial, the servals, exposed to their first animate "company" in years, leaped more than two body lengths vertically to catch the meat" (Markowitz, 1982, p.176). The interest generated by these early studies led to the servals being moved to an outdoor enclosure, which Markowitz (1982) describes as "more adequate" (p.176). Work continued there on the flying prey object ("birdie").

The serval's outdoor enclosure (17.5 m x 4.5m x 6.2m) was constructed of welded wire and steel, with a concrete floor (partly strewn with wood-chips) and housing a 1m high (2m diameter) heated pedestal. During very cold weather, the servals were housed indoors at night. The first "birdie" prototype tested in the new enclosure still consisted of a Zu/Preem meatball "carried" across the enclosure. The height and pattern of travel across the enclosure varied randomly. If the servals leapt at the container and struck it, the "meatball" was released. However, the meatballs tended to fall by themselves as a result of the "erratic path of the apparatus". To overcome this problem the meatballs were fitted into the container "more securely", but "this made it difficult if not impossible for the servals to release" the meatball (Mellen et al, 1981, p.197).

Following a number of "trial and error" variations a teflon rod "birdie" was designed. This rod was approximately 25cm in length, suspended from a 5mm cable. When not in use the "birdie" was kept out of the servals' reach. When in operation, it was lowered to between 1.5 metres and 2.5 metres off the ground, within reach of a leaping serval. In this final version of the "birdie" the food was not attached to the rod. If a serval successfully leapt and hit the "birdie", a piece of Carnifare (prepared carnivore diet) was delivered at the "home" end of the run, serving as reinforcement for the leap. Each run of the apparatus lasted for one minute, covering a distance of 13 metres (across the enclosure, & back to the starting point). Not surprisingly, "quite often one animal would earn the food and another consume it" (Mellen et al, 1981, p.197).

The "birdie" was in use for 20-minute sessions, run once or twice a day. Data were collected from October 1976 to March 1977, and October 1977 to January 1978. The second female had died prior to commencement of the second period. Data collected included: amount of contact with the teflon "birdie", jump frequency, number of food pieces consumed, threat displays, and general activity- defined as: "moving one or more body lengths in a given one-minute interval" (Mellen et al, 1981, p.197).

Striking individual differences emerged for the relative frequency of jumps and amount of earned food consumed by each serval. During the first observation period (October 1976 - March 1977) the male only made one percent of the total jumps per session, and consumed one percent of all earned food per session. Female "1" made 81% of all jumps per session, and consumed more than her "earned" share (98% of all earned food). The second female ("2") made 18% of the jumps per session, but only consumed one percent of the earned food per session.

During the second period of observations (October 1977 - January 1978), when the second female was no longer alive, the first female's percentage of jumps per session rose to 97%, and she still consumed 98% of the earned food per session. The mean number of jumps made by the female per hour was 94.4. The male's percentages rose slightly to 3% of the jumps per session, and he consumed 2% of the earned food. The mean number of jumps made per hour by the male was 3.3. Mellen et al (1981) point out that the reinforcement food (Carnifare) only constituted 25% to 30% of their daily diet, so servals obtaining only minimal amounts of the "birdie" food did not starve.

Statistically significant differences for general activity levels were found for the female between the experimental "birdie" sessions and the "non-sessions" (second study period). During "birdie" sessions, the female was active for 59.2 minutes of the hour. During the "non-sessions" this figure dropped to 18.2 minutes of the hour. Unfortunately, there were no baseline data (prior to installation of the "birdie"). It is not surprising that activity levels would be higher when the "birdie" was in operation, since "activity" was being reinforced anyway. However, there was no difference (statistical) for the activity of the male during sessions and "non-sessions". When the "birdie" was in operation, he was active for a mean of 10.9 minutes of the hour. For "non-sessions" he was active for 8.7 minutes of the hour. This finding puzzled Mellen et al (1981), since the male was dominant, often threatening the females, rarely receiving threats in return. In addition, he rarely earned or consumed food during "birdie" sessions but was able to obtain extra food by threatening the females.

Typically, during "birdie" sessions, the male slept or watched the females from a stationary position. His lack of interaction with the feeding device was attributed to a possible minor injury during earlier trials with different "birdies" or for "idiosyncratic" reasons (Mellen et al, 1981, p.198). These researchers posit that the subordinate female was prevented from participating fully by the dominant female. Instead, she "intently" watched both the birdie and dominant female, from a position near the "birdie's" path. The frequency, duration and severity of threats and fights evoked by the feeding activity "were never critically high" (Mellen et al, 1981, p.198).

The male's low level of participation in the enrichment task "aided the veterinary staff in diagnosing a congenital diaphragmatic hernia" (Mellen et al, 1981, p.198). In particular, the male's behaviour was observed to change suddenly when he "halted" at the start of a prey-capture session. Behavioural enrichment tasks may alert keepers and vets to possible injuries or illnesses, which may otherwise remain undetected if the animals are typically inactive anyway (Markowitz, 1982). Mellen et al (1981) maintain that the servals benefited from the leaping task, as did the zoo visitors.

> "Ordinarily the servals received little attention, but when the birdie was in operation the staff were inundated with questions about these cats and their remarkable hunting style" (Mellen et al, 1981, p.198).

However, Markowitz (1982) describes the enrichment task as only "partially successful", since not all the servals used it to the same degree. He posits that: "Since servals are rather skimpy eaters, there was not the motivation to exercise at the greatly increased level" (p.176).

5.5.3 SERVALS HUNTING ARTIFICIAL "HAIRY RODENTS", WHIFFLE BALLS AND PIGSKIN SACKS

Markowitz and LaForse (1987) discuss the use of artificial prey as behavioural enrichment devices for tigers and servals. The "leaping for birdie" device used with servals at Portland Zoo (Oregon) has already been described. At a zoo near Hilo (Hawaii), tigers were provided with the opportunity to "hunt" molded plastic replicas of a rabbit and a squirrel, which "ran across the surface of 4-foot hills" (Markowitz & LaForse, 1987). Fresh chunks of meat were automatically delivered at the completion of a successful hunt.

Following these two studies, a pilot project was conducted with two five-year old servals at San Francisco Zoo. Three different artificial hunting apparatus were designed, including a variety of small balls, a hanging pigskin sack (with sheepskin bits sewn onto it) and a "hairy rodent" (stuffed toy), which was pulled through cast acrylic tubing. The servals could initiate a "hunt" if they explored the tree stump areas, when they heard squeaking "prey" sounds (produced by a concealed microphone & sound synthesiser). Thus, the servals were able to "flush out a fast-moving prey object whenever they foraged for it after hearing a sound representing the presence of the prey" (Markowitz & La Forse, 1987, p.41). The artificial rodent moved through the tube, and if pounced on by the servals, a meatball was delivered through a food tube. Fifty sessions of the "hairy rodent" chase were conducted over a three-month period (one-hour in the mornings & one-hour in the afternoons).

The responses directed at the balls varied between the two servals. The male merely sniffed at the "whiffle" ball. The female, on the other hand, swatted, chased or carried the ball continuously for twenty minutes, before dropping and ignoring it. Over the remaining days, she occasionally swatted the ball around. Other balls were played with initially, and then were largely ignored. Markowitz and La Forse (1987) suggest that these simple novel objects (balls) elicited some play, but the cats quickly habituated to them, and thus they were ineffective as long-term enrichment devices.

The hanging pigskin sack was rubbed, swatted and scent-marked by the servals when it was first introduced in a morning session. By the afternoon the cats were directing fewer response towards it, and for the next two days it was ignored (& then removed by the experimenters). After one week, the sack was reintroduced, and explored by the cats during the morning, before being ignored. Again, the servals quickly habituated to this simple object.

The "tube chase apparatus" (or "hairy rodent") had the greatest impact on the servals' behaviour. The female engaged in foraging, chasing, leaping and pouncing when the hunting apparatus was in operation. These behaviours were rarely (or never) observed during baseline sessions. When the servals were not provided with the opportunity to "hunt", more time was spent walking or pacing. The female spent between seven and fifty minutes of each allocated "hunting" hour engaged in hunting activities. She also did not habituate to the rodent "squeaking" sound. The female continued to hunt in the presence of free food. The male was less responsive (but he was de-clawed, "hostile" towards humans, and may have had a hearing deficit), but he spent more time out of the den when the apparatus was in use. More hunting took place during morning sessions, before feeding, and after rodent "squeaks".

Markowitz and La Forse (1987) point out that the meatballs were delivered in response to the servals' behaviour, and were "slightly animated", since they often bounced or rolled. These researchers stress that prey or play objects should be removed when not in use (to retain novelty). They also maintain that acoustic stimuli should be included, artificial prey should be animated, and the accessibility of "prey" should be contingent upon the serval's behaviour.

5.5.4 NATURALIZED OPERANT ANIMATED HABITATS: THE "CAT-A-PULL"

> "even a 17-year-old, captive-born ocelot could reach up and grab a fake lizard, pull it down a track in the side of a 7-foot fake tree trunk, and eat the snack dispensed into the recess at the base of the tree. During these occasions, an exhibit can be transformed into a dynamic predatorial theater where the prey always succumbs to the cat's lunges, much to the delight of visitors photographing this spectacle" (Bacon, 1992, p.7).

Bacon (1993) proposes that the prey-capture repertoire of caracals, servals and ocelots involves: spotting, stalking, crouching, running, leaping, reaching, grabbing, pulling and biting (& sometimes tripping & swatting). He suggests that a "naturalized operant exhibit" would use an artificial and reusable "mock prey", which would be captured and subdued by the cat, which would be "immediately rewarded with a nutritious snack at or near the site of capture" (p.7). The device tested on the ocelot in the quote was a modified version of the "Cat-A-Pull", an operant device designed for domestic cats.

The "Cat-A-Pull" is an upright three-foot (six-inch wide) tube, supported by a wide base, with two mice (one on either side), which can be pulled downwards through a track. As one mouse moves down, the other moves up, and cat chow is dispensed into a food-trough at the base. Bacon (1993) maintains that after a few sessions: "any healthy eight-week-old kitten can learn to jump, reach, grab, pull, and bite the rubber mouse and drag it to submission" (p.7). The response required to obtain reinforcement is not dissimilar to the standard operant bar-pressing response in the laboratory rat. That is, instead of pressing the bar, the cat stretches up and pulls down the mouse/lizard (which is essentially a rubber, animal-shaped manipulandum). Even the food "reservoir" is just like the standard food-trough. Although certainly an interesting addition to an exhibit, which provides no simulating hunting opportunities, a flying-fox style, moving device would no doubt elicit a wider range of behavioural topographies (see Chapter 10 for more information).

Unfortunately, Bacon (1993) alienated a number of zoo researchers by subsequent published criticisms of whole carcass feedings. That is, he does not support the feeding of a whole carcass to a captive cat, since this "obviates hunting" (p.10). In response, Graham Law (1993) stresses that captive exotic cats may no longer recognize prey, if they are only fed "prepared pulp", and deprived of the opportunity to engage in plucking behaviour (of fur or feathers from the prey item). Law (1993) rather sarcastically comments that:

> "I have observed both my own house cat and my cats at the zoo flinging mice and chickens into the air and performing mock stalking and hunting behaviour on the already dead prey. I have yet to see my house cat fling its tinned food into the air and then stalk it. It seems, therefore, that dead, whole foods can stimulate hunting behaviour" (p.10).

This debate, and indeed division between the mechanical/operant and naturalistic techniques used, will be discussed subsequently. Common sense would suggest that a combination of techniques and approaches would be appropriate.

5.5.5 ACOUSTIC "PREY" AS ENRICHMENT FOR LEOPARDS

Mechanical artificial prey devices (such as the "run-and-fun lift" mentioned previously) can be expensive to design, build, install and maintain. Once installed, they are difficult to move. At San Francisco Zoo, Markowitz, Aday and Gavazzi (1995) developed an "acoustic prey" device for a sixteen-year old leopard (*Panthera pardus*), which could be easily transported or reinstalled into new exhibits. These researchers maintain that prey vocalisations can form part of "an active environmental enrichment protocol" (p.376). The apparatus consisted of a number of components that were computer-operated.

The enrichment device simulated the "flight of a bird, roused by a hunting leopard" (Markowitz et al, 1995, p.373). Over eleven sessions (30 - 90 minutes in duration), the leopard was shaped by successive approximations to forage around and follow the acoustic prey sounds. The computer was on from 10 a.m. until 4 p.m. (or until all the 24 food reinforcements had been delivered). A bird sound was played through a speaker (near the top of the enclosure & tree branch), which typically attracted the leopard. This speaker was usually activated 30-60 seconds after the last trial (pseudo-random time schedule). If she foraged around that area within the set amount of time (which was picked up by a motion sensor), the bird sound then moved down a branch (from speaker 2-3) to a fourth speaker at the other side of the cage. If the leopard then foraged around the fourth speaker (which was again picked up by a motion sensor) within 60 seconds, a piece of meat was delivered from a feeder.

Over a period of 16 months, the leopard foraged every day, and this behaviour did not extinguish. Of the 327 trials or days, the leopard successfully obtained the maximum number of reinforcements (24) in one-third of cases, and the successful completion of the behavioural sequence varied depending on the meat used (chicks > horse meat > frankfurters). When the apparatus was in use, walking, jumping, pouncing and rolling increased and stereotypic pacing (& time off-exhibit in some cases) decreased, when compared to baseline and sessions when the apparatus was switched off.

Markowitz et al (1995) stress that the behavioural changes facilitated by the acoustic enrichment device were varied and interesting. Stereotypic hunting patterns were not elicited. Sometimes the leopard moved at speed along various routes. At other times she slowly crept along the shortest route. The bird sounds occurred randomly, and were often ignored. Thus the leopard decided when to hunt. This acoustic prey device allows researchers to set up various contingencies (or schedules of reinforcement). It provides captive carnivores with the opportunity to control part of their environment. Markowitz et al (1995) conclude that although:

> "it is not feasible to reproduce exactly the contingencies of nature in a captive setting, the apparatus described here does serve to occupy the animal in healthy exercise and increase her involvement in the feeding procedure" (p.377).

A later version of the device varied the location of the first bird sound.

5.6 MORE "NATURALISTIC" TECHNIQUES

In the late 1970s and early 1980s a group of researchers affiliated with Woodland Park Zoo (*e.g.*, Hancocks, 1980; Hutchins, Hancocks & Calip, 1978a, 1978b, 1979) rejected the mechanical approach. They preferred to use "technology and information from field studies" to "make naturalistic modifications in physical and social environments" (Forthman Quick, 1984, p. 66). In fact, the mechanical approach was clearly excluded from the Woodland Park Zoo's *Research*

Policy and Procedure document as outlined by Foster and Freeman (1977). They state that it would:

> "be contradictory to our objectives to accept investigations that would require manipulation of the animals with furniture or devices that might result in abnormal behavior or distract from the naturalistic appearance of the exhibit" (Foster & Freeman, 1977, p.10).

Researchers of the 1980s and 1990s, such as David Shepherdson (London Zoo & Portland Zoo, Oregon), Graham Law (Glasgow Zoo) and Arnold Chamove (Stirling University) have not completely rejected the mechanical approach or use of devices (Figure 5.6). Instead, they have opted for "soft" environments, which: "incorporate as much natural material as possible; and laboratory-style devices, if they are employed at all, are given a more natural mien" (Tudge, 1991, p.220).

5.6.1 WOOD-CHIP SUBSTRATES WITH SCATTERED FOOD FOR PRIMATES

Between 1979 and 1986, Chamove and his co-workers conducted a series of experiments that investigated the behavioural effects following the introduction of wood-chip litter in the large cages of eight species of primate (Chamove, 1989). The primary aim of these studies was to "improve welfare". In particular, their aim was to reduce abnormal and undesirable behaviours (*e.g.*, self-mutilation & aggression) and to increase activity. In each instance, the cage floor was covered with 4cm deep wood-chips, and small items of food were scattered throughout the litter. Chamove (1989) makes a distinction between emulating and simulating nature, stating:

> "The choice of floor-covering was not one of emulation-to copy nature, as this is impractical for almost all captive environments; rather the aim was simulation-to provide certain, possibly critical, components of the natural environment" (p.170).

Apart from the enrichment technique itself, the importance of Chamove's (and co-worker's) contributions to behavioural enrichment lies in the fact that his studies involve the systematic testing of hypotheses. The technique in thoroughly evaluated in terms of costs and benefits to the animals, technicians and institutions involved. Each study was run over several months. Behavioural change, costs and benefits were measured, including technician workload, odour and cleanliness of cages, and the "bacterial vigour" of wood-chips (Chamove, 1989, p.170). Two predictions were made, based on the hypothesis that: "enrichment would be more effective when targeting behaviour more common to the animal in its natural setting" (Chamove, 1989, p.170). It was posited that substantial changes in behaviour would be observed, if the opportunity to engage in foraging were changed. In addition, terrestrial primate species would be more affected

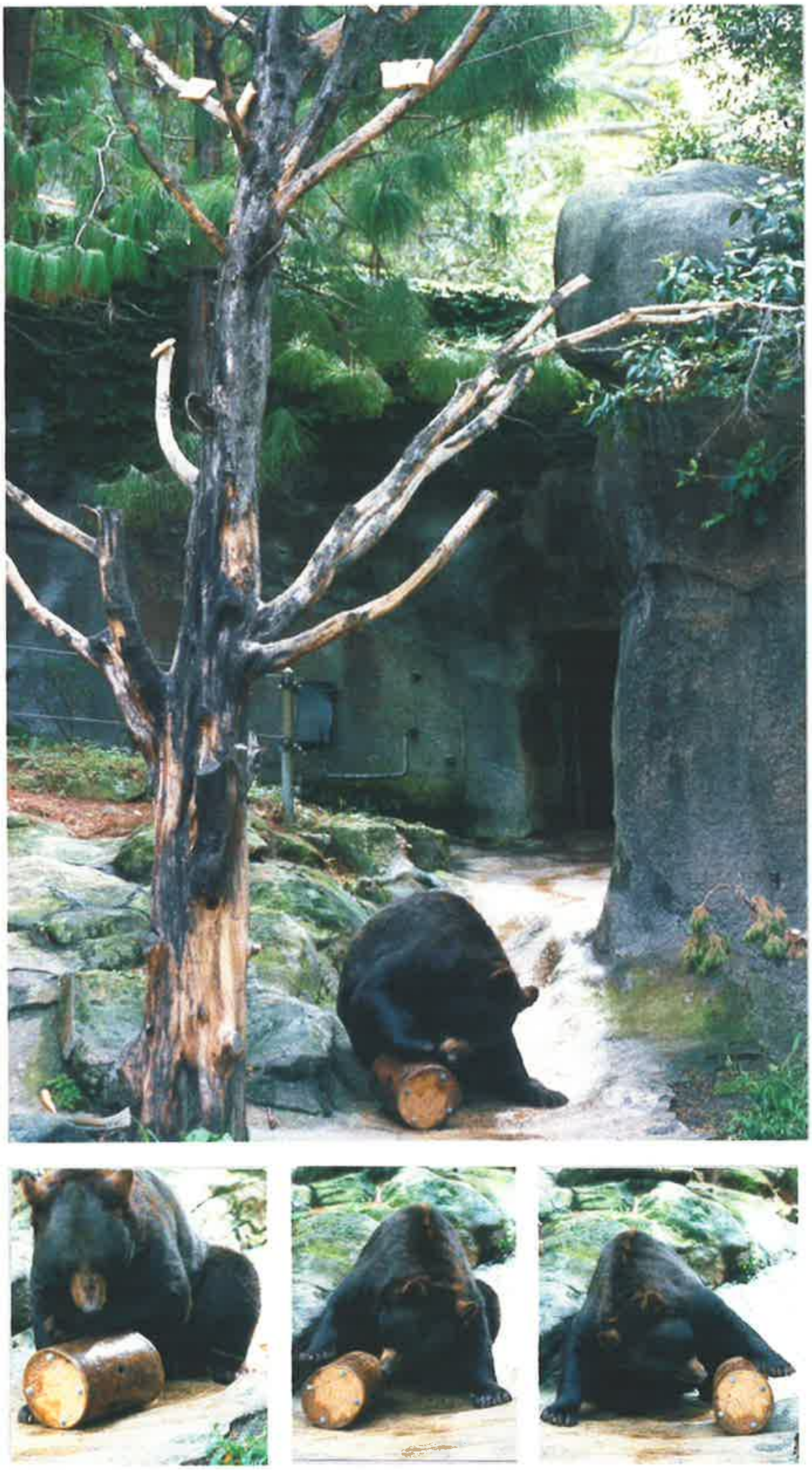


Figure 5.6. Bears can be encouraged to engage in more foraging by providing them with "natural" looking puzzle "boxes" or by simply scattering food (note the pieces of bread located at the top of the tree for this bear at Taronga Zoo)

if floor covering were provided, than arboreal primate species, which spend less time foraging on the ground (in order to avoid predators).

Chamove (1989) suggests that wood-chips are highly cost-effective in terms of the behavioural changes achieved. The initial studies were carried out on stump-tailed macaques. "Self-injury" behaviour decreased by more than 50%, and aggression was decreased in adults and juveniles by a factor of two and ten respectively. Similar findings emerged in seven of the eight other species investigated. Chamove (1989) compares the percentage of waking time spent foraging by macaques under four experimental conditions, namely: bare floor (almost no time); wood-chips only (5%); wood-chips and scattered grain with a concurrent source of grain (15%); and wood-chips with scattered grain throughout (>30%). In the last condition, in which grain was only available scattered amongst the wood-chips, the monkeys foraged for over 30% of their day, which "more closely resembles the behaviour of free-ranging macaques" (Chamove, 1989, p.171). Interestingly, even the arboreal species of primate tested spent more time on the floor. The provision of wood-chips and scattered food resulted in increased foraging, and decreased inactivity, aggression and abnormal behaviours. Some reductions in play and affiliative behaviour were also noted. However, some changes may be expected in a variety of behaviours (including "desirable" behaviours), when a behaviour such as foraging (which takes up a substantial portion of a wild counterpart's activity budget), is increased substantially.

The use of wood-chips as a floor covering was also found to be cost-effective, when assessed in monetary and practical terms. Chamove (1989) maintains that cleaning time per enclosure dropped from five to two hours per week; walls and windows were considered cleaner; and even after four weeks of use, the wood-chips were rated less "smelly" than a bare floor after one day. In addition, the longer the wood-chips were in use, the "more inhibitory it was to bacterial survival" (Chamove, 1989, p.171). This latter finding was based on samples of wood-chips that were collected over eight weeks, tested for bacteria and inoculated with *Salmonella* bacteria to measure its survival time. Thus, based on a number of criteria, wood-chips as a substrate, when incorporated with scattered feed, can be considered a successful method of behavioural enrichment for both terrestrial and arboreal primates, in a variety of cage or captive enclosures (Chamove, 1989).

5.6.2 PLANTS, SOFT SUBSTRATES AND ENCLOSURE FURNISHINGS FOR FELIDS

Carnivores also benefit from having plants, soft substrates and interesting exhibits. As Law et al (1997) point out, plants provide felids with shade and places to hide (or visual barriers). Subdued lighting and plants are particularly recommended for forest-dwelling felids, such as clouded leopards. Soft substrates (*e.g.*, wood chips) rather than abrasive concrete floors can prevent leg injuries or paw pads from becoming sore, and the use of water and disinfectants (minimising phenol absorption) is reduced. Furnishings may include a number of objects that add complexity to the environment, and provide areas to rest, from where they can observe their surroundings (e.g., trees or logs, & observation platforms).

Mertens and Schär (1988) stress, that high space quality must be the aim if space quantity is at a minimum. It is unlikely that many zoos (unless they are open-range zoos) are able to provide a range that is comparable in size to the range of free-ranging counterparts (even a semi-feral suburban female cat ranges over 200 sq m, Mertens & Schär, 1988). As already mentioned, male ranges are typically larger than female ranges, which in practical terms suggests that females may adapt better to captive environments, since they require less space.

Where information about the free-ranging behaviour of a particular cat species is lacking, researchers can use information from studies of farm cats or feral cats as a guide (Mertens & Schär, 1988). Farm cats tend to choose elevated resting places (warm, dry, & sheltered on one or two sides) and sleeping places are often concealed. Observation posts, on the other hand, allow a good view of the surroundings (often sunny & not far from cover). Importantly, farm and feral cats do not soil feeding o sleeping areas, and rarely defecate and urinate in the same location. Therefore, enclosures should provide sufficient space (with appropriate substrates) for at least two "litter" areas, and food, water and resting areas should be as far away as possible from these areas (Mertens & Schär, 1988).

As Mertens and Schär (1988) point out, all free-ranging cats hunt and explore, and captive environments must compensate for deficiencies in opportunities to engage in these behaviours. Moving objects can stimulate simulated hunting behaviour and new objects can promote exploratory behaviour (as already mentioned). Some naturalistic enrichment techniques will be discussed in the following pages.

5.6.3 MULTIPLE FEEDINGS OF HIDDEN FOOD FOR LEOPARD CATS

In addition to the fishing cat study already mentioned, Shepherdson et al (1993) conducted a study of leopard cats at the National Zoological Park, in which the feeding routines were altered, rather than the type of food, as a possible means of behavioural enrichment. Four captive-bred leopard cats (two males & two females) served as subjects. They ranged in age from three to ten years, and were singly housed in off-exhibit enclosures (in the lion & tiger complex). Each enclosure consisted of concrete and wire-mesh (2.4m x 3.0m x 2.7m in size), containing three elevated resting platforms, two hollow logs, tree branches, an animal carrier, and three pans of sand, dirt or mulch. Behind each of the cat enclosures was a 2.4m x 1m x 1.5m wire-mesh run, which the cats had access to.

Prior to the study, the cats were fed once daily from an aluminium pan, which was placed on the floor. Feeding time varied, depending on the keeper's schedule. The daily cat feed consisted of 0.25kg of Nebraska brand feline processed meat diet, one egg, and either one or two dead mice or a dead chick. The enclosures were hosed clean once a day (between 7.30 a.m. & 2p.m.), with the cat remaining in the enclosure when keepers entered, rather than being moved into an adjacent area.

Shepherdson et al's (1993) study was divided into three phases: one baseline condition and two experimental conditions (multiple feeding & hidden food). The baseline data were collected on the first eight days of the study, when the feeding regime remained unchanged. Following this stage, the researchers changed the feeding routine from one large meal, to four small meals, spaced at irregular intervals between 7a.m. and 5p.m.. Thus, feeds began slightly earlier and finished later than before. Each small feed consisted of an egg, a chick, a mouse or 0.125kg of the feline diet. Each meal was placed on the floor. This second phase was run for one month, with data collected on the last six days. The third phase continued the four feeds a day for another month. In addition, these four meals were hidden in one of two possible brush piles. The large pile was comprised of between five and seven 2m long branches, which were located in the centre of the enclosure. The second smaller pile consisted of three or four 1m long branches located in the run behind the enclosure. On the last five days of this third phase, the data were collected.

The most significant differences between the three methods of feeding were found for locomoting/exploring and stereotypic pacing. If multiple feedings were hidden, the amount of locomoting/exploring almost tripled, pacing decreased by half, and behavioural diversity increased (when compared with baseline). In addition, exploratory behaviour occurred throughout the day, not just at feeding time.

5.6.4 FISHING AS ENRICHMENT FOR SQUIRREL MONKEYS

Although this review has focussed on behavioural enrichment in zoos, the work of researchers in laboratories can provide a rich source of ideas for enrichment of captive environments. King and Norwood (1989) investigate the use of "free-environment" rooms, and fishing as a form of behavioural enrichment for squirrel monkeys in a laboratory situation. Two "free-environment" rooms were established to house a total of 38 squirrel monkeys that had previously been housed in individual and "gang" cages in colony rooms. Features of the "free-environment" rooms included ropes, plastic chains, small live trees, tree branches, step ladders, racks without cages, and a long rack of 12 rodent gang cages with the fronts removed (King & Norwood, 1989, p.106). A number of injuries were initially reported in the monkeys, attributed to falls as a result of "their rustiness in leaping and climbing" (King & Norwood, 1989, p.109). Interestingly, the new rooms were far quieter than the old environment, which was characterised by the noise of cage and perch rattling.

The most notable feature of the study described by King and Norwood (1989) is the provision of fishing pools in the "free-environment" rooms. These researchers were prepared to employ a source of enrichment, to enhance and facilitate foraging, problem solving strategies and other natural patterns of behaviour, despite the fact that fishing *per se* is not a "natural" behaviour for squirrel monkeys. That is: "squirrel monkeys undoubtedly do not capture live fish in their natural arboreal habitat" (King & Norwood, 1989, p.110). Squirrel monkeys do, however, capture rapidly moving flying insects, and are thus adept at visually tracking and seizing small, fast prey items.

Three weeks prior to testing, the monkeys were introduced to the taste of fish, by adding sardines to their monkey chow feeds. During the experimental phase, ten goldfish were placed daily into a small ceramic water-filled bowl. Despite the monkey's inexperience with live fish, the "appearance of the first crock of fish elicited a frenzy of excited attempts to grab them" (King & Norwood, 1989, p.110). Of the 18 monkeys in the study, only one did not attempt to catch fish, and two were unsuccessful in capturing a fish. The "hunting success" was 26%. The second phase of the experiment increased the difficulty of fishing by using small wading pools instead of crocks. In this situation, 12 of the 18 monkeys successfully captured a fish during the first 22 days of testing, with a "hunting success" of 22%. "Handedness" was also recorded, with most fishing attempts made with the left hand (57.5%) or both hands (25%).

A number of interesting patterns of behaviour emerged as a result of introducing the fishing pools. The method of capture, usually involved "tracking" a particular fish (separated from the main school). The successful monkey usually retained its catch, despite being watched and followed by conspecifics, and attempted "thefts" being made. Prior to eating, monkeys typically removed the scales (by rubbing the fish on preferred tree branches), bit the head off, and disembowelled the fish. Whilst, the catcher rejected the entrails, other monkeys often ate these portions.

Apart from behaviours related to fish capture and feeding, other behavioural changes were also observed. King and Norwood (1989) suggest that the introduction of live fish in pools may lead to interesting and complex social interactions in monkey groups, including: "Dominance, cooperation, imitative learning, food sharing, social roles of skilled fisher-monkeys, and patterns of attentiveness among monkeys" (p.112). The fishing opportunity provides squirrel monkeys with a challenge that requires concentration, skill, and the expenditure of time and effort. Further, this form of enrichment is cost effective, since goldfish, bowls and wading pools are relatively inexpensive.

Some may criticise this study for facilitating an "unnatural" behaviour. However, "natural" patterns of behaviour emerged concurrently, and mental and physical stimulation eliciting foraging and problem solving skills was provided. The provision of live fish in water pools might be considered for squirrel monkeys in zoo enclosures (provided fish are not included in a "no live-prey" policy). This form of enrichment could also be considered for other primate species, such as chacma baboons, which have been observed to fish in Namibian desert water holes (Hamilton & Tilson, 1985).

5.6.5 PROVIDING LIVE PREY (FISH) TO FISHING CATS

Shepherdson, Carlstead, Mellen and Seidensticker (1993) provided a ten-year old captive-born female fishing cat with the opportunity to capture live fish prey. She was housed at the Metro Washington Park Zoo, in an indoor, glass-fronted, off-exhibit enclosure (4.9m x 5.2m x 2.4m). The enclosure contained a number of elevated platforms constructed of artificial gunite rock, and two pools (1.5m x 0.6m x 0.2m & 1.8m x 0.6m x 0.15m), with a small waterfall flowing into the larger pool. Hiding places for the fish in the pool consisted of loose rocks. Every morning (between 8.30 & 9.30a.m.) the cat was moved into a holding area, where she was fed her daily meal of 0.4kg of Hills Prescription Diet (a processed meat diet). Whilst she was eating, her enclosure was cleaned and hosed by the keeping staff. The only exposure this cat had to live fish was three times during a pilot study, which had been conducted two months earlier.

The study conducted by Shepherdson et al (1993) was run over two months, in three phases (two baselines). During the first baseline (six non-consecutive days), the fishing cat was fed in the usual manner. The second phase (six non-consecutive days) involved the introduction of the live fish as behavioural enrichment. On these days the cat was still fed in the adjoining holding area, whilst the enclosure was cleaned and hosed out. Ten to twenty minutes prior to the cat's re-entry, one or two live fingerling trouts or goldfish (5cm to 8cm in size) were placed in one or both of the pools. According to Shepherdson et al (1993), by the time the cat had re-entered her enclosure, the fish had explored and become acclimatised to the pools. The second "post-fish" baseline phase was run on the day after live-fish feeding, when the feeding regime was the same as during the first baseline. After the fourth occasion on which live-fish were provided, behavioural observations were made on day three, six, seven and eight, in order to determine how long it would take for the cat's behaviour (following live-fish feeding) to return to the initial baseline levels.

Behavioural observations were made twice daily, at 10a.m. (30-minutes after feeding) and 3p.m. (1,000 hours & 1,500 hours, respectively). Observation periods were thirty minutes long, with behaviours scored by instantaneous point sampling at 30-second intervals. Behavioural categories included stereotypic pacing, locomotion, sleeping, resting/alert, sniffing, grooming and hunting- defined as "active and visual searching for fish in the pool" (Shepherdson et al, 1993, p.205). The cat's location in the enclosure was also recorded. On "fish" days, the cat's behaviour was recorded on videotape.

During the first baseline condition, the fishing cat was inactive for 91.8% of observation time, and sleeping accounted for 66.8% of this inactive time. During the live-fish phase, sleeping dropped to 20.9%, with increased hunting replacing the inactive behaviour. Sleeping increased to 32.5% during the post-fish baseline, and slightly less than 20% of the fishing cat's time was still spent hunting. That is: "behavior had not returned to baseline levels 24 hours after fish presentation" (Shepherdson et al, 1993, p.207). During the eight-day observation period, following the fourth live-fish feeding, hunting gradually declined, but did not cease completely even after eight days. The cat slept considerably less than during the first baseline period.

Behavioural diversity was measured using the Shannon index, with higher values indicating greater diversity. The highest value was obtained for live-fish days (0.55), and the lowest for the first baseline (0.31), indicating that behavioural diversity had increased upon presentation of live-fish. Use of the enclosure space was evaluated by the "spread of participation index (SPI)", with the value of 1 representing minimum utilisation of the enclosure (staying in one area only), and 0 representing maximum utilisation (using all areas of the enclosure equally; Shepherdson et al, 1993). Not surprisingly, enclosure utilisation was lowest during the first baseline, with 86% of the cat's time spent in 16.6% of the enclosure, which was the preferred sleeping or resting area (SPI of 0.84). Use of the area containing the pools increased on live-fish days, becoming the area of "most intense use" (SPI of 0.62). Maximum utilisation of enclosure space occurred on the post-fish baseline days, when the cat spent time resting and hunting in different areas (SPI of 0.4).

Perhaps the most interesting findings are the topographical descriptions of the hunting or fishing behaviour. A pattern of predatory behaviour emerged upon analysis of videotapes and notes. On the days when live-fish were presented, and on post-fish baseline days, the cat immediately approached the pool, sat or stood next to it, and "stared intently" into the pool.

> "On sighting a fish, she entered the water and attempted to follow the fish's movement with her head, fishing with a paw under rocks if it disappeared" (Shepherdson et al, 1993, pp.207-208).

If the fish continued to remain out of sight for more than a few seconds, the cat moved back onto land, and again took up a watchful position from the side of the pool.

> "If the fish failed to escape under a rock, she attempted to pounce on it with both forepaws held together. At no point was she observed to strike the fish out of the water...but she did submerge her head several times" (Shepherdson et al, 1993, p.208).

In the wild, Breeden (1989) observed fishing cats diving for fish:

> "The cat positioned herself on a log overhanging the water and held her nose just a short distance from the water surface, presumably to cut down on refraction. Then she launched herself head first into the water grabbing the fish in her mouth" (Kitchener, 1991, p.73).

Shepherdson et al (1993) also provide information on how the fish were consumed after successful capture. If a fish was captured via the "pounce", it was then picked up in the cat's mouth, and taken onto land. The smallest fish (<5cm in size) were typically swallowed, whereas, the cat typically ate the head first of larger fish, before consuming the body tail first. Whilst consuming the body of one fish, the cat "squeezed out" the intestines as she ate. Captured fish were not always eaten immediately, with some carried back to the pool and then "recaptured". The fish were all successfully captured within 24 hours of release, with some fish being caught in less than five minutes, and others taking up to 5 hours to be caught. Capture time: "seemed to depend on how well the fish evaded capture, rather than on the cat's increasing experience" (Shepherdson et al, 1993, p.208).

The results of the fishing cat study, led Shepherdson et al (1993) to conclude that: "Provision of live-fish to small felids can result in long-lasting and beneficial behavioral changes: increases in activity, behavioural diversity, and space use" (p.215). As these researchers point out, the live fish were introduced after the cat had already consumed her daily quota of food. That is, she was presumably "satiated". However, the provision of live prey: "increased active behaviors associated with the search, location and capture components of predation", and decreased "less desirable" sleeping and inactivity (Shepherdson et al, 1993, p.212). Further, the behavioural changes were maintained over a number of days (up to eight), more of the enclosure was utilised by the cat, the implementation of the enrichment technique was simple and presumably relatively inexpensive. Shepherdson et al (1993) suggest that provision of fish can be an "efficient" and "effective" enrichment technique (p.212).

5.6.6 PLAY OBJECTS AND SWIMMING POOLS FOR CRAB-EATING MACAQUES

Another interesting source of behavioural enrichment for monkeys comes from a laboratory situation. Gilbert and Wrenshall (1989) discuss a variety of play objects, and a portable swimming pool in the playroom of a behavioural toxicology laboratory in Ottawa, Canada. The playrooms included stainless steel perches, swings, shelves and a "jungle gym". Finding objects that were indestructible and an appropriate size was a matter of "trial-and-error". Golf balls were too small and could be cracked open. Rawhide dog bones became unsanitary and hard to clean. Fisher-Price Butterfly Balls (large with colourful butterfly inside) broke when dropped from a height of six feet. "Wolf" and "regular" size hard nylon "Nylaball" balls were popular with the monkeys and easily cleaned. Red and black rubber "Kong Toys" (various sizes) specifically designed for monkeys provided new challenges when filled with raisins or other food. Stainless steel chain-segments and feeding-bowls (for cats) provided opportunities for "endless games". Gilbert and Wrenshall (1989) point out that natural substrates such as wood-chip litter may not be suitable in monkeys used for toxicology studies, since pesticide residues may be present in the wood-chips.

The most interesting behavioural enrichment technique described by Gilbert and Wrenshall (1989) is the provision of a portable swimming pool in the monkey playrooms. The pool consisted of a stainless steel frame on wheels, with 3/8th inch thick Plexiglas sides (121cm x 80cm x 78cm). The younger monkeys adapted quickly and easily to water and were "instinctively good swimmers", whilst the older monkeys took longer (Gilbert & Wrenshall, 1989, p.251). Placing raisins at the bottom of the pool resulted in monkeys swimming "with their eyes open looking for the raisins and playing with each other" (Gilbert & Wrenshall, 1989, p.251). The pool was considered a great success, since play was facilitated, activity was increased and fur was kept clean. Pools of a similar size (but more naturalistic in appearance) might be considered for zoos that house this species of monkey, since in the wild these "crab-eating" monkeys are no strangers to water, inhabiting "Forest edge, swamp, banks of water courses and coastal forest" (Rowell, 1984, p.88). Swimming pools may also be considered for other primate species, such as, talapoins which: "are said to dive for fish" (Rowell, 1984, p.80).

5.6.7 OBJECTS FOR CHIMPANZEES AT QUÉBEC ZOO

Paquette and Prescott (1988) investigated the effect of presentation of novel objects upon the behaviour ("normal" & aberrant) of four young (7 & 8-year old) hand-reared chimpanzees at the Jardin Zoologique du Québec. The objects were plastic or rubber children's toys, and one object in each experimental condition squeaked when squeezed. For the baseline condition (0 novel objects presented), two rubber balls and a tyre were present in the playroom (enclosure). The other experimental conditions involved presentation of one, three, six or ten novel objects for eight-hours per day, until the mean object manipulation frequency of the group fell below 15% of the total session time (with an interval of three days without objects between conditions).

The percentage of total time for the first three days of each condition showed a marked increase for the manipulation of objects. During the baseline condition, only 8% of the group's time was spent manipulating the balls and tyre, whilst 37% of their time was spent inactive. By contrast, when ten objects were present, 54% of the group's time was spent manipulating the objects, and only 10% (16% for one subject) was spent inactive. Self-grooming and abnormal behaviours (*e.g.*, licking & coprophagia) also decreased when novel objects were present. Importantly, aggression did not increase, even when the number of objects presented were less than the number of subjects. However, the more dominant individuals secured more objects, which was reflected in higher frequency of object manipulation.

Habituation occurred more rapidly if fewer objects were present. That is, the criterion of 15% manipulation frequency was reached within three days if only one object was present, whereas it took seven days if ten objects were available. Paquette and Prescott (1988) suggest that the habituation period could be extended by reducing the daily exposure period (*i.e.* < 8 hours) or by increasing the interval between object presentations (*i.e.* > 3 days). They conclude that presentation of toys- large, bright and moveable objects (particularly ones that produce auditory or visual changes)- can enhance the environments of captive chimpanzees (resulting in decreases in inactivity & abnormal behaviours).

5.6.8 OBJECTS FOR CHIMPANZEES AT COPENHAGEN ZOO

In 1984, the “Ape Jungle” was opened at Copenhagen Zoo. An activity room was built between the chimpanzee and lowland gorilla exhibits, which incorporated a number of feeding enrichment devices (Lunding Andersen, 1987). The two species take turns in using the activity room (although, Lunding Anderson only refers to the chimpanzees using it). This activity room proved so popular with the zoo visitors, that the zoo was forced to stop announcing when the chimpanzees would be given access to this area, as there was not enough room to accommodate the “inrush” of visitors to the viewing areas (Lunding Andersen, 1987, p.49).

Unlike the simple balls and toys provided to chimpanzees at Québec Zoo (& elsewhere), the enrichment devices used at Copenhagen Zoo were far more complex and innovative. Furthermore, the devices were numerous. Metal “sunflower castors”, which dropped sunflower seeds and other grains if turned upside down, were suspended within the chimpanzee and gorilla enclosures. An acrylic tube, simulating a long “hollow tree trunk” (with acrylic blocks inside to make the task more difficult by creating obstructions), was filled with fruit and nuts, which the chimpanzees had to push to the ends with branches. A “nut maze” attached to a tree could be turned, and eventually a nut would fall out (with more complicated partitions creating a more difficult “labyrinth”). Wooden “raisin blocks” were provided, with raisins stuffed into small holes, which could be removed with the aid of thin twigs. A “shaking table”, with an acrylic lid and internal maze structure, allowed the chimpanzees to obtain sunflower seeds or grains if the table was shaken (Lunding Andersen, 1987).

Other enrichment devices, which were later installed to increase the novelty of the activities, were the “fruit organ”, made up of a number of tubes holding balls and fruit, which required the chimpanzees to use a branch to manipulate fruit past the obstructing balls, and the “tilting table”, which had to be tilted to allow the fruit to role to the centre, and out through a hole (Lunding Andersen, 1987). Although the feeding devices are innovative, there are no published studies or data to show whether use of this activity room has resulted in less aberrant behaviours or increased the range of behaviours. These enrichment devices (including diagrams) will be discussed further in Chapter 10.

5.7 CAPTIVE ENVIRONMENTS DESIGNED AROUND THE BEHAVIOURAL NEEDS OF THE ANIMALS

Obviously, the ideal captive environment provides challenges and appropriate stimulation, which meets the behavioural needs of each species. This section will discuss the optimal captive environments for chimpanzees and caracals.

5.7.1 OPTIMAL CAPTIVE ENVIRONMENTS FOR CHIMPANZEES (PRIMATES)

Behavioural enrichment for chimpanzees in zoos aims to allow the chimpanzees to behave as closely as possible to those living in the wild. This is achieved by providing the zoo chimpanzees with a more challenging and stimulating environment that elicits "natural" chimpanzee behaviours. Thus, behavioural enrichment seeks to increase the range and diversity of natural behaviour patterns, as well as attempting to reduce or eliminate aberrant behaviours (Shepherdson, 1989a). To assess whether behaviour is natural or aberrant, it is vital to have information on the behaviour of chimpanzees in the "wild", and fortunately, there are many excellent books and articles to turn to (*e.g.*, Chapman & Wrangham, 1993; Goodall, 1986). The points discussed in this section are also relevant to other primate species.

As mentioned previously, zoo chimpanzees tend to spend less time and effort in foraging for food, than wild chimpanzees. As a result, many behavioural enrichment studies aim to provide food in more naturalistic or challenging ways. That is, the chimpanzees have to search for food, or use their exploratory and manipulative skills to gain access to food sources. ***Feeding enrichment*** is not the only option for creating an optimal zoo situation for chimpanzees. After all, chimpanzees in the wild do not spend the whole day engaged in foraging. Natural behaviour patterns, other than feeding alone, can be elicited by other forms of enrichment. Social, physical, sensory and occupational enrichment are all equally important for chimpanzees in zoos (Bloomsmith, 1992). The different categories of enrichment proposed by Bloomsmith (1992) are not always mutually exclusive, since some forms may fit into more than one category, but separating the various forms gives some idea of the many options available, and indeed may point to areas of neglect in some zoos.

Social enrichment for chimpanzees is perhaps one area that has been poorly addressed by some zoos. Chimpanzees in the wild live in large social groups, and yet even today, chimpanzees can be found housed alone, in pairs, or in very small groups. Of course, not all zoos have the space, facilities, staff and finances to care for a large group of chimpanzees. The days of keeping one or two chimpanzees in a zoo, purely as a display species, are vanishing. If a zoo cannot comfortably house chimpanzees as a social group, perhaps it should not house chimpanzees at all. This is a decision that many zoos have had to face, for the sake of chimpanzees. Social contact, and the opportunity to engage in a variety of complex social interactions, is important for a chimpanzee's psychological well-being. Young chimpanzees engage in play and contact behaviour with mothers, siblings and adult males (Bloomsmith, 1992). In a study examining interactions between adult male and juvenile captive chimpanzees (<6 years of age), Bloomsmith (1989) found that on average, 10.7 interactions took place per hour. Most of these interactions took the form of play behaviour, with only 2% of the interactions being agonistic in nature. This is important from an animal management perspective, since it allows adult males to live in a large social group in captivity. However, as Bloomsmith (1992) points out, the prosocial relationships that can develop between adult males and juveniles in captivity, do not reflect a species-specific behaviour, since in the wild males in general do not interact with juveniles to the same extent. For a zoo infant chimpanzee to develop into an adult that displays natural behaviour patterns, he or she should ideally be mother-reared in a social group, within a spacious and stimulating environment.

Physical enrichment ensures that zoo chimpanzees are housed in well-designed and spacious enclosures that allow the chimpanzees to engage in a variety of activities. Maple (1979) discusses both habitat and activity requirements for adequate housing of chimpanzees, and other Great Apes. Wherever possible, zoos should aim for optimal rather than simply adequate housing. There should be utilisation of vertical space, with the provision of climbing structures, ropes and elevated areas, or platforms. Areas of cover are important, to give chimpanzees refuge and privacy from the public, as well as protection from the heat or cold. The "flight distance" requirement must also be met, allowing spacial separation (at least 20 feet) from human intrusion. Foraging, activity and play are all requirements that must be taken into account, if chimpanzees are to engage in healthy and natural behaviours. Various objects can be introduced into the chimpanzee enclosure to encourage manipulation, exploration and play.

The outdoor enclosure is not the only physical environment that zoo chimpanzees find themselves in. At night, they have access to night rooms, or indoor sleeping quarters. Since chimpanzees in the wild sleep in trees, in fresh leafy nests they build for themselves every night, zoos must provide their chimpanzees with plenty of bedding material (see Figure 5.7). This may include shredded paper, straw or wood wool. Shredded paper appears to be the softest, cleanest and most absorbent of the three. The chimpanzees use such bedding to build a comfortable nest to sleep in, above ground on shelf areas, if they are available. Again various objects or tasks can be provided for activity in these indoor areas.

As Bloomsmith (1991) points out, the ***sensory environment*** of chimpanzees is too often forgotten. This is particularly important for chimpanzees that are housed indoors or alone instead of in a social group. Such indoor or solitary environments can deprive chimpanzees of interesting and varied sights, sounds, smells and tastes. If the chimpanzee's welfare and health is important, then they must be provided with different sights and sounds, smells and tastes. Although, the way of providing this sensory stimulation may be far from natural, it helps alleviate boredom. It should be added, that the following forms of enrichment are mainly for use in laboratory, rather than typical zoo situations. Sights and sounds can be provided by slides, television, mirrors for seeing around corners, videos of other chimpanzees, and audio recordings of music or other sounds (Bloomsmith, 1991).

Occupational enrichment is one way of providing chimpanzees with cognitive challenges. In other words, problem solving skills and strategies are required. Using a computer and software, or various mechanical devices, is one form of such enrichment (Bloomsmith, 1991). One might argue, that a chimpanzee punching the keys of a computer keyboard is not displaying species-typical behaviour, but the accompanying problem-solving behaviour is appropriate, since survival in the wild requires problem-solving skills (Bloomsmith, 1991).

Feeding enrichment has received much attention in the scientific literature, with a variety of alternatives suggested for providing food to chimpanzees in more naturalistic or challenging ways. The enrichment technique can be as simple as scattering and hiding food, or increasing the number of feeds per day, or it can take the form of a complex maze or simple food puzzle (Figure 5.8). Irrespective of the complexity of technique used, all aim to increase the time spent foraging, and require chimpanzees to use foraging skills, that are not used if the food is just placed in front of them.

5.7.2 OPTIMAL CAPTIVE ENVIRONMENTS FOR CARACALS (FELIDS)

There does not appear to be any behavioural enrichment work directed specifically at caracals. However, a number of enrichment techniques have been used for other medium or small sized felids (*e.g.*, servals, fishing cats & leopard cats). A substantial proportion of the 1997 *International Zoo Yearbook* is devoted to articles concerning behavioural enrichment techniques for felids. Although many of the suggestions for enrichment are concerned with alternative feeding methods, the underlying theme throughout is the emergence of an integrative approach to enrichment. As Mellen and Shepherdson (1997) point out, a biologically appropriate captive environment involves researchers being familiar with a species' natural habitat and behavioural repertoire in the wild. Optimal captive environments for felids provide appropriate social structures, suitably complex enclosures, increased interactions with keepers, positive reinforcement training, more natural diets and alternative feeding methods, and novel objects and scents (Mellen & Shepherdson, 1997). Just adhering to a single enrichment method is not recommended, since cats quickly habituate to novel objects, scents or changes to enclosures.

Figure 5.7. Hessian sacks can be tied securely throughout a tall tree, to provide inexpensive yet effective nests for captive chimpanzees (photo of orphaned chimpanzees at rest in "sack" nests in Burundi taken by Debby Cox in 1995)

Figure 5.8. Ice blocks and simple food puzzles or blocks (with holes filled with food) are also inexpensive enrichment techniques that have been used at sanctuaries for orphaned chimpanzees in Africa (photos taken by Debby Cox in Burundi in 1994 & 1995)

Mellen and Shepherdson (1997) stress that the most successful enrichment techniques are those that "most closely mimic aspects of the animal's natural environment" (p.195). Since the introduction of Markowitz's (1982) "ingenious" operant tasks, the:

> "scope of environmental enrichment has since expanded to include almost any variable that impinges upon the perceptual world of an animal in captivity" (Mellen & Shepherdson, 1997, p.192).

Typically, recent research focuses on the provision of naturalistic substrates, climbing structures, foraging opportunities, novel food, and opportunities to learn new behaviours and engage in intellectual tasks. That is, an integrated approach provides captive "animals with some of the same behavioural opportunities that their wild conspecifics would experience" (Mellen & Shepherdson, 1997, p.192).

Despite the fact that most felids are solitary, zoos continue to house cats as pairs or trios. This can lead to breeding problems and increased pacing. Mellen and Shepherdson (1997) assert that in most cases cats should be housed singly, and only introduced to a member of the opposite sex for breeding or enrichment purposes. A rotation system can be used to utilise space, with different cats spending time on and off exhibit. These researchers also recognise the importance of good keeper-animal bonds. Jill Mellen and her coworkers have found that reproductive success is greater, and pacing is less, in cats which spend more time interacting with their keepers- through mesh or fence (Mellen & Shepherdson, 1997).

A negative relationship between time spent pacing and exhibit complexity appears to exist for small cats (see Figure 5.2 for pacing in a large cat). That is, pacing reduces with increased complexity. Mellen and Shepherdson (1997) refer to studies by Mellen and coworkers, which found that pacing was reduced (or even non-existent) for cats housed in enclosures that provided seven or more physical barriers, which the cats could use to hide from each other. Enclosures should also provide aerial pathways (*e.g.*, logs suspended by chains, which can be moved around), areas of subdued lighting (*e.g.*, by using netting over or around the enclosure), and new layers of soft mulch on the ground every couple of months.

Mellen and Shepherdson (1997) suggest that positive-reinforcement training has only recently been recognised as a method that can facilitate veterinary and husbandry procedures as well as provide a means of enrichment. That is, it makes use of an animal's cognitive abilities, which may enhance psychological well-being. They refer to a Siberian tiger at Portland zoo that has been trained to present different parts of his body for inspection by staff. Between fifteen and thirty minutes a day are set aside for positive reinforcement training, with portions of his daily food allowance used as the reinforcer. This may appear quite new in the published literature, but Taronga Zoo employed this technique (in the 1980s) to train a diabetic chimpanzee to present her shoulder for her insulin injections (personal observation).

5.7.3 ENRICHING PRERELEASE ENVIRONMENTS FOR CAPTIVE-RAISED ANIMALS INTENDED FOR REINTRODUCTION

Although the goal of reintroduction or release to the wild may be "overly optimistic" (Snowdon, 1991), some captive-born animals have already been reintroduced to the wild (*e.g.*, golden lion tamarins in Brazil, Castro, Beck, Kleiman, Ruiz-Miranda & Rosenberger, 1998; black-footed ferret, Miller, Biggins, Vargas, Hutchins, Hanebury, Godbey, Anderson, Wemmer & Oldemeier, 1998). It should be pointed out, that researchers often appear to use the term reintroduction as referring to any release of animals back to the wild. However, the golden lion tamarin project is actually a "reinforcement/ supplementation" strategy. The four main terms used to describe "re-introduction" projects, as defined by the IUCN (the World Conservation Union, 1995; 2000), are as follows:

- **Re-introduction** – an attempt to establish a population in an area that was once part of the range of the species but from which it has become extirpated or extinct (*e.g.*, Père David's deer, Arabian oryx, & swift fox);
- **Reinforcement of an existing population (or Supplementation)** – the addition of individuals to an existing population of the same species (*e.g.*, golden lion tamarin);
- **Conservation introductions (or Beneficial or Benign introductions)** – an attempt to establish a species, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat and eco-geographical area – if there is no remaining area left within the species' historic range (*e.g.*, endangered birds on off-shore islands in New Zealand);
- **Translocation** – deliberate and mediated movement of wild individuals or populations from one part of their range to another.

Rearing animals in an environment that is as close to natural as possible is recommended for individuals that are intended for release to wild environments (Miller et al, 1998). Enrichment of pre-release environments can ensure that the two main (interrelated) factors linked to survival of captive-raised animals in wild environments, is enhanced (Miller et al, 1998). These two factors are: proficiency of skills needed to survive (gained from earlier experience); and flexibility to learn and adapt skills in the constantly changing natural environment (Miller et al, 1998).

An enriched environment should attempt to reproduce natural cues and recreate a natural environment, but that is not always possible, and may be almost impossible. For example, Miller et al (1998) posit that it may be difficult to restore learned behaviours (*e.g.*, those that are culturally transmitted & depend on the correct cues at critical periods of development) or transmit some vital information (*e.g.*, migration routes). However, if captive animals are reared in an enriched environment, the "risk of missing specific stimuli during an early sensitive period" may be reduced (Miller et al, 1998, p.100).

Castro et al (1998) posit that behavioural training for reintroduction could be more effective if stress components are added. That is, they maintain that free-ranging animals in natural environments are exposed to stressful experiences, and if natural habitats are to be emulated in pre-release environments, then short-term threatening events could be beneficial. Castro et al (1998) also point out that provisioning released animals with food and providing post-release training further increase a captive-reared animal's chance of survival in natural habitats.

5.7.3.1 OPPORTUNITIES FOR SOCIAL INTERACTIONS: FACILITATING SOCIAL AND OBSERVATIONAL LEARNING

Snowdon (1991) stresses that if many of the important skills of a particular species are acquired through observational learning and social reinforcement, then an adequate captive environment must provide the relevant opportunities. Parental care, predator recognition and avoidance, prey recognition and capture, social communication and foraging are all behaviours that require observational or social learning (Miller et al, 1998; Snowdon, 1991).

Primates, in particular, acquire parental care skills by observing and interacting with other conspecifics (parents & offspring). Juvenile chimpanzee females gain valuable mothering skills by observing their mothers rearing younger siblings (Goodall, 1986). Snowdon (1991) states that cotton-top tamarins: "must have direct experience with two successive sets of infants in order to acquire parental competence", which means that captive environments must provide enough space to house a large number of these monkeys (p.106). If marmosets and tamarins do not have prior experience with infants, they may bite or push infants off their backs, or females may not nurse them in the correct position (Snowdon, 1991).

If animals are to survive in natural environments, they must recognise and avoid predators. Captive-born monkeys (*e.g.*, rhesus macaques & tamarins) may show few fear responses to snakes, which may also readily habituate, whereas wild monkeys show strong fear responses, which do not habituate (Snowdon, 1991). These monkeys learn the appropriate fear of snakes through observation of conspecifics. Vervet monkeys acquire and use appropriate predator alarm calls (& other vocalisations, *e.g.* grunts) by observational learning (adult modelling) and social reinforcement (Cheney & Seyfarth, 1990; Snowdon, 1991).

Predator avoidance skills (*e.g.*, freezing, fleeing or fighting) may be largely innate, but even these can be reduced by "depauperate" environments (Miller et al, 1998, p.102). Miller et al (1998) suggest that pre-release exposure to mock or real predators (avian & terrestrial) may improve antipredator reactions and skills in a number of species of birds and mammals. However, these researchers stress that the potential predator or stimulus: "may have to be presented in such an unnatural context that animals may not recognize the cue in a natural setting. In addition, if exposure is frequent without sufficient aversive conditioning, there is a danger of habituation to the predator" (Miller et al, 1998, p.103).

Miller et al (1998) stress that a number of carnivore species must be exposed to prey items as juveniles, or they do not kill efficiently as adults. However, simply allowing captive animals to kill prey items in their captive environments may not increase survival rates after release to natural environments, since the capture situation is far too simple. As Miller et al (1998) point out, an efficient predator must learn to search for prey in appropriate places, use effective search strategies, know when to attack, use specialised hunting techniques, and have an appropriate "search image". Each unsuccessful hunt tires and weakens predators, which make subsequent kills more difficult. Therefore, captive-reared carnivores that are intended for release must be provided with enriched pre-release environments that allow them to locate and capture prey.

Promoting appropriate foraging skills may be one of the most challenging tasks for captive management. Primates must be able to find food that is seasonal and distributed in patches scattered over large areas (Goodall, 1986). Wild chimpanzees may feed on 200 different plants in a year (Goodall, 1986). They must be able to handle whole fruits, and therefore, pre-release environments must not provide food that is cut-up into small chunks. Snowdon (1991) also emphasises that marmosets excavate holes in trees to extract sap, and captive environments should provide sap feeders.

Post-release movements (distance travelled & dispersal from the release site) of captive-reared animals appear to be affected by whether the animals have been cage-reared or pen-reared (Miller et al, 1998). If animals disperse too far, they may be more susceptible to predators. If they don't disperse far enough, they may not find enough resources. Birds may also choose post-release nest sites (elevated or on the ground) according to where their own nests were located in captivity (Miller et al, 1998). This highlights the fact that researchers must take every aspect of the pre-release and post-release environments into account.

5.7.3.2 OPPORTUNITIES FOR ENVIRONMENTAL INTERACTIONS: FACILITATING PHYSICAL SKILLS

As Snowdon (1991) points out, the actual structure of the physical environment must allow expression of species-typical behaviours. For example, arboreal monkeys must be provided with a complex environment, consisting of different elevated levels, that helps develop the "careful eye-limb coordination to move in a three-dimensional environment" (Snowdon, 1991, p.107). A natural forest environment would include trees and plants of different sizes and heights- some flexible, others unmoving- and monkeys would at times have to leap between branches, which requires the ability to accurately judge distances. They would also have to find their way through a canopy environment (which may be dense), and be able to climb up and down tree trunks of varying diameter. Survival in the natural environment depends on well-developed locomotor skills. Therefore, a pre-release environment must be complex, use different wood and fibre structures, and provide trees (or climbing frames) of different diameters and flexibility. Importantly, the environment must be changed relatively frequently, in order to remain novel, provide challenges and "sanitize" the environment (Snowdon, 1991).

Miller et al (1998) maintain that mammals, which experience environmental complexity at an early age: "are able to better employ cues in problem solving" (p.101). Laboratory experiments with rats and ferrets have shown that experience with enriched environments leads to better food-finding and prey-capture abilities, less time being spent out of burrows (reducing risk of predation), and increased skill in moving through unfamiliar mazes (Miller et al, 1998). Miller et al (1998) stress that:

> "when animals scheduled for reintroduction are raised in an enriched environment, they can acquire beneficial neural changes that can increase problem-solving abilities later in life. This process could enhance survival for a captive-raised individual that is introduced into a novel and dynamic wild environment" (p.101).

Miller et al (1998) conclude that researchers must systematically test factors that could affect survival after release. Laboratory studies have already provided valuable information about effects of rearing animals in impoverished or enriched environments. Zoo studies can provide information about behaviour in naturalistic enclosures. Field studies should determine which factors are the most ecologically relevant and which behavioural traits must be performed efficiently. Importantly, Miller et al (1998) emphasise that reintroductions must be monitored intensively, so that mortality, movements, and breeding success can all be determined after release. “Postrelease analysis of behavioural traits may, therefore, provide important information about release strategies and contribute clues to increase survival in future attempts” (Miller et al, 1998, p.107).

5.8 AN INTEGRATIVE APPROACH TO BEHAVIOURAL ENRICHMENT: COMBINING NATURALISTIC AND MECHANICAL TECHNIQUES

Forthman Quick (1984) provides an analysis of the "natural versus unnatural" debate that has emerged in the field of environmental enrichment, as a result of two seemingly incompatible approaches. As already mentioned, the techniques used for environmental enrichment fall into two major categories, namely, naturalistic or mechanical. Opponents of the mechanical approach suggest that mechanical devices are "unnatural". Forthman Quick (1984), however, points out that the two approaches are not mutually exclusive, concluding that an integrative approach or "an integration of feeding apparatus with a more naturalistic physical layout" would be beneficial (p.69). In her analysis of the "natural" versus "mechanical" approach, Forthman Quick (1984) separates the debate into four basic issues: natural versus unnatural activities; free versus earned food; altering activity levels; and novelty versus predictability. To arrive at the solution of an integrative approach, a brief discussion of these four issues is necessary.

The suggestion that the mechanical approach is "unnatural" is based on the premise that conditioning techniques and the operation of mechanical devices are unnatural. However, the assumption that: "conditioning has no influence on animals as they learn where, when, and how to find food, shelter, and mates in the wild" is certainly fallacious, since: "some combination of operant and Pavlovian conditioning occurs routinely in all creatures, humans included" (Forthman Quick, 1984, p. 67). Few would argue that zoos and researchers should employ naturalistic methods of enriching environments wherever possible. However, if the cost of redesigning a zoo enclosure is prohibitive or not possible (*e.g.*, in a lab situation), then an alternative must be considered. This might involve using a less naturalistic mechanical device as a means of improving a sterile environment, and eliciting more "natural" patterns of behaviour (Forthman Quick, 1984).

Forthman Quick (1984) suggests that concentrating on a "simplistic dichotomy between natural and unnatural" may be inappropriate, since captivity itself is an "unnatural" state (p.68). Whilst zoo enclosures should aim to simulate natural habitats, this alone may be insufficient to ensure the psychological wellbeing of the animal (see Figures 5.9 – 5.11). Forthman Quick (1984) does not use the term "psychological wellbeing". However, this concept is addressed with her insistence that captive animals be:

> "healthy and happy; this can be defined and measured objectively as maintenance of good physical condition, display of ecologically valid behavior, with concomitant absence of stereotypies, and successful reproduction" (p.68).

"That free food (the zoo norm) is unnaturalistic is a belief held in common by both groups" (Forthman Quick, 1984, p.68). Animals in their natural environments must actively hunt or search for food, with considerable time and energy expended. The mechanical and naturalistic approaches may agree on the need to increase foraging, but they differ in the techniques used. Forthman Quick (1984) separates the techniques into two groups. One involves interaction with responsive apparatus, whilst the other involves natural methods of food presentation (*e.g.*, scattering food throughout substrates for primates, providing browse for primates & herbivores, providing carnivores with whole carcasses, & providing insectivores with live crickets & moths to hunt).

Forthman Quick (1984) addresses the issue of altering activity levels by focusing on two criticisms aimed at the mechanical approach by fervent supporters of the naturalistic approach. The mechanical approach has been accused of concentrating on foraging and locomotion, to the exclusion of other behaviours, such as reproduction, communication, aggression and parental behaviours (Hutchins et al, 1978a, 1978b, 1979). However, Forthman Quick (1984) points out that these other behaviours: "do not usually occupy as much of a wild animal's daily time budget as do foraging and locomotion" (p.68). The mechanical approach has also been criticised for its: "indiscriminate or inappropriate use of feeding devices" (Forthman Quick, 1984, p.68). The classic example of a mechanical feeding device leading to problems and aberrant behaviour is that of the "hunting" apparatus set up for pumas at Brookfield zoo, where the artificial prey was "hunted" up to 200 times per day (Tudge, 1991, p.220). Forthman Quick (1984) maintains that the abnormal response rates elicited by the apparatus may have been reduced if the schedule of reinforcement had been altered. Thus, it is not the philosophy behind the use of machines to stimulate foraging behaviour that is at fault, but rather the actual application of the devices used (Tudge, 1991).

Information concerning hunting success rates in the wild for a particular carnivore species could aid in the selection of an appropriate schedule of reinforcement. In natural habitats, the success rate for various cat species can range from 8% to 82% (Kitchener, 1991, p.86). In addition:

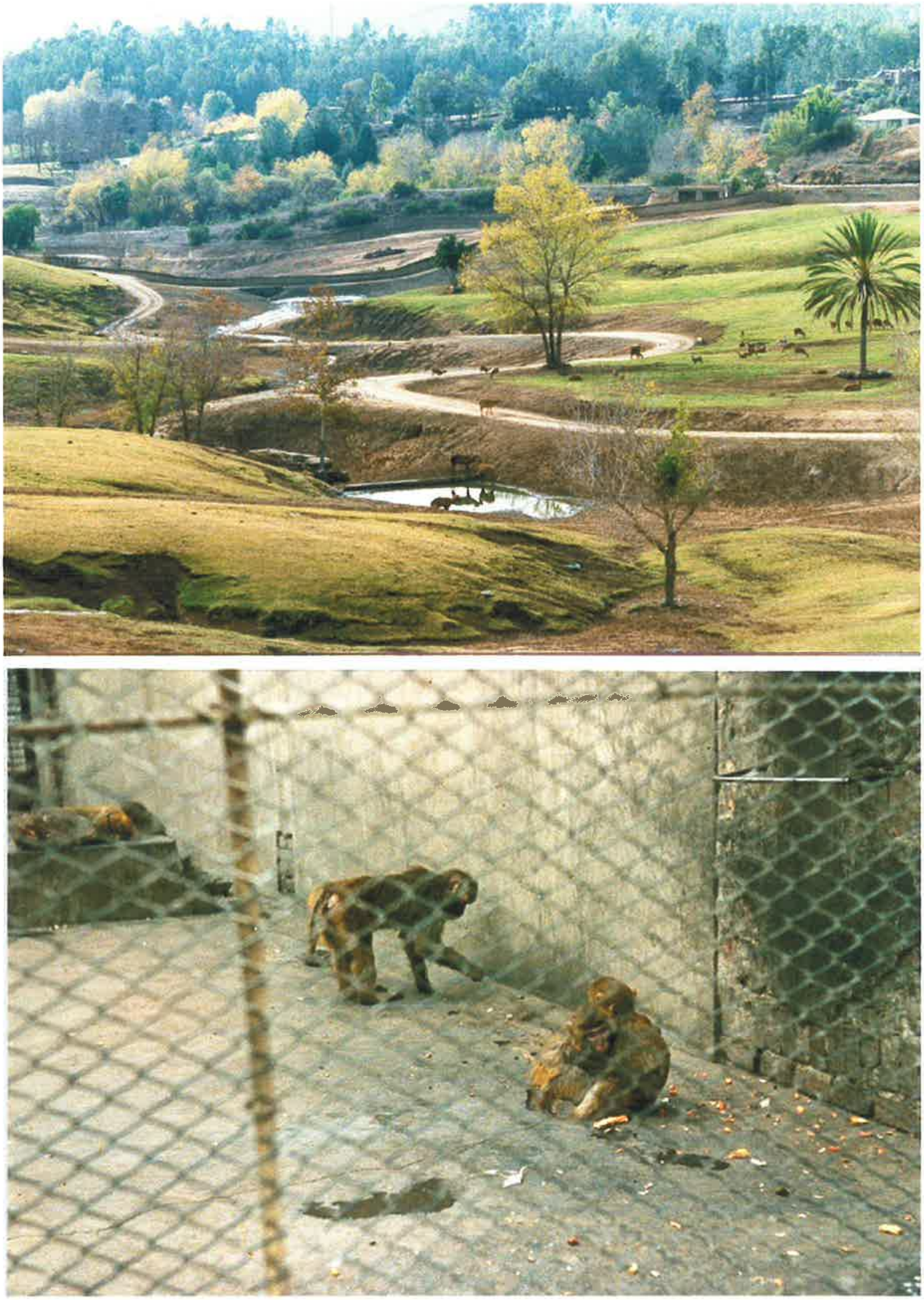


Figure 5.9. The open-range "naturalistic" San Diego Wild Animal Park (Dec. 1991) provides a stark contrast to a barren macaque enclosure in China (taken by Anita O'Hair)

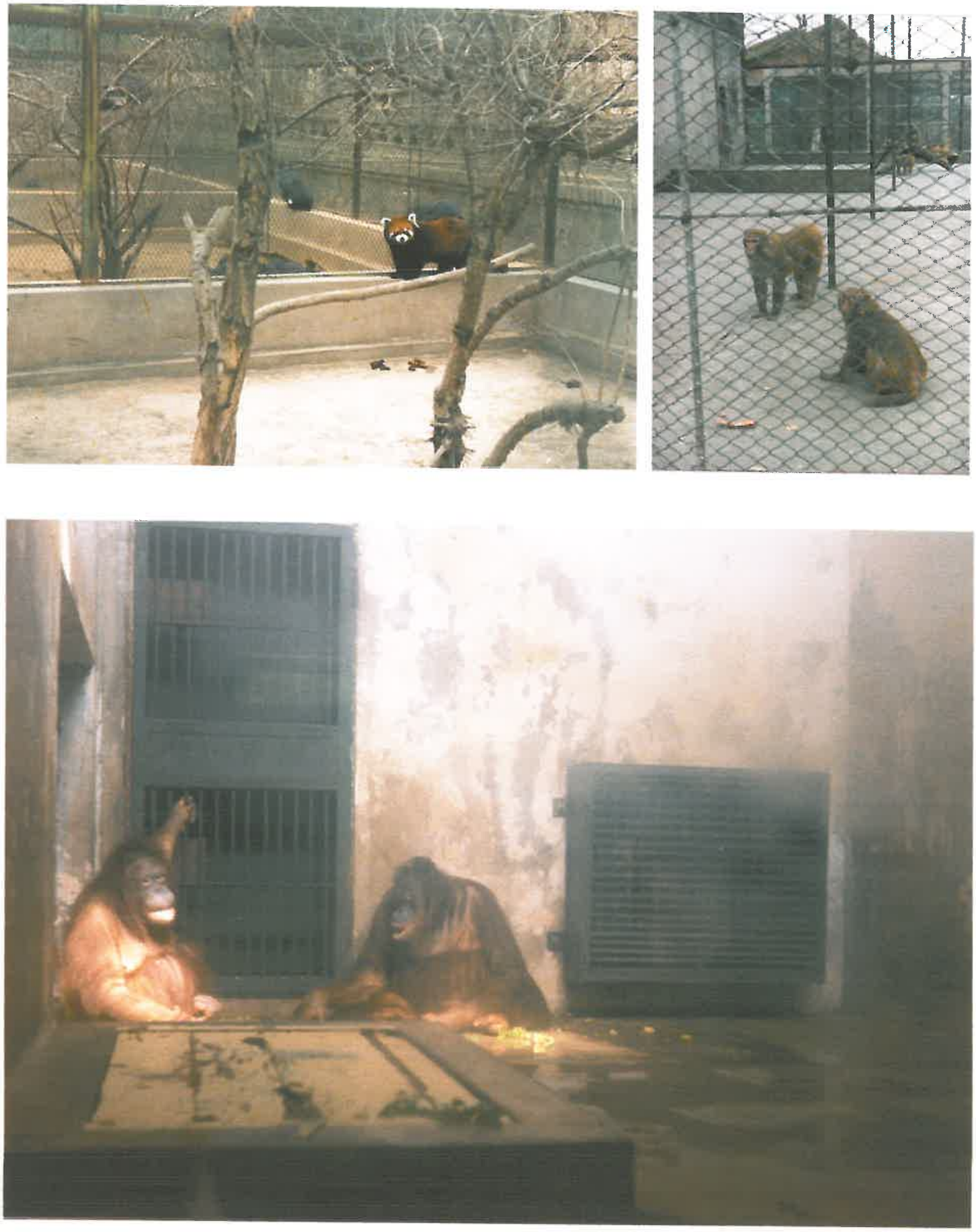


Figure 5.10. Some zoos provide neither naturalistic nor mechanical methods of behavioural enrichment (photos of red panda, macaque, and orangutan zoo enclosures in China taken by Anita O'Hair in 1995)

Figure 5.11. Barren enclosures that provide little physical or psychological stimulation are not only found in developing countries. Indoor primate and lion enclosures at Cheyenne Mountain Zoo in Colorado in 1991 (top and center left) and golden monkey and macaque enclosures at a zoo in China (top and center right, taken by Anita O'Hair) illustrate this point. Naturalistic cotton-top tamarin (Perth Zoo) and snow leopard (Taronga Zoo) enclosures in Australia provide a sharp contrast.

"there are often great differences between the natural activity patterns of opportunistic generalists and animals with specialised feeding strategies" (Forthman Quick, 1994, p.69). Activities can be stimulated by naturalistic techniques or enclosure alterations, such as natural substrates, vegetation, rocks, trees and bodies of water (Forthman Quick, 1994).

The fourth issue touched upon by Forthman Quick (1984) concerns the possible causal factors that lead to "boredom" and "abnormal" behaviour in captive animals. Supporters of the naturalistic approach (*e.g.*, Hutchins et al, 1978a, 1978b, 1979) suggest that predictability, rather than sterility of environments, is the critical factor. However, as Forthman Quick (1984) points out, having concluded that *predictability* is the key problem, Hutchins et al (1978a, 1978b, 1979) also maintain that the use of electronic apparatus programmed with *unpredictable* schedules becomes rapidly boring for animals. It should be noted, that as a result of novelty, naturalistic changes to an enclosure may increase the complexity of the environment and facilitate a number of behavioural changes. However, over time, the animals become accustomed to the changes, which have become "predictable". Forthman Quick (1984) warns that constant change, stimulation or novelty may not be desirable in all instances since: "a certain amount of stability is crucial to reproductive success in those species that form strong pair bonds [eg, wolves...]" (p.69). From a practical point of view, it is not always possible to completely rebuild or restructure enclosures, or alter the social groupings of animals, whereas, it may be easier and: "less disruptive to program variability in a computer" (Forthman Quick, 1984, p.69).

Following a discussion on the mechanical and naturalistic approaches to behavioural enrichment, Tudge (1991) also concludes that: "the ideal must be to combine the best of the two traditions" (pp.212-213). As he points out, an enclosure can look naturalistic but provide "no more freedom of expression than it would have in a simple box" (p.212). Trees can provide captive animals with the opportunity to probe and bore into trunks, climb or smell them, touch and scent-mark them. But, trees can easily be destroyed or become less stimulating over time. If protected by electric fences, they merely become a scenic "prop". Since "trees, earth, sand and water are infinitely variable", changes in the naturalistic elements of an enclosure can provide stimulation (Tudge, 1991, p.213).

Tudge (1991) maintains, that interactive machines, or other artificial environments or elements: "have to be very ingenious, complex, and expensive (at least in keeper time) if they are to compete with the sheer exuberance of nature" (p.213). This is open to dispute, since puzzle boxes, raisin boards and artificial simulations of termite mounds for chimpanzees are simple, challenging and easy to clean and maintain (Figure 5.12). Further invention and assessment of simple apparatus could be useful for animals kept in third world zoos, sanctuaries, farms (Figure 5.13) or laboratories where there is little opportunity to provide large naturalistic enclosures. An integrative approach could encourage the use of browse, manipulative ground coverings and other naturalistic features, but also provide further challenges and stimulation in the form of apparatus. Apparatus could be constructed of wood or be made to "blend" in with the naturalistic features of an enclosure.

5.9 EVALUATING THE SUCCESS OF BEHAVIOURAL ENRICHMENT

> "Recently there is increasing research interest in improving the welfare of captive animals, but there has been less interest in the rigorous operational definition of terms used in the description of environmental `improvement' or enrichment, in evaluating the cost-effectiveness of enrichment, or in the development of theoretical models that guide research and integrate divergent studies" (Chamove, 1989, p.155).

Bloomsmith, Brent and Shapiro (1991) stress the importance of evaluating any enrichment program. Without evaluation, it is impossible to determine whether the enrichment technique used is in fact improving the animal's psychological or physical wellbeing. As Bloomsmith et al (1991) suggest, the provision of toys or larger cages does not always ensure an improvement in psychological well-being. Animals may even be harmed, and money and time wasted by institutions, if techniques are not evaluated. Wherever possible, the evaluation should include quantitative measurement and analysis of the animals' responses to the introduced enrichment technique (Bloomsmith et al, 1991).

One cannot assume that the provision of behavioural enrichment devices will always have a positive effect. In fact: "devices for environmental enrichment may do harm - and that harm may be far from obvious" (Tudge, 1991, p.232). If an enrichment technique is introduced into a group of animals, not all individuals may benefit. Chamove (1989) discusses a study by Rosenblum and Smiley (1984), in which a foraging task was introduced to a group of isolation-reared bonnet macaques. This technique was successful in reducing self-directed aggression and abnormal posturing in individuals that were high or low in the dominance hierarchy. However, those individuals that were ranked as intermediate displayed increases in abnormal behaviours.

Tudge (1991) refers to the provision of a peanut puzzle box for a group of chimpanzees at an American Zoo. The task involved the insertion of fingers into holes in the front of a metal box with shelves, and pushing the peanuts down shelf by shelf, until they fell out at the bottom. The dominant chimpanzees used the puzzle box most, and a reduction in aggressive and stereotypic behaviours was recorded for these individuals. However, since the dominant chimpanzees

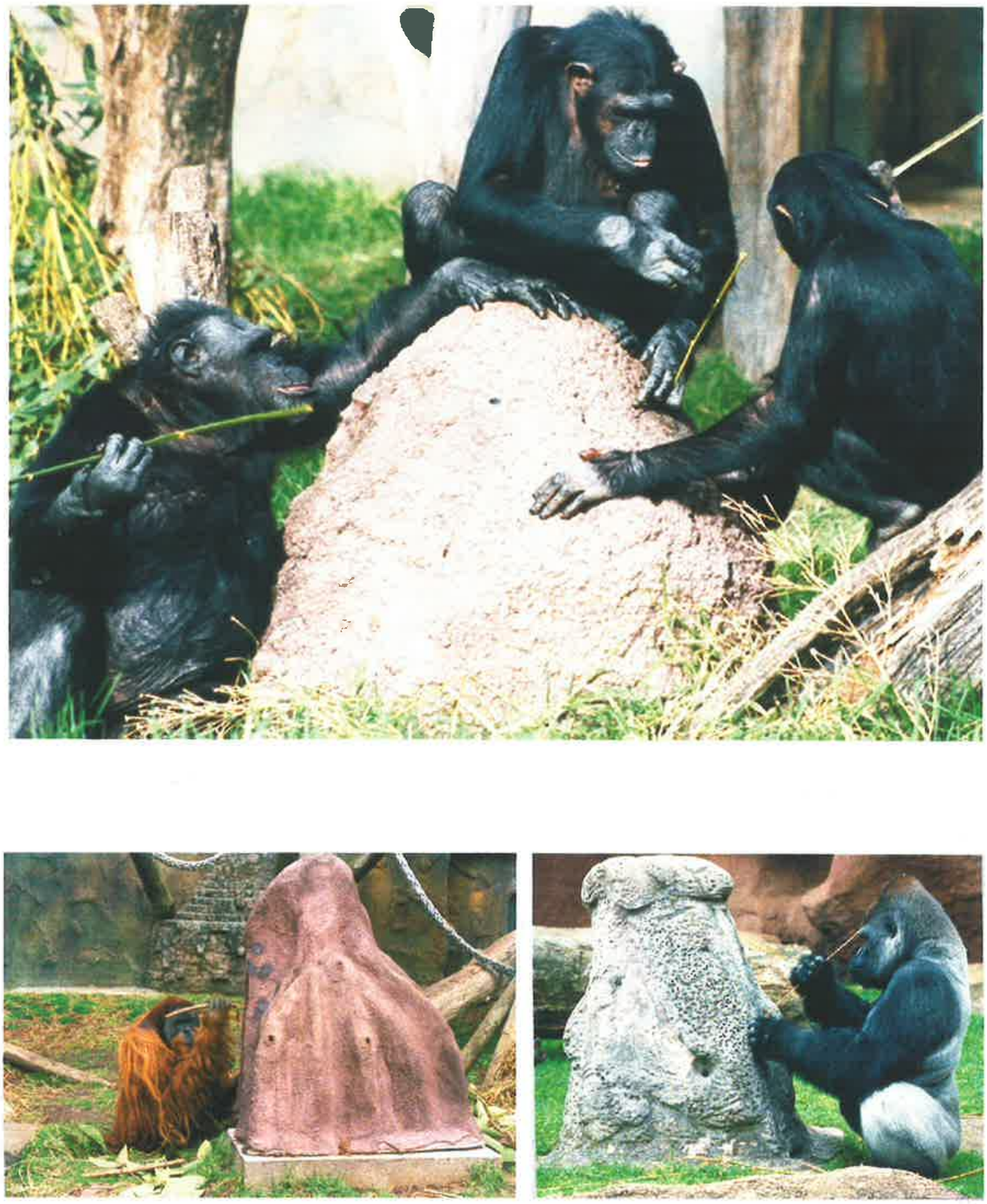


Figure 5.12. Artificial termite mounds are used by chimpanzees, orangutans and gorillas at Australian Zoos (chimpanzee and orangutan at Adelaide Zoo, and gorilla at Melbourne Zoo)

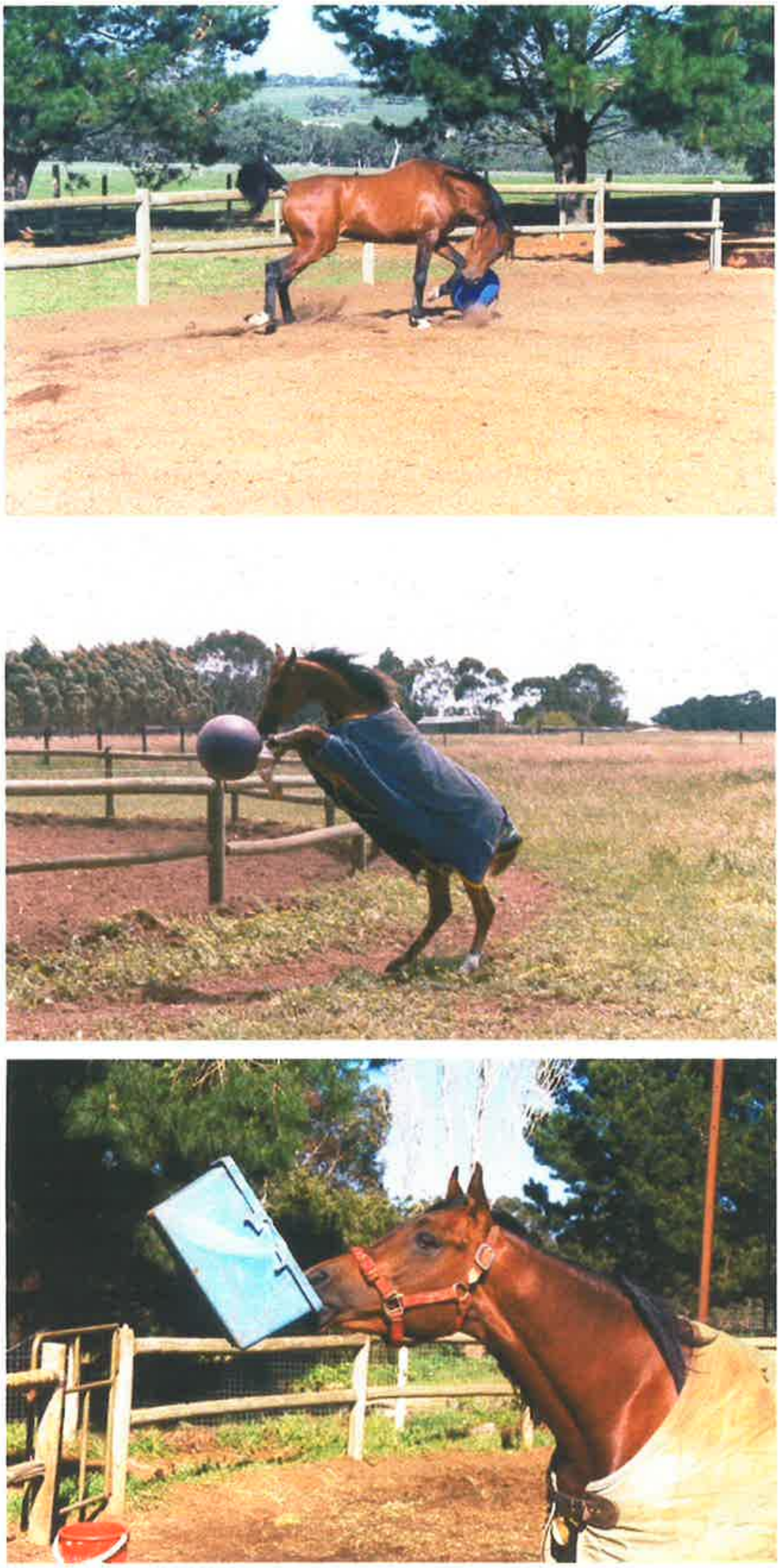


Figure 5.13. Horses can be provided with a variety of simple objects to play with

monopolised the object, the subordinate animals became frustrated, which was reflected in an increase in stereotypic behaviour for these animals (Tudge, 1991). Bloomstrand, Riddle, Alford and Maple (1986) reported similar findings. In fact, their study may be the one referred to by Tudge (1991), although it was in fact carried out at the chimpanzee facility at the University of Texas Science Park. Individual differences were noted, with respect to the amount of aggression and abnormal behaviour (*e.g.*, coprophagy & repeated regurgitation) demonstrated, after the introduction of the peanut puzzle box. These researchers stress, that dominance alone may not account for the individual variations in behaviour. Other possible factors that must be taken into account when evaluating enrichment techniques include:

> "the animals' histories of exposure to such an apparatus, individual responses to novel stimuli, individual motivation as determined by hunger or other factors and the responses of other animals" (Bloomstrand et al, 1986, p.299).

Evaluation of the responses of this group of chimpanzees to the food puzzle, allowed Bloomsmith, Alford and Maple (1988) to avoid similar problems. Instead of one puzzle box, multiple food puzzles were provided to the chimpanzees as part of the enrichment program. Without proper evaluation, the negative reactions of some individuals in the studies mentioned may have been overlooked (Chamove, 1989).

5.10 CRITERIA FOR EVALUATING CAPTIVE ENVIRONMENTS

Snowdon (1991) provides three criteria, which must be met before a naturalistic environment can be considered successful. Although he restricts his discussion to primate environments, the criteria set are equally applicable to other animals housed in captivity. The three criteria are as follows:

- **Veterinary criterion** – animals must be in good physical and nutritional health and disease-free (*i.e.*, diets are nutritionally adequate; air, temperature & lighting are stable & adequate; & surroundings are sanitary);
- **Biological criterion** – animals can reproduce successfully & care for their own offspring (*i.e.*, infants are not hand-reared);
- **Behavioral-ecological criterion** – animals retain motoric, social, cognitive, and other skills needed by animals were they to be reintroduced to the wild.

The third criterion, in particular, has been discussed at length in section 5.7.3. As Snowdon (1991) points out, these criteria must also be met, if the psychological well-being of captive animals is to be enhanced and maintained.

5.11 CRITERIA FOR SELECTING SPECIES FOR BEHAVIOURAL ENRICHMENT

This discussion of behavioural enrichment has focused on mammals, but enrichment techniques have also been employed for birds. King (1993) criticises researchers in the area of enrichment for largely ignoring birds altogether. The importance of providing social species of mammals with conspecifics is recognised, as is the need for providing stimulation for "intelligent" species and the opportunity for engaging in natural behaviour patterns and reducing aberrant behaviours. King (1993) stresses that many bird species are also social, require the opportunity to engage in natural behaviour patterns (especially if they are to be released back into the wild), and also demonstrate "abnormal" behaviours (*e.g.*, feather-plucking & severe self-mutilation) if socially or environmentally deprived.

Birds too may require mental stimulation, especially "intelligent" species, such as parrots: "which have in fact been likened to primates" who "share many behavioral and ecological characteristics" (King, 1993, p.511). A number of parrot species have been shown to "solve "object permanence" tasks, indicating an ability to assimilate and use environmental information" (King, 1993, p.511). Various bird species have been found to "relocate cached and recached food stores and even learn where these are through watching other birds, displaying use of memory" (King, 1993, p.511).

Reptiles can also benefit from the provision of novel objects. For more than fifty years, a Nile soft-shelled turtle was housed alone in a glass-fronted concrete tank at the National Zoo in Washington, D.C. In an attempt to alleviate this turtle's self-inflicted injuries, Burghardt, Ward and Rosscoe (1996) added a number of objects (a familiar brown basketball, an unfamiliar orange basketball, a round hoop of garden hose, the rubber fill hose & fish) to the sticks already present in his tank. These researchers observed the equivalent of tug-of-war and hoop "games", and the objects allowed him:

> "to perform behaviors that he normally would use in other contexts such as exploring, chasing, attacking, biting, dismembering, and eating" (p.236).

Burghardt et al (1996) point out that the turtle had never been provided with a soft substrate over the concrete floor of his tank. They conclude by appealing to researchers to develop enrichment techniques for reptiles, other than the provision of "toys" or novel objects. Unfortunately, due to funding or staff/time shortages, zoos and researchers are required to somehow select the species that require high levels of stimulation or opportunities for exploratory behaviour.

Wood-Gush, Stolba and Miller (1983) pose the questions:

> "how much exploratory behaviour do they require for their mental well-being? Would adequate exploratory behaviour cut down the high levels of aggression and abnormal behaviour often seen in intensively housed animals?" (p.206).

They are referring primarily to farm animals, but the questions are just as relevant for animals in a variety of captive environments. These researchers suggest that the function of patrolling is both appetitive and exploratory in wild animals. However, for farm animals housed in cramped and unvarying environments, the investigation of objects is the main expression of exploratory behaviour.

To decide how much exploratory behaviour is necessary for psychological well being, Wood-Gush et al (1983) state that a number of factors should be taken into account.

- Exploratory behaviour is likely to be particularly "prominent" in species whose essential resources are patchily distributed (temporal & spatial), by comparison with those whose resources are easily obtained.
- Species with greater cognitive abilities may show more exploratory behaviour than other species exploiting the same food sources.
- A high correlation appears to exist between levels of manipulative play (rather than social play) shown in the young of a species and the level of exploratory behaviour observed in adults.
- Exploratory behaviour may vary according to the developmental stage of an animal. Highest levels are likely to be observed during the emergence of the behaviour in ontogeny (usually in young mammals).

Mench (1998) suggests that all animals must be provided with stimulation and enrichment in captive environments. She also provides a set of three guidelines, indicating the species for which opportunities for exploration must be given the highest priority, namely:

- Species that are generalists or are adapted to environments that are highly variable in terms of resource availability (*i.e.*, patchy or seasonally variable)- similar to the first factor mentioned by Wood-Gush et al (1983).
- Species that exhibit complex antipredator behaviours (*e.g.*, learn & use escape routes).
- Species that have a complex social structure (& higher cognitive abilities)- similar to the second factor given by Wood-gush et al (1983).

Mench (1998) stresses that for these species enrichment devices must be designed around their patterns of exploratory behaviour, so that their information-gathering needs are met.

5.12 BEHAVIOURAL ENRICHMENT STUDIES CONDUCTED AT ADELAIDE ZOO

For a decade, researchers have been conducting behavioural studies at Adelaide Zoo (The Royal Zoological Society of South Australia). Many have been in the area of behavioural enrichment, providing a number of species with the opportunity to investigate novel objects, encounter artificial predators, hunt artificial prey or engage in a variety of foraging tasks based on principles of ecological learning theory. Three recent studies will be mentioned here.

5.12.1 A FORAGING TASK BASED ON OPERANT CONDITIONING FOR MALAYAN SUN BEARS

Landrigan (1998) attempted to reduce stereotyped pacing in a pair of Malayan sun bears (*Helarctos malayanus malayanus*) by designing a foraging task based on principles of operant conditioning. The bears were conditioned to climb to a manipulandum located in a tree, and press a response bar with the front paws. When the bear pressed the response bar (which could be attached at three different heights of the trunk), a feeder suspended from the outer limbs of the same tree was activated, and a small amount of food (one - five grapes or nuts) was dropped to the ground. An auditory discriminative stimulus was used to indicate when the apparatus was in use and reinforcement was available.

Some interesting differences between the behaviour of the male and female were observed (Landrigan, 1998). Surprisingly, increases in visitor numbers resulted in decreases in the male's pacing, whilst there was no apparent effect on the female's pacing. If the door to the "night dens" was closed, the male's level of pacing increased (especially prior to the midday feed), whereas the female's level of pacing was again not affected. The female spent more time within the trees (climbing & stationary), whilst the male was constantly moving or retreating into the dens (if the door was open). The female was considered to be the dominant animal. If the apparatus was in use, her pacing was completely suppressed.

Fewer reinforcements were received as the response bar was positioned higher in the tree. Landrigan (1998) attributed this to the greater effort required to register a response. In addition, when the response bar was located higher in the tree, longer consummatory PRPs were observed in the female. Again, Landrigan (1998) suggests that more energy is expended, and the bear is less likely to begin climbing after consuming the reinforcement. The male, on the other hand, engaged in bursts of responding, interspersed with long breaks. Landrigan (1998) concludes that visitors to the zoo were able to observe the bears climbing and foraging to a greater extent, but suggests that a feeder capable of dispersing food over a wider area would further increase foraging.

5.12.2 SIMULATED HUNTING BEHAVIOUR IN AFRICAN WILD DOGS, CARACALS AND PERSIAN LEOPARDS

Mills (1998) provided three species of predator with the opportunity to perform simulated hunting behaviour. The behaviour systems approach (ecological learning theory) provided a theoretical framework. Initially, a moving object (rectangular section of tyre with the tread removed) was employed as the conditioned stimulus (CS). Subsequently, a visual stimulus (white circle on a black background hooked to the fence outside the enclosure) and auditory stimulus (tone of 400 hertz frequency, set at 60 decibels for the wild dogs & 50 decibels for the caracals) was used to signal the moving object. Finally, subjects were run on three schedules of reinforcement. The rubber stimulus object was attached to the apparatus during non-rewarded trials, and was rubbed with meat so that a successful "capture" was necessary for the animals to discover whether meat was attached or not. During rewarded trials, the meat was cut into the same shape as the rubber object. The Persian leopards were only used in the initial phase.

For the leopards, the moving object was propelled along a track on the ground. For the African wild dogs and caracals a "flying fox" style apparatus was used, with the stimulus propelled around the exhibit via an overhead steel cable (Figure 5.14). Two pieces of equipment of varying height were used for the caracals. Meat (horsemeat or occasionally chicken) was used as the unconditioned stimulus (US), and experimental sessions were fifteen minutes long (or five minutes long for the auditory and visual stimulus sessions) and session times were randomly allocated.

During the baseline experimental sessions the moving stimulus was found to "release components of the felids' predatory sub-systems" (Mills, 1998, p.124). That is, the caracals and leopards directed contact responses and bouts of predatory behaviour towards the moving stimulus. The cats rapidly habituated to the moving stimulus within seven sessions. The wild dogs, on the other hand, tended to avoid the stimulus all together. Mills (1998) found that the artificial prey condition (when compared with the operant condition) "produced substantially higher levels of naturalistic responses" (p.261).

A VR10 schedule for caracals and a VR3 and CRF schedule for the wild dogs produced the most complete sequences of predatory behaviour. Mills (1998) attributes this to species-typical hunting success rates. Estes (1991) maintains that wild dogs are efficient predators with prey capture rates of up to 85%. For cats such as servals, the hunting success rate is usually lower at around 50% (Kitchener, 1991). In addition, the wild dogs responded less during sessions held in the middle of the day, whereas the caracals responded throughout the day.

Figure 5.14. African wild dogs chasing (left) and "capturing" (right) meat during a practice run for Vanessa Mill's study at Adelaide Zoo in March 1996

Figure 5.15. One of the aerial silhouettes used by Monique Kardos at Adelaide Zoo (top) with the meerkats (bottom) in September 1996

5.12.3 THE EFFECTS OF AERIAL PREDATOR SILHOUETTES ON MEERKAT AND DWARF MONGOOSE FORAGING PATTERNS

One of the studies conducted by Kardos (1999) investigated the effect of feeding schedules on the foraging patterns of three male meerkats and a dwarf mongoose group. Food was delivered at from a feeder apparatus ("non-contingent" or "operant") hidden within a hollow log. After initial baseline observations, aerial silhouettes were presented at random times (Figure 5.15). The silhouette was either predatory (African hawk eagle, Martial eagle & dark chanting goshawk) or non-predatory (greylag goose & square neutral stimulus). Kardos monitored the meerkats' and mongooses' behaviour, in an attempt to determine whether foraging patterns were sensitive to the presence and frequency of aerial predators (or whether they were able to discriminate between the different silhouettes).

The meerkats tended to ***flee*** upon presentation of the predatory silhouettes, and demonstrated a relatively rapid recognition of non-predatory silhouettes. However, multiple presentations resulted in increased ***watching*** rather than ***fleeing***, indicating that habituation towards the predatory silhouettes was taking place. This was not unexpected, since "there was no actual attack component associated with the passing of the shapes overhead" (Kardos, 1999, p.261). Interestingly, the dark chanting goshawk tended to elicit the ***threaten*** response. Kardos (1999) points out that this species of bird is not a natural predator of meerkats, and in flight is somewhat similar to the pigeons and seagulls that occasionally land in the meerkats' enclosure at the zoo, and are ***attacked*** by the meerkats. In fact, Kardos (1999) states that: "the subjects in this study were twice observed to attack and hold onto pigeons which had landed in the enclosure. Both pigeons escaped these attacks, although they sacrificed rather a large number of tail feathers in the process" (p.261).

The dwarf mongooses tended to display more consistent ***fleeing*** responses to the aerial predator silhouettes, but some habituation was also evident after multiple presentations. Kardos (1999) found that: "the younger animals displayed an inclination to threaten and attack birds which landed in their enclosure, despite the size of the birds and the chance that they may have been taken by these birds as food" (p.261). Interestingly, when a watching response was elicited on a first run, a flight response was often observed on the return run. Kardos (1999) suggests that the return pass of a predatory bird may pose a greater threat, since the bird may have selected a target prey animal. With respect to the habituation effect, Kardos (1999) points out that the maintenance of flight responses: "would require some type of adverse outcome following at least some proportion of silhouette presentations which may present ethical problems" (p.261).

5.13 APPLYING PRINCIPLES OF EXPLORATORY BEHAVIOUR TO BEHAVIOURAL ENRICHMENT

Knowledge about the different forms of exploratory behaviour engaged in by wild animals should be taken into account when designing or improving captive environments. For example, sex differences in the size of home ranges are evident for both caracals (Weisbein & Mendelssohn, 1990) and chimpanzees (Goodall, 1986), with males ranging over far larger territories. Therefore, smaller captive enclosures may be particularly inappropriate for males. There also appear to be differences in the amount of object manipulation that occurs, with female chimpanzees using tools more often (McGrew, 1992), whilst male kittens appear to make more "object contacts" (Barrett & Bateson, 1978). Clearly, young chimpanzees and adult females must be provided with extra opportunities to engage in tool-use. In addition, young animals engage in large amounts of exploratory play and object manipulation. As a result, captive environments must provide extra opportunities for young animals.

Differences in the amount of object manipulation are also observed within species, in natural environments. For example, chacma baboons living in swampy environments show a more extensive repertoire of social object manipulation than those living in desert river ravines (Hamilton, Buskirk & Buskirk, 1978). This highlights the fact that researchers must remain flexible in their thinking, when addressing enrichment options for captive environments.

Perhaps the three most important principles, or stimulus determinants, that must be applied to (or taken into account) the enrichment of captive environments are the complexity of the novel object or environment, the degree of control that the animal has over the novel object or environment, and the actual novelty of the object or environment (Birke & Archer, 1983; Mench, 1998; Sambrook & Buchanan-Smith, 1997). Each of these will briefly be discussed in turn (although they have already been mentioned in section 1.8).

5.13.1 COMPLEXITY OF NOVEL OBJECTS OR ENVIRONMENTS

Sambrook and Buchanan-Smith (1997) point out that many enrichment studies focus on increasing the complexity of the physical environment and of the behavioural repertoire, since level of activity and environmental complexity have been shown to be positively correlated. Complexity can be increased in three ways, namely by including the presence of other animals (conspecifics or other species), by presenting novel manipulable objects, and by altering the physical structure of enclosures. Typically, researchers manipulate stimuli in terms of ***visual*** complexity. Laboratory studies have shown that primates show preferences for visual stimuli that are more complex (Sambrook & Buchanan-Smith, 1997).

Although researchers recommend increasing "complexity" as an enrichment tool, Sambrook and Buchanan-Smith (1997) stress that most do not explicitly quantify the properties of the concept used. The visual complexity of an object is surprisingly difficult to define, but Sambrook and Buchanan-Smith (1997) maintain that it is usually defined in terms of the "number of features" included, which can be relatively few (*e.g.*, dimensions of principle axes, such as length & width) or many (*e.g.*, geons, which include about 50 basic shapes). Despite the great variation in possible definitions of complexity, in: "practice, a subjective estimate is probably sufficient" (Sambrook & Buchanan-Smith, 1997, p.208) Importantly, visual complexity should not be confused with the complexity of the interactions that may be observed in the captive animals.

To focus only on visual complexity or characteristics of enclosures and objects, is to ignore the other senses that could and should be stimulated in captive animals. That is, odours, sounds and tactile features may also vary in terms of "complexity", but these are likely to be far more difficult to define than visual complexity. A number of features of the actual enclosure must be taken into account when defining complexity. For example, a three-dimensional analysis of an enclosure would include height, width, angles, crevices, the actual floor area, and the number of levels (Mench, 1998). Again, it must be stressed that field researchers must also define and quantify features of the natural environment, and stimuli within these environments, in terms that can be translated into relevant dimensions or properties in captive environments (Miller et al, 1998). That is, it is not enough merely to state that the natural environment is "complex".

5.13.2 DEGREE OF CONTROL OVER NOVEL OBJECTS OR ENVIRONMENTS

> "The attractiveness that the ability to control holds for animals should not surprise us since control is *the* adaptive aspect of behaviour: control over what you eat, what eats you (within certain limitations), with whom you mate, etc. It is fair to describe the process of learning as acquisition of control through the learning of rules...Object play during development (human and non-human) serves an exploratory function...enabling individuals to establish control over the mechanical affordances of objects" (Sambrook & Buchanan-Smith, 1997, p.210).

For decades, researchers have been aware of the adverse effects of perceived lack of control, such as learned helplessness, apathy, depression, and learned inhibition (Seligman, 1975). However, Sambrook and Buchanan-Smith (1997) point out that total control (the other extreme) does not alleviate boredom, and in fact may encourage new aberrant behaviours (*e.g.*, excessive use of operant feeders in some captive environments). Therefore, researchers attempting to enrich captive environments must discover a "middle ground for controllability", which does not confuse controllability with predictability (Sambrook & Buchanan-Smith, 1997, p.210).

Sambrook and Buchanan-Smith (1997) maintain that the process of acquisition of control, rather than the actual repeated execution of acquired control is most enriching. They suggest that ***neophilia*** is the key to enrichment, since it: "serves the clear function of motivating individuals to learn about their environment, to control their interactions with it, to be accurate predictors and to be ready to adapt to changing circumstances" (p.210). Thus, researchers should design and use objects, which evoke neophilia and "suggest controllability", but in actual fact "resist control", which maintains responsiveness (Sambrook & Buchanan-Smith, 1997, p.210). This is linked to the concept of novelty, which will be discussed in the following section.

Table 5.3
The dimensions of "controllability" in novel objects as proposed by Sambrook and Buchanan-Smith (1997; Table 1, p.212).

GRADE OR DIMENSION OF CONTROLLABILITY	**DEFINITION & EXAMPLES**
FIXED (least sophisticated cause-effect relationship)	Animal can move only with respect to the object (*e.g.*, swinging on bars, extra substrates on which animals can move)
MOVEABLE	Animal & object are free to move with respect to each other & the enclosure (*e.g.*, throwing or pushing objects, transfer between animals, many enrichment toys)
MALLEABLE	Action applied to a point on the object results in an effect at the same location (*e.g.*, squeezing a rubber ball, bouncing on tree limbs, many enrichment toys)
ANALOGUE	Action applied at one point generates an analogue effect at another point (*e.g.*, use of levers, computer tracking games- joystick movements result in movements of a cursor on a computer screen, mirrors)
DIGITAL (most sophisticated cause-effect relationship)	No analogue relationship between cause & effect (*e.g.*, most electronic mechanisms, switch-operated control of white noise or radios)

Table 5.3 provides a set of five grades of controllability, as proposed by Sambrook and Buchanan-Smith (1997). They suggest that these (largely qualitative) dimensions provide a unifying framework, which will allow researchers to compare enrichment devices that are used in captive environments. Although "analogue" and "digital" enrichment devices are unlikely to

promote the exact species-specific behaviours observed in natural environments, they may promote psychological well-being in otherwise barren captive environments.

Sambrook and Buchanan-Smith (1997) discuss three other aspects of controllability that must be considered when choosing appropriate novel objects for enrichment purposes (the third has already been discussed). These are:

- **Number of controllable features & interactions between them** – most enrichment toys are simple "activity boxes", which may nevertheless afford multiple responses.
- **Predictability of the response** – ranges from certain to random. "Puzzle feeders" can deliver food at random or fixed intervals (or be contingent upon or non-contingent upon the animal's response).
- **Grade of controllability** – ranging from fixed to digital (*i.e.*, from least to most sophisticated cause-effect relationship), as presented in Table 5.3.

Since novel stimulation may elicit fear responses, as well as exploratory responses, captive animals should be provided with the option to seek and interact with, or avoid the novel stimuli, or to enter or avoid the novel environment (Mench, 1998). This choice of options clearly increases the degree of control that the animal has, and reduces any stress associated with novelty. Thus, captive enclosures must be large enough and complex enough to provide cover or areas to allow hiding or other avoidance responses, or animals must be given time to enter new enclosures in their own time.

5.13.3 NOVELTY OF OBJECTS AND ENVIRONMENTS

As already discussed in Chapter 1, novelty is difficult to define. However, Sambrook and Buchanan-Smith (1997) maintain that from a cognitive perspective, a system or object retains novelty: "until the individual is satisfied that the means of controlling all properties in its range of interest that can be controlled are discovered. Novelty is thus defined in terms of neophilia rather than vice versa" (pp. 210-211). These researchers stress that the provision of novel objects elicits novel behaviours (thus expanding the behavioural repertoire), since new challenges require animals to search for solutions, which provokes behavioural flexibility. Sambrook and Buchanan-Smith (1997) point out that:

> "Behaviourism recognizes that the viability of operant conditioning rests on an innate tendency for animals to generate new behaviours spontaneously, from which rewarded ones are then selected…Thus it is through the learning context that we have most hope of breaking stereotypies and encouraging a wider range of behaviour" (p.211).

Since animals habituate to novel stimuli, sometimes within minutes (Sheldon, 1969) or hours (Forster, 1992), researchers must carefully monitor the animal's responses to the stimuli. If a simulated predator is to retain its effectiveness in eliciting flight responses, it should probably only be presented on a few occasions, with long intervals between presentations. If an object is to retain its effectiveness in eliciting exploratory responses, it should be removed periodically, with long intervals between presentations (so that the object can "regain novelty").

As already mentioned elsewhere, researchers must constantly be adding to the potential list or reservoir of suitable novel objects or enrichment devices, which can be interchanged (Birke & Archer, 1983). Similarly, researchers could use some successful enrichment devices amongst a more diverse range of species. For example, artificial termite mounds need not only be made available for chimpanzees, since orangutans and gorillas also use them if these enrichment devices are provided (Figure 5.12). O'Connor (2000) has shown that captive Rodrigues fruit bats (at the Jersey Wildlife Preservation Trust) can benefit from the use of mealworm dispensers, which provide an unpredictable source of food (& have been successfully used for a range of species). Natural exploratory and foraging behaviours increased in the fruit bats, and the presence of mealworms resulted in decreases in aggression and number of bats on the enclosure floor.

5.13.4 PRACTICAL APPLICATIONS: IMPROVING CAPTIVE ENVIRONMENTS & MANAGEMENT OF PROTECTED AREAS

Although this chapter has focused on improving captive environments, the principles of exploratory behaviour can and should be applied to improving the management of protected areas. The destruction of natural environments in Uganda (& other countries) has already resulted in National Parks and other protected areas shrinking, and these areas may already be too small to adequately maintain the populations of animals within them (Wrangham, 1998). This may force animals to crop raid outside the boundaries of the protected areas, which puts their lives at risk (personal observation). Managers of protected areas must ensure that the size of the home range is adequate for all the populations within the park, and that corridors exist between protected areas (for exchange of genetic materials). Thus accurate information about patrolling and home ranges is vital for planning and maintaining of protected areas.

When managers of protected areas are setting up and developing wildlife tourism programs, they must be aware of the potential devastating effects that ***neophilia*** (object approach & contact) may have. "Wild" animals that have been habituated to the close proximity of humans may also become attracted to the novel objects that tourists, researchers and other visitors may bring along. That is, backpacks, drink bottles, hats, food items may all attract the attention of animals (see Figure 2.1). Contact with these items can increase the risk of disease transmission, or other dangers (*e.g.*, choking on, or swallowing an object). Tourist camp areas must be well away or suitably fenced off from animals, which may otherwise investigate rubbish tips, rooms or tents, or other items/areas.

Finally, if reintroductions are planned, managers and researchers must ensure that the animals, which are to be released, have had adequate experience in dealing with complex environments, and again, the tendency for ***neophilic*** reactions must be monitored. If an animal is too prone to investigate any novel object, it may be more vulnerable to becoming caught in a trap or snare, or exploring outside the protected area (e.g., bordering agricultural properties), and therefore may not be a suitable candidate for reintroduction. An awareness of principles of exploratory behaviour may thus help improve wildlife management (captive & free-ranging).

5.14 AIMS OF THE PRESENT STUDY

The following experimental chapters investigate exploratory behaviour, particularly in response to the presentation of novel stimulus objects, in two different environments (laboratory & zoo) and with three different species (rats, chimpanzees & caracals). In addition, the effect of novel stimulus objects on patterns of adjunctive (in the laboratory) or other aberrant behaviours (in the zoo) is also investigated.

The first two experiments complete a set of five simple intermittent schedules of food-reinforcement. That is, Litchfield (1987) investigated exploratory (& other) behaviour during ***fixed-ratio*** (FR30), ***continuous reinforcement***, and ***extinction*** sessions. Experiment 1 investigates responses to novel objects (& other behavioural patterns) during ***fixed-interval*** (FI60s), ***variable-interval*** (VI60s) and subsequent ***extinction*** sessions. Experiment 2 investigates exploration and other behaviours during ***variable-ratio*** (VR30), ***differential reinforcement of low rates*** (DRL15s) and subsequent ***extinction*** sessions. The widest range of behaviours possible is included in the investigation: behaviour directed at the stimulus objects (sniff object, sniff & touch object, & chew/bite object), behaviour directed at the peripheral areas of the box (propping & jump at lid), behaviour directed at the bar and food-trough area (bar pressing & bar-related behaviour), and grooming/scratching, digging/burying, rearing and pica. Of particular interest, are: the amount of behaviour (frequency & duration) that occurs during the post-reinforcement pauses on each schedule (with or without novel objects present), and the resistance to extinction observed following each schedule (with or without prior exposure to novel objects).

Experiment 3 seeks to determine whether ***polydipsia***, or other excessive behaviours (such as aggression towards the water bottle or escape-directed behaviours) occur during a ***fixed-interval*** (FI60s) schedule in the more naturalistic open-field Skinner box, if a concurrent water source is available. It is possible that the presence of novel objects may reduce any polydipsia observed (if it occurs). The behaviours included in the analysis are: behaviour directed at the stimulus objects (sniff object, sniff & touch object, & chew/bite object), behaviour directed at the bar and food-trough area (bar pressing & bar-related behaviour), behaviour directed at the water bottle (sniff bottle, sniff & touch bottle, chew/bite bottle & drinking), and propping, displacement, digging/burying and resting/sleeping. This experiment creates a link between the laboratory open-field environment- where it is possible that aberrant behaviours occur (if a water source is available & food is presented on at predictable intervals)- and the zoo environment, in which a water source is always available, and food is presented intermittently (& somewhat predictably)- where it is also possible that aberrant behaviours occur.

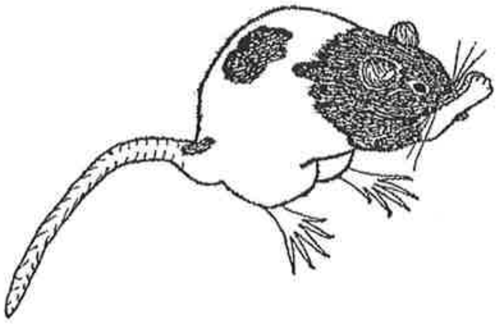
The final preliminary experiments present a qualitative analysis of exploratory behaviour and other behavioural changes upon presentation of novel stimulus objects (food-related & non-food-related), to a group of six chimpanzees and a pair of caracals. It is expected that some aberrant behaviours would be observed in these two species, since captivity tends to pose particular problems for the Great Apes (high cognitive abilities & therefore need extra mental & physical stimulation), and carnivores (who are unable to hunt). However, the studies conducted at Adelaide Zoo seek to provide suitable objects that will facilitate exploratory behaviour and play, whilst reducing any aberrant behaviours observed. These final studies attempt to show that the principles of exploratory behaviour, schedules of reinforcement, and patterns of aberrant behaviours that have been largely gleaned from laboratory studies, can and should be applied to improving captive environments (irrespective of whether the species is a rodent, primate or felid).

CHAPTER 6

EXPLORATORY BEHAVIOUR IN THE LABORATORY RAT:

EXPERIMENT 1:

FI60 AND VI60 SCHEDULES OF INTERMITTENT FOOD REINFORCEMENT



6.1 INTRODUCTION TO EXPERIMENT 1

Laboratory rats have been found to engage in ***exploratory behaviour*** under conditions of FR30 intermittent food-reinforcement, ***continuous reinforcement*** and ***extinction*** (Litchfield, 1987). By combining operant (experimental) and ethological (observational) techniques, Litchfield (1987) was able to investigate exploration and other behaviours under "controlled" experimental conditions, but in a more "naturalistic" environment than the conventional Skinner box. The behaviours scored included: ***exploratory behaviour directed at stimulus objects***; ***behaviour directed at the bar and food-trough area***; ***displacement behaviour*** and ***exploratory*** (or "escape") ***behaviour directed at the peripheral areas of the box***.

During FR30 sessions, at least a third of the total frequency measure of behaviours scored occurred during the post-reinforcement pauses (PRPs). The percentage of the total duration measure for behaviours present during the post-reinforcement pauses was over 50% in some cases. As Litchfield (1987) points out, rats do not remain passive during the post-reinforcement pauses. Instead, they use this time after the consumption of a food pellet to explore their surroundings, or engage in other behaviours. By engaging in behaviours other than instrumental responding, the rat:

> "...is able to investigate the objects and other areas of the apparatus, in an effort to locate alternative sources of food, maintain familiarity with the surroundings it is faced with every day, or seek sources of novel-stimulation. After a while, the rat then returns to the manipulandum and its known food source" (Litchfield, 1987, p.91).

Such behaviours can be considered to have adaptive significance to rats. No single behaviour was engaged in to an excessive degree. Thus, Litchfield (1987) concludes that the behaviours observed were unlike the ***schedule-induced behaviours*** reported by Falk (1971).

The subsequent two studies follow on from Litchfield's (1987) investigation of ***exploratory behaviour*** during schedules of intermittent food-reinforcement. Since behaviours other than the instrumental response were found during FR30, ***CRF*** and ***extinction*** sessions, then exploratory and other behaviours may also occur during other schedules of reinforcement. Experiment 1 focuses on behaviour during a Fixed- Interval 60-second schedule (FI60) and a Variable-Interval 60-second schedule (VI60), and subsequent ***extinction*** sessions. Different schedules of intermittent food-reinforcement should be investigated- especially those that most closely emulate conditions in natural environments, with their unpredictability of reinforcement, that evoke particular foraging strategies. Experiment 1 and Experiment 2 seek to do this.

Variable-interval schedules in particular are considered to demonstrate a "powerful hold" on an animal's instrumental responding (*e.g.*, ***bar pressing***), since these schedules make it impossible for the subject to predict when the next reinforcement is due (Litchfield, 1987). Steady, constant rates of instrumental responding occur as a result, with few (or no) post-reinforcement pauses (Weiten, 1998). Do ***exploratory behaviours*** or other behaviours occur during a ***variable-interval*** schedule, and if so, when do they occur? Are post-reinforcement pauses created, lengthened, or do these other behaviours interrupt runs of ***bar presses***? The "unpredictable" nature of reinforcement on ***variable-interval*** schedules may also result in a higher ***resistance to extinction***, since the unpredictable ***variable-interval*** schedule is less distinct initially from the new ***extinction*** schedule. ***Fixed-interval*** schedules, on the other hand, deliver reinforcements predictably. This results in the typical post-reinforcement pauses and scalloped effect of instrumental responding. There is a lower ***resistance to extinction***. Discrimination between ***extinction*** and previous predictable reinforcement conditions is easily made.

Although different subjects were used for this experiment and the initial 1987 study, and the experiments were run at different times, the experimental apparatus and procedures used were the same (except for the actual schedules run). In addition, the number of subjects in each group was the same, and the behavioural categories were defined and scored in the same way, in an attempt to provide as much comparability as possible. The range of behaviours scored in the following experiment has been increased from the initial set investigated by Litchfield (1987). These additions include ***digging/burying***, ***pica***, ***rearing***, and ***chew/bite objects***, thus providing a "more complete "ethogram" of the rat's behavioural repertoire during schedule and extinction sessions" (Litchfield, 1987, p.93).

Experiment 1 aims to demonstrate that exploration and a number of other behaviours occur during ***fixed-interval*** (FI60) and ***variable-interval*** (VI60) schedules of food-reinforcement. The first part of Experiment 1 proposes that a significant proportion of such behaviours will be present during the post-reinforcement pauses for the FI60 schedule. This hypothesis is based on Forster's (1986) finding that extinction produces exploration, and on the ***discrimination hypothesis*** which indicates that a large ***fixed*** schedule is in some degree similar to ***extinction***, since it is itself composed of periods of ***extinction***, namely the post-reinforcement pauses. Further, Litchfield (1987) found that at least a third of each behavioural measure (frequency & duration) took place during the post-reinforcement pauses on a FR30 schedule.

The premise of behaviours other than the instrumental/target response occurring during the post-reinforcement pauses is based on the findings of Dinsmoor, Lee and Brown (1986). These researchers found that stimuli associated with post-reinforcement pauses are negative predictors of food, and as such, are negative reinforcers. As a result, operant responding is inhibited. Falk (1971) lends further support for the occurrence of exploratory and other behaviours during the post-reinforcement pauses. His studies show that various ***schedule-induced*** or ***adjunctive behaviours*** occur during intermittent food-schedules. Along with Litchfield's (1987) study, this study aims to falsify Falk's (1971) notion of adjunctive behaviours being analagous to displacement activities. Instead, a postulation, that such behaviours are examples of attempts to find sources of novel stimulation (or alternative sources of food), will be presented. To merely label all schedule-induced or extinction-induced behaviours as ***displacement activities*** is to undermine the complexity and variety of such behaviours. Behaviours pertaining to exploration are not "out-of-context", but rather are highly relevant to the situation.

Unlike the ***fixed-interval*** schedule with its predictable delivery of reinforcements, the ***variable-interval*** schedule is unpredictable with respect to delivery of reinforcements. Thus, a regular post-reinforcement pause is unlikely to develop. As a result, it is expected that lower proportions (or none) of behaviours will be present during post-reinforcement pauses for the VI60 schedule.

It is also expected that ***fixed-interval*** rats may engage in exploration and behaviours other than ***bar pressing*** to a greater extent during extinction sessions. This postulation is based on the ***discrimination hypothesis*** (Church, 1963), which states that: "resistance to extinction will be enhanced the greater the similarity between conditions in pretraining (acquisition) and testing (extinction)" (Fantino & Logan, 1979). Extinction of ***bar pressing*** should occur more rapidly in the ***fixed-interval*** groups, since these rats should discriminate more readily between the ***fixed-interval*** and ***extinction*** conditions. Intuitively, one might expect an increase in the time spent engaged in other behaviours to occur, as a result of decreased time spent ***bar pressing***. A greater ***resistance to extinction*** would be expected to appear in the ***variable-interval*** groups, since the differences between the ***variable*** intermittent schedule and ***extinction*** sessions would be less readily discriminated. As a consequence, it is expected that more of the ***variable-interval*** rats' time will be spent in ***bar pressing***, leaving less time to engage in alternate behaviours.

The experimental design used two different groups, ***fixed-interval*** or ***variable-interval***, further subdivided into two groups depending on whether stimulus objects were first present during ***schedule*** running (***fixed-interval*** or ***variable-interval***), or during ***extinction***. (It should be noted that ***extinction*** is also a "schedule", but in order to simplify the terminology used, ***schedule*** refers to the intermittent schedule used prior to ***extinction***). The four groups are referred to as:

- FIOS (***fixed-interval***, objects first present during ***fixed-interval*** sessions);
- FIOE (***fixed-interval***, objects first present during ***extinction*** sessions);
- VIOS (***variable-interval***, objects first present during ***variable-interval*** sessions);
- VIOE (***variable-interval***, objects first present during ***extinction*** sessions).

Table 6.1 presents the experimental design in more detail.

6.1.1 HYPOTHESES PERTAINING TO THE PRPs

Hypothesis One: Proportion of behaviours occurring during PRPs of FI60-s and VI60-s schedules

Fixed-interval *schedules are characterised by the existence of regular PRPs.* ***Variable-interval*** *schedules, on the other hand, do not typically produce regular PRPs. Thus, it is expected that a larger proportion of each of the scored behaviours will occur during the PRPs for rats run on the* ***fixed-interval*** *schedule, when compared with the* ***variable-interval*** *counterpart* ***(FIOS*** *compared to* ***VIOS*** *&* ***FIOE*** *compared to* ***VIOE****).*

Hypothesis Two: Effect of novel stimulus objects on proportion of behaviours occurring during PRPs of FI60-s and VI60-s schedules

*It is predicted that the presence or absence of novel stimulus objects during **fixed-interval** and **variable-interval** running may have some effect on the proportions of behaviours occurring during the PRPs. Thus, it is expected that there will be a difference between the "OS" groups with objects present, and the "OE" groups with objects absent during **fixed-interval** and **variable-interval** sessions (**FIOS** compared to **FIOE** & **VIOS** compared to **VIOE**).*

6.1.2 HYPOTHESES PERTAINING TO CHANGES IN BEHAVIOUR OVER SCHEDULE AND EXTINCTION SESSIONS

Hypothesis Three: Effect of novel stimulus objects on frequency and duration of behaviours during FI60-s and VI60-s schedules

*If objects are absent during **fixed-interval** and **variable-interval** sessions, more time and effort can be devoted to behaviours that are not object-directed. Thus, it is expected that higher frequencies and durations of non-object behaviours will be observed in the **FIOE** and **VIOE** groups during schedule sessions, when compared to their same schedule counterparts. In addition, without objects present to "distract" them during schedule sessions, the frequency and duration of **bar pressing** scores is expected to be higher in the **FIOE** and **VIOE** groups (**FIOE** compared to **FIOS** & **VIOE** compared to **VIOS**).*

Hypothesis Four: Effect of novel stimulus objects on frequency and duration of behaviours during extinction

*For rats previously run on a **fixed-interval** schedule, when objects are first encountered during extinction, it is expected that higher frequencies and durations of object-directed behaviours will be observed. That is, the **FIOE** group will direct more behaviour towards novel stimulus objects during extinction sessions than the **FIOS** group. No firm expectations are held for the other behavioural categories.*

*Since extinction is less readily discriminated after a **variable-interval** schedule, and the VIOE group are more likely to be under the "control of the schedule", less behaviour will be directed towards novel stimulus objects (lower frequencies & durations) during extinction sessions (than for the **VIOS** group). No firm expectations are held for the other behavioural categories.*

Hypothesis Five: Frequency and duration of behaviours during FI60-s and VI60-s schedules

*Rats run on the more predictable **fixed-interval** schedule should demonstrate lower frequency and duration of **bar pressing** and higher frequency and duration of other behaviours than their counterpart rats run on the less predictable **variable-interval** schedule (**FIOS** compared to **VIOS** & **FIOE** compared to **VIOE**).*

Hypothesis Six: Frequency and duration of behaviours during extinction

*During extinction, the **fixed-interval** rats should more readily discriminate between the previous **fixed-interval** schedule and new extinction sessions, than their counterpart rats previously run on the **variable-interval** schedule (**FIOS** compared to **VIOS** & **FIOE** compared to **VIOE**). Thus, **fixed-interval** groups should demonstrate lower frequency and duration of **bar pressing** and higher frequency and duration of other behaviours.*

6.2 METHOD FOR EXPERIMENT 1

6.2.1 SUBJECTS

Twenty experimentally naive male Hooded Wistar rats, bred at the Waite Institute Central Animal House, served as subjects. They were obtained at approximately 73 days of age, and subsequently, housed in separate cages (28cm x 19cm x 18cm) in the Psychology Department's animal holding room, at the University of Adelaide.

Four of these rats were used in a pilot study (to check the apparatus). The remaining sixteen rats were randomly divided into four groups of four animals. The two experimental groups were designated as (1) Variable-Interval/ Objects during Schedule running group (VIOS) and (2) Variable-Interval/ Objects during Extinction group (VIOE). Similarly, the two control groups were designated as (3) Fixed-Interval/ Objects during Schedule running group (FIOS) and (4) Fixed-Interval/ Objects during Extinction group (FIOE). The FIOS group had the VIOS group matched to it, with respect to, the experimental conditions being followed. The FIOE and VIOE groups were similarly matched. Thus, the two ***fixed-interval*** groups were each matched with a separate ***variable-interval*** group.

The rats were housed under controlled temperature and illumination conditions (12/12-hour light-dark cycle). All animals received *ad libitum* water, with *ad libitum* food received during the handling sessions. Prior to the start of testing, each rat was individually handled once daily for seven days. Testing commenced at approximately 80 days of age. Table 6.1 presents the experimental design in detail.

6.2.2 APPARATUS FOR EXPERIMENT 1

6.2.2.1 EXPERIMENTAL APPARATUS

The experimental apparatus consisted of an exploration box fitted with a bar manipulandum, food trough and light on one wall (as in a Skinner box). A buzzer, pellet dispenser and pellet counter were situated on the other side of this wall. The exploration box was made of stainless steel, with a perspex lid (raised slightly for ventilation). Its dimensions were 50cm x 49cm x 25cm (Figure 6.1). The floor of the exploration box was covered by sawdust, to a depth of approximately 1cm.

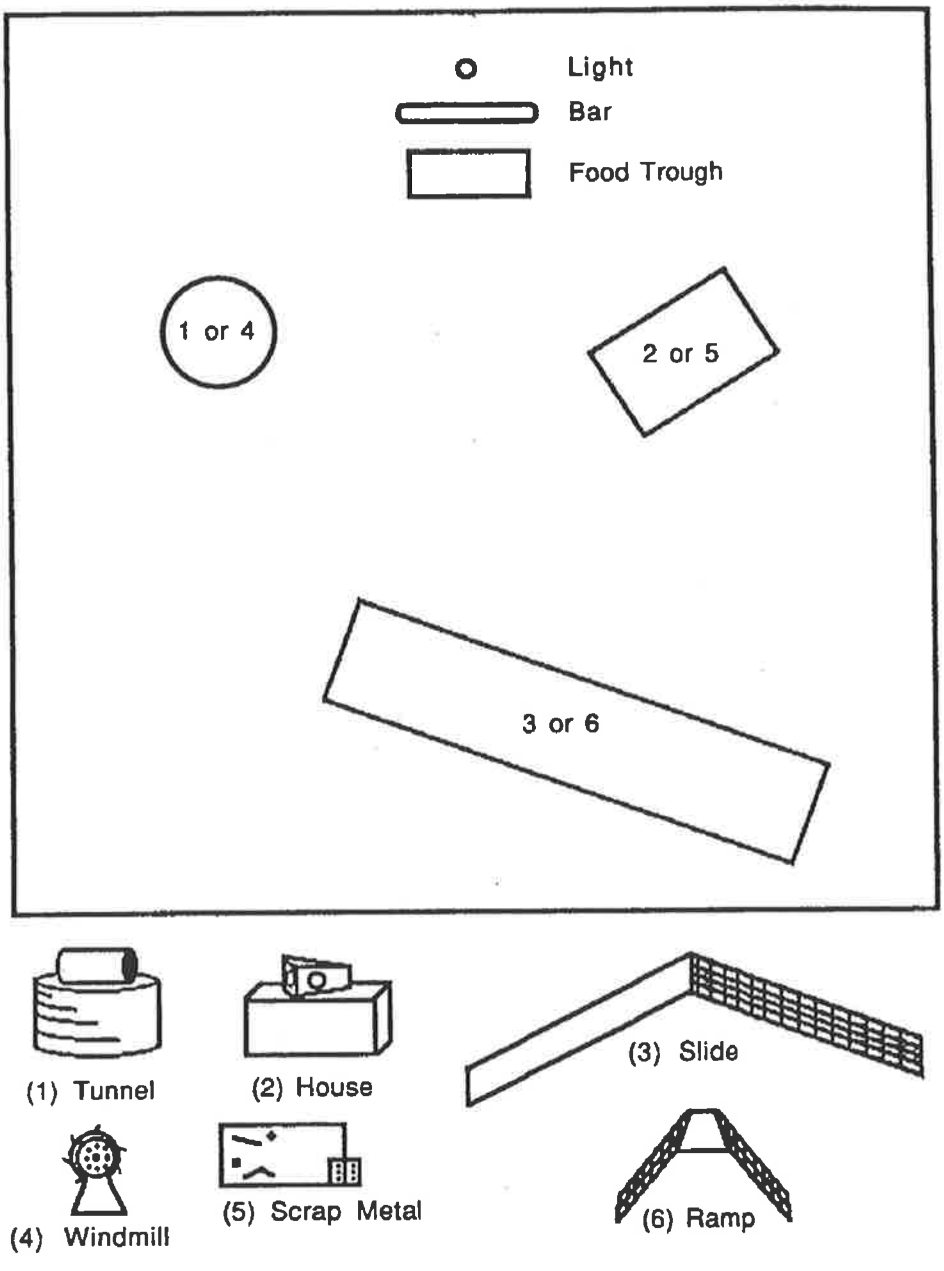


Figure 6.1. Diagram of the exploration box showing the placement of stimulus objects

A Gerbrands cumulative recorder, and hand-operated pellet dispenser were also connected to the box. A PDP11 computer controlled the whole system. All program commands were entered into the computer via a Decwriter terminal located in the room adjacent to that in which testing took place.

Two groups of three removable objects (Figures 6.2 & 6.3) were clipped onto the floor of the exploration box when required. These stimulus objects were as follows:

Group A objects

- **"TUNNEL":** a solid stainless steel cylindrical block (4.9cm in diameter & 4.5cm in height), with a piece of aluminium tubing (2.8cm in diameter & 3.3cm in length) mounted across it
- **"HOUSE":** a solid stainless steel rectangular block (7.8cm x 5.7cm x 3.3cm), with an open triangular structure (3.8cm in height) containing two holes, mounted upon it
- **"SLIDE":** a ramp / slide consisting of a metal grid on one side (21.8cm x 6.6cm), with the other side covered by a plain aluminium sheet (20cm x 6.8cm), which was 14cm from the floor at its highest point

Group B objects

- **"WINDMILL":** an upright triangular piece of aluminium (7.4cm in height, with a 5.7cm base), with a free spinning wheel (4.2cm in diameter) bolted on near the top, and a free spinning electric motor cooling fan (4.7cm in diameter) bolted on the other side
- **"SCRAP METAL":** a brass spring-loaded structure (4.2cm in length & 4cm in height), a free moving brass "arm" (3.9cm in length and 3.4cm in height) resting against an upright piece of brass (3.5cm in height), and an upright piece of plastic (4.2cm high), all mounted upon a 12.7cm x 8.9cm flat stainless steel rectangular base
- **"RAMP":** a metal grid ramp with a flat rectangular aluminium top (8.7cm x 8.1cm), 13.6cm from the floor at its highest point

6.2.2.2 OBSERVATIONAL EQUIPMENT

Experimental sessions were recorded onto VHS tapes, using a National WVP 100N video camera with an in-built timer, and a National NV 7800 videocassette recorder (VCR). The video camera on a tripod was situated on the edge of a table, directly above the exploration box (Figure 6.4). The Gerbrands cumulative recorder was set on the floor against a wall and the VCR and monitor were located behind a partition, thus separating them from the exploration box and camera (Figure 6.5).

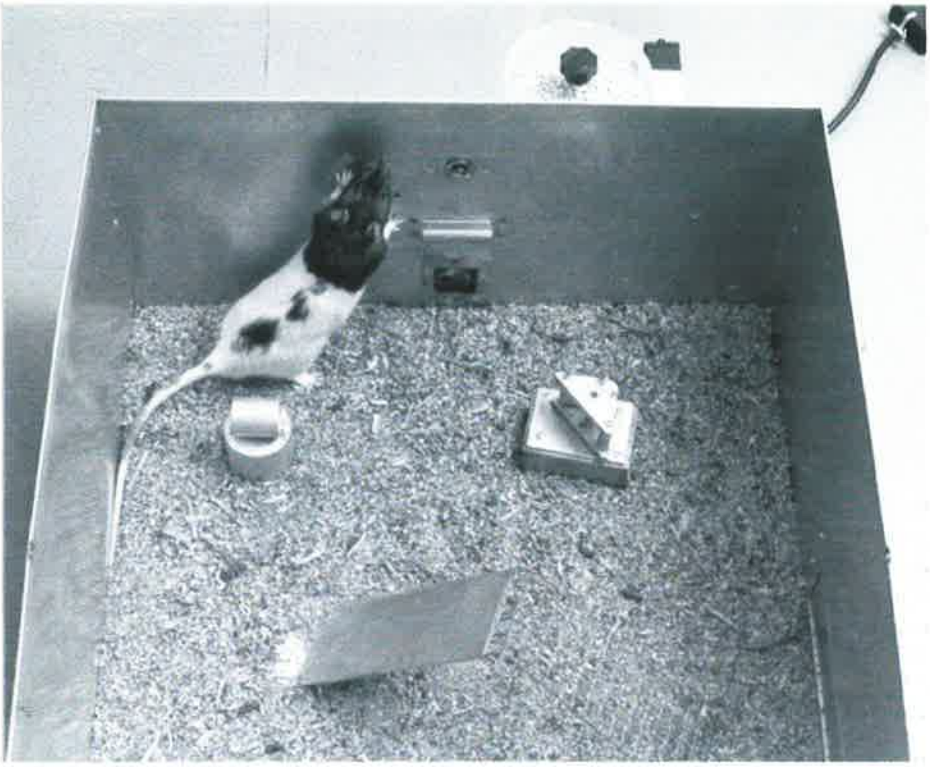


Figure 6.2. The exploration box with Group A objects clipped into place

Figure 6.3. The exploration box with Group B objects clipped into place

Figure 6.4. View of the video camera located directly above the exploration box

Figure 6.5. The Gerbrands cumulative recorder (top) and the video-cassette recorder and video monitor behind the partition (bottom)

Videotapes of all sessions were viewed on a National TC-2633 video monitor and transcribed to behavioural records, via an event recorder. A series of buttons, each representing a specific behaviour, and an event recorder program were used to enter the behaviours onto computer files. Each time one of the buttons was depressed, the duration and frequency of one event was recorded.

6.2.3 PROCEDURE

6.2.3.1 EXPERIMENTAL DESIGN

The experimental design used two different groups, ***fixed-interval*** (FI) or ***variable-interval*** (VI), further subdivided into two groups depending on whether stimulus objects were present during schedule running (OS), or during extinction (OE). The rats were allocated to a group at random. Table 6.1 presents the experimental design in more detail.

Table 6.1
The experimental design, showing which stimulus objects are present in each session (*i.e.*, objects from group A or B or none at all).

PHASE OF EXPERIMENT	SESSION	GROUP 1: FIOS	GROUP 2: FIOE	GROUP 3: VIOS	GROUP 4: VIOE
SCHEDULE	**1**	Group A Objects	No Objects	Group A Objects	No Objects
SCHEDULE	**2**	Group A Objects	No Objects	Group A Objects	No Objects
SCHEDULE	**3**	Group A Objects	No Objects	Group A Objects	No Objects
EXTINCTION	**4**	Group B Objects	Group A Objects	Group B Objects	Group A Objects
EXTINCTION	**5**	Group B Objects	Group A Objects	Group B Objects	Group A Objects
EXTINCTION	**6**	Group B Objects	Group A Objects	Group B Objects	Group A Objects

6.2.3.2 HANDLING, CONDITIONING AND OBSERVATION SESSIONS

The experimental procedure consisted of three phases: handling, conditioning and observation, and was adhered to for all four groups of rats.

HANDLING

Each rat was individually handled for the same amount of time before the experiment commenced. All rats were handled on a daily basis for seven days. Consequently, each rat received handling on seven separate occasions at the same time every day. Each handling session lasted for ten minutes, during which time the rat was removed from its home cage and gently stroked.

CONDITIONING

Throughout the experimental sessions the animals were maintained on a 23-hour food-deprivation schedule. All rats were subjected to the same initial procedures of conditioning. ***Bar pressing*** was shaped in each rat over a number of (individualised) training sessions. No objects were present in the box during this period. Subsequently, all rats were placed on a ***continuous*** (food) ***reinforcement*** (CRF) schedule of reinforcement. The number of training sessions required by each rat varied, with a minimum of 200 ***bar presses*** in 50 minutes being the criterion set before the next stage could be attempted. The duration of each training session was 50 minutes. Following CRF training, rats in the FIOS and FIOE groups were placed on a Fixed-Interval 60-second (FI60-s) schedule of reinforcement. Similarly, rats in the VIOS and VIOE groups were placed on a Variable-Interval 60-second (VI60-s) schedule of reinforcement.

Prior to conditioning, each rat was given a ***familiarisation*** session in the exploration box. During this phase three pellets were placed in the food trough. The rat was able to explore the box freely, until these pellets were consumed. Throughout the conditioning sessions the exploration box (with its bar & food-trough) was devoid of stimulus objects. Once the rat was placed into the box, a free reinforcement was delivered by a button (operated by hand), which was connected to the pellet dispenser. Accompanying the button press and reinforcement delivery were a light and buzzer.

The next stage to be undertaken was ***magazine training***, followed by ***shaping of bar pressing by successive approximations***. Reinforcements were automatically delivered for every ***bar press*** following the first such successful instrumental response. Once all rats had reached the criterion (*i.e.*, 200 ***bar presses*** in 50 minutes) the next phase commenced. Rats in the FIOS and FIOE groups were each run for one half-hour session per day, for 14 days, by which time their FI60-s baseline running was considered to be stable. Rats in the VIOS and VIOE groups were also run for one half-hour session per day, for 14 days, by which time their VI60-s baseline running was considered to be stable.

OBSERVATION

All rats were observed on six different occasions: three ***fixed-interval*** or ***variable-interval*** schedule sessions, and three ***extinction*** sessions. Each observation session was of 30 minutes duration. During the observation sessions the stimulus objects were either present, or not present, according to the experimental conditions laid out in Table 6.1.

Exploratory behaviour (directed at the stimulus objects & the peripheral areas of the box), ***bar pressing*** and various other behaviours (to be detailed subsequently) were recorded under all the conditions specified.

Video recording commenced at the start of each observation session, as did the video camera timer. All rats were placed into the exploration box in the same way. The right hand side of the rat's body was side-on to the bar and object (1 or 4). This minimised potential positional biases, which may have favoured exploration of the object over the bar-area (or vice-versa). The perspex lid was then closed and the session commenced.

The rat was left alone for the entire session. Viewing took place from behind the partition, via the video monitor. The rat was removed from the box when the video monitor timer reached 30 minutes. In addition, the light above the manipulandum came on at the end of the session. Upon removal from the exploration box, the rat was returned to its home-cage where it received *ad libitum* food for one hour. Following each experimental session, the stimulus objects were wiped clean, and the sawdust was smoothed out to an even distribution, after faeces and urine-soaked areas of sawdust were removed (& more sawdust added), if necessary.

6.2.3.3 EVENT RECORDING

The observation sessions were all viewed upon completion of the experimental running. Scoring behavioural events was accomplished by means of an event-recording program, which was activated at the start of each viewing session. The event recorder consisted of a custom built board (fixed to the top of a table) with 15 buttons, each representing a different behavioural event. The criteria for each behavioural category are now presented.

Behaviour directed at the bar and food-trough area

- ***Bar pressing*** - consists of the complete depression of the bar, by one or both front paws, with or without the aid of the snout (Forster, 1986; Litchfield, 1987).

- ***Bar-related behaviour*** – is a category that includes sniffing, touching or digging in and around the food-trough area. "Bar-related" is perhaps a misnomer, since it is in fact behaviour directed at the food-trough. Litchfield (1987) originally intended this category to include sniffing and touching of the manipulandum, and sub-criterion ***bar presses***. However, it was virtually impossible to distinguish sub-criterion ***bar presses*** from successful ones. Thus, the literally ***bar-related behaviours*** were omitted from this category.

Behaviour directed at the stimulus objects

- ***Sniffing objects (i.e., "Sniff Object")*** - includes orientation of the rat's snout towards the stimulus objects, without physical contact (Figure 6.6). Bolles and Woods (1964) describe *sniffing* as the rapid "wiggling" of the rat's nose and whiskers, with the snout oriented towards an object, but without its body actually touching the object. Such *sniffing* occurs immediately prior to *sniffing while touching or manipulating objects* (Gojak, 1984; Forster, 1986; Litchfield, 1987).

- ***Sniffing while touching or manipulating objects (i.e., "Sniff and Touch Object")*** - includes sniffing whilst simultaneously: touching objects with the front paws; rearing onto objects; or climbing onto objects (Figure 6.7). Digging at the base of the objects is also included in this category (Gojak, 1984; Forster, 1986; Litchfield, 1987). However, unlike Litchfield's (1987) study, it does not include mouthing or biting of the objects. These behaviours now fall into a separate category.

- ***Chewing or biting objects (i.e., "Chew/Bite Object")*** – is a category that includes mouthing, biting or chewing of the stimulus objects. The rat may also be touching the object with its paws or other parts of its body, whilst biting the object.

Behaviour directed at the peripheral areas of the box

- ***Propping*** - is described by Renner (1986) as the placement of the forepaw(s) against the wall of the test box, with or without sniffing the wall (Figure 6.8). This category also incorporates "scrabbling", which is defined by Shettleworth (1973), for golden hamsters, as: "a behaviour in which the hamster claws at the wall, often hopping up and down and moving along the wall as if trying to climb out" (p.247). Rats also display this behaviour.

- ***Jumping at the lid*** - consists of leaping at the perspex lid of the box, with all four paws off the ground. Typically, the rat hunches down, and then pushes off with the back legs. Alternatively, the rat props itself against the wall, hunches, and propels itself off the wall, and into the air. The leap may include a somersault-like twist in the air, touching the lid momentarily with the paws, before landing again on all four paws (Litchfield, 1987).

Other behavioural categories

- ***Grooming / scratching (i.e., "Displacement")*** - behaviours are not directed at the objects or surroundings. Such displacement activity incorporates the grooming or scratching of any part of the rat's body. An example of this category is face washing (Figure 6.9).

- ***Digging / burying*** - includes any digging or burying with the forepaws in the sawdust (Figure 6.10).

- ***Rearing*** - includes any rearing in the open. That is, the rat is standing on its hind legs, with its forepaws in the air, and not in contact with any walls or objects.

- ***Pica*** - involves ingestion of the wood-shavings (sawdust) that cover the exploration box (Davey, 1981). ***Coprophagia*** (ingestion of feces) was also included in this category, with instances of this behaviour noted by the observer at the end of the session.

Figure 6.6. An example of ***sniff object***

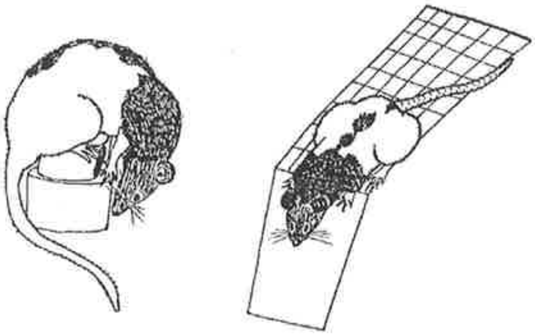


Figure 6.7. Examples of the behavioural category ***sniff and touch object***

Figure 6.8. An example of ***propping***

Figure 6.9. Examples of the behavioural category ***displacement***

Figure 6.10. An example of ***digging/burying*** in which the rat rapidly pushes sawdust forwards with the forepaws

Frequency and duration measures were recorded for all behavioural events. The appropriate button was depressed for the full duration of each event, and released upon the completion of the behaviour. Prior to the commencement of event recording, one ***fixed-interval*** session (30 minutes duration) and one ***variable-interval*** session (30 minutes duration) were chosen at random. Event recording of these sessions was performed in order to reduce possible biases as a result of practice effects in the experimenter. The data obtained from these trial sessions was not included in later analyses.

6.2.3.4 INDEPENDENT JUDGING

To ensure observer reliability and replicability of behavioural findings, three independent judges scored the behaviour of an animal chosen at random. The session was of 30 minutes duration. Prior to commencement of scoring, the independent judges were individually familiarised with the event recording apparatus. Each button was clearly labeled with the behaviour it represented. The behavioural categories were described, the task explained, and any ensuing questions pertaining to the behavioural scoring answered.

The independent judge was then given a ten-minute practice session, selected at random from the remaining animals. Subsequently, the judge was required to score the behaviours from the 30-minute session. The total frequency and duration of behaviours was calculated, and compared with the behavioural measurements scored by the experimenter for the same session. In addition, the agreement amongst all the judges was examined.

6.3 RESULTS FOR EXPERIMENT 1

6.3.1 THE PRESENCE OF EXPLORATORY AND OTHER BEHAVIOURS DURING THE POST-REINFORCEMENT PAUSES

In order to test Hypotheses 1 and 2, a separate table of means for each frequency and duration measure was set up for subjects classified by the two grouping (or independent) variables, group and session. (These tables of raw data can be found in Appendix A). Each mean was based on the behavioural responses of four subjects (four rats per group). The mean for each session was summed to give the sum of means for individual rats in the VIOS, VIOE, FIOS and FIOE groups for the three schedule sessions combined. The same procedure was followed for the behavioural measures during the PRPs. This PRP sum of means value was then calculated as a percentage of the sum of means of that particular behavioural measure for the three sessions combined (*i.e.*, as a % of the total occurrence). Table 6.2 presents the sum of means and percentages of each frequency and duration measure for the FIOS and FIOE groups, and Table 6.3 presents the sum of means and percentages of each frequency and duration measure for the VIOS and VIOE groups.

6.3.1.1 HYPOTHESIS ONE: PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s AND VI60-s SCHEDULES

Fixed-interval *schedules are characterised by the existence of regular PRPs.* ***Variable-interval*** *schedules, on the other hand, do not typically produce regular PRPs. Thus, it is expected that a larger proportion of each of the scored behaviours will occur during the PRP's for rats run on the* ***fixed-interval*** *schedule, when compared with the* ***variable-interval*** *counterpart (****FIOS*** *compared to* ***VIOS*** *&* ***FIOE*** *compared to* ***VIOE****).*

The frequency measures for the *fixed-interval* groups

In order of increasing percentage of total frequency for the FIOS group, the behavioural measures were: ***bar-related behaviour***; ***displacement***; ***propping***; ***chew/bite object***; ***rearing***; ***sniff and touch object***; ***sniff object***; ***pica*** and ***digging/burying***. The score for the percentage of total occurring during the PRPs ranged from 23.85% to 83.2%. With the exception of ***bar-related behaviour*** (23.85%) and ***displacement*** (48.67%), over 50% of each behavioural category occurred during the PRPs (Table 6.2).

In order of increasing percentage of total frequency, the behavioural measures for the FIOE group were: ***bar-related behaviour***; ***propping***; ***displacement***; ***rearing***; ***pica***; ***jump at lid***; and ***digging/burying***. The value for percentage of total occurring during the PRPs ranged from 16.82% to 75.39%. With the exception of ***bar-related behaviour*** (16.82%) and ***propping*** (40.33%), over 50% of each behavioural category occurred during the PRPs in ***fixed-interval*** sessions. For, ***pica***, ***digging/burying*** and ***jump at lid***, over two thirds occurred during the PRPs (Table 6.2).

The duration measures for the *fixed-interval* groups

The behavioural measures in order of increasing percentage of total duration (in seconds) for the FIOS group were: ***chew/bite object***; ***bar-related behaviour***; ***rearing***; ***sniff and touch object***; ***displacement***; ***propping***; ***sniff object***; ***pica***; and ***digging/burying***. The value for the percentage of total occurring during the PRPs ranged from 46.61% to 90.63%. With the exception of ***chew/bite object***, at least 50% of each of the duration measures occurred during the PRPs, in the FIOS group. An exceptionally high percentage (90.63%) of total duration of ***digging/burying*** occurred during the PRPs (refer to Table 6.2).

Table 6.2
The mean frequency and duration of behaviours occurring during the PRPs (for the FIOS & FIOE groups) summed over the three ***fixed-interval*** sessions as a percentage of the (total) mean frequency and duration of each behaviour summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS * FIOS GROUP**	**SUM OF MEANS * FIOE GROUP**	**SUM OF MEANS IN PRP's * FIOS GROUP**	**SUM OF MEANS IN PRP's * FIOE GROUP**	**% OF TOTAL * FIOS GROUP**	**% OF TOTAL * FIOE GROUP**
FREQUENCIES						
Pica	13.25	25.5	10.5	17	79.25	66.67
Digging/Burying	31.25	64	26	48.25	83.2	75.39
Rearing	259.5	439.75	138	242	53.18	55.03
Propping	433.5	612.5	221.25	247	51.04	40.33
Displacement	178.75	129.5	87	67.25	48.67	51.93
Bar-related behaviour	1196.25	1551.5	285.25	261	23.85	16.82
Sniff object	368.75	no	220.75	no	59.86	no
Sniff & Touch object	250.75	objects	146.75	objects	58.52	objects
Chew/Bite object	16.25	present	8.5	present	52.30	present
Jump at lid	0	35.75	0	26.25	-	73.43
DURATIONS (in seconds)						
Pica	55.71	80.73	43.89	62.21	78.79	77.06
Digging/Burying	18.68	45.03	16.93	35.55	90.63	78.95
Rearing	335.88	599.31	186.38	369.08	55.49	61.58
Propping	543.03	751.16	330.91	400.83	60.94	53.36
Displacement	186.78	200.1	112.98	126.46	60.49	63.20
Bar-related behaviour	718.91	843.73	393.31	472.23	54.71	55.97
Sniff object	168.78	no	106.5	no	63.10	no
Sniff & Touch object	523.28	objects	315.13	objects	60.22	objects
Chew/Bite object	33.6	present	15.66	present	46.61	present
Jump at lid	0	11.56	0	8.38	-	72.49

Note. There were no objects present during the ***fixed-interval*** sessions for the FIOE group. A dash (-) indicates that no instances of the behaviour were observed, whereas a zero (0) indicates that the behaviour did occur but all instances took place outside the PRPs.

The behavioural measures in order of increasing percentage of total duration (in seconds) for the FIOE group were: ***propping***; ***bar-related behaviour***; ***rearing***; ***displacement***; ***jump at lid***; ***pica***; and ***digging/burying***. The values for the percentage of total occurring during the PRPs ranged from 53.36% to 78.95%, for the FIOE group. Thus, at least half of each duration measure (& >75% of ***pica*** and ***digging/burying***) occurred during the PRPs (Table 6.2).

The frequency measures for the *variable-interval* groups

In order of increasing percentage of total frequency for the VIOS group, the behavioural measures were: ***jump at lid***; ***bar-related behaviour***; ***propping***; ***sniff and touch object***; ***displacement***; ***rearing***; ***sniff object***; ***pica***; ***digging/burying***; and ***chew/bite object***. The percentage of total occurring during the PRPs ranged from 13.49% to 66.67%. For this group, less than a third of each behavioural category occurred during the PRPs. The one exception was ***chew/bite object***, two thirds of which occurred during the PRPs (Table 6.3).

Table 6.3

The mean frequency and duration of behaviours occurring during the PRPs (in the VIOS & VIOE groups) summed over the three ***variable-interval*** sessions as a percentage of the (total) mean frequency and duration of each behaviour summed over the three ***variable-interval*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS * VIOS GROUP**	**SUM OF MEANS * VIOE GROUP**	**SUM OF MEANS IN PRP's * VIOS GROUP**	**SUM OF MEANS IN PRP's * VIOE GROUP**	**% OF TOTAL * VIOS GROUP**	**% OF TOTAL * VIOE GROUP**
FREQUENCIES						
Pica	22.75	0	7	0	30.77	-
Digging/Burying	54	14	17	2	31.48	14.29
Rearing	175.25	607.25	41.75	77.75	23.82	12.80
Propping	334	1196	65.75	126	19.69	10.54
Displacement	95.5	160.25	21.25	12.5	22.25	7.8
Bar-related behaviour	973.5	1204	132.25	130	13.59	10.80
Sniff object	367.75	no	93.25	no	25.36	no
Sniff & Touch object	200	objects	42.5	objects	21.25	objects
Chew/Bite object	0.75	present	0.5	present	66.67	present
Jump at lid	53.75	150.5	7.25	15.25	13.49	10.13
DURATIONS (in seconds)						
Pica	90.03	0	31.4	0	34.88	-
Digging/Burying	26.83	10.46	8.06	1.43	30.04	13.67
Rearing	175.2	555.46	41.36	81.41	23.61	14.66
Propping	353.76	1006.69	83.85	126.28	23.70	12.54
Displacement	78.03	156.43	16.64	12.04	21.33	7.7
Bar-related behaviour	351.79	493.76	71.48	113.66	20.32	23.02
Sniff object	147.98	no	43.08	no	29.11	no
Sniff & Touch object	296.36	objects	60.26	objects	20.33	objects
Chew/Bite object	2.03	present	0.43	present	21.18	present
Jump at lid	19.63	44.93	2.51	4.69	12.79	10.44

Note. There were no objects present during the ***variable-interval*** sessions for the VIOE group. A dash (-) indicates that no instances of the behaviour were observed, whereas a zero (0) indicates that the behaviour did occur but all instances took place outside the PRPs.

In order of increasing percentage of total frequency for the VIOE group, the behavioural measures were: ***displacement***; ***jump at lid***; ***propping***; ***bar-related behaviour***; ***rearing***; and ***digging/burying***. The value for percentage of total occurring during the PRPs ranged from 7.8% to 14.29%. Thus, only a small percentage of each of the behaviours occurred during the PRPs (Table 6.3).

The duration measures for the *variable-interval* groups

In order of increasing percentage of total duration (in seconds) for the VIOS group, the behavioural measures were as follows: ***jump at lid***; ***bar-related behaviour***; ***sniff and touch object***; ***chew/bite object***; ***displacement***; ***rearing***; ***propping***; ***sniff object***; ***digging/burying***; and ***pica***. The percentage of total occurring during the PRPs ranged from 12.79% to 34.88%. Six of these behavioural measures fell between 20% and 24%. With the exception of ***pica*** (34.88%), less than a third (or indeed in most cases, a quarter) of each duration measure occurred during the PRPs (Table 6.3).

In order of increasing percentage of total duration (in seconds) for the VIOE group, the behavioural measures were: ***displacement***; ***jump at lid***; ***propping***; ***digging/burying***; ***rearing***; and ***bar-related behaviour***. The values for the percentage of total occurring during the PRPs ranged from 7.7% to 23.02%. With the exception of ***bar-related behaviour*** (23.02%), all the other values fell below 15%. That is, a small percentage of time was spent engaged in these behaviours during the PRPs (Table 6.3).

Summary

Table 6.4 provides a summary of the percentage of total mean frequency and duration of behaviours occurring during the PRPs (summed over the three ***schedule*** sessions) for all four groups in Experiment 1 (taken from the last two columns of Table 6.2 & Table 6.3).

The frequency measures

With respect to the frequency measures, ***Hypothesis 1 was supported*** (with a couple of exceptions). As expected, for the groups with objects present during ***schedule*** sessions (FIOS & VIOS), the percentage of total frequency occurring during the PRPs was much higher in the ***fixed-interval*** group for all behavioural categories, except ***chew/bite object*** and ***jump at lid***. ***Jump at lid*** was not observed in the FIOS group during ***schedule*** sessions (Table 6.4).

As predicted, for the groups with objects absent during ***schedule*** sessions (FIOE & VIOE), the percentage of total frequency occurring during the PRPs was markedly higher in the ***fixed-***

interval group for all behavioural categories. ***Pica*** was not observed in the VIOE group during ***schedule*** sessions (Table 6.4).

Table 6.4

The percentage of the (total) mean frequency and duration of each behaviour occurring during the PRPs (summed over the three ***schedule*** sessions) for all four groups.

BEHAVIOURAL MEASURE	**% OF TOTAL * FIOS GROUP**	**% OF TOTAL * VIOS GROUP**	**% OF TOTAL * FIOE GROUP**	**% OF TOTAL * VIOE GROUP**
FREQUENCIES				
Pica	79.25	30.77	66.67	-
Digging/Burying	83.2	31.48	75.39	14.29
Rearing	53.18	23.82	55.03	12.80
Propping	51.04	19.69	40.33	10.54
Displacement	48.67	22.25	51.93	7.8
Bar-related behaviour	23.85	13.59	16.82	10.80
Sniff object	59.86	25.36	no objects present	no objects present
Sniff & Touch object	58.52	21.25		
Chew/Bite object	52.30	66.67		
Jump at lid	-	13.49	73.43	10.13
DURATIONS (in seconds)				
Pica	78.79	34.88	77.06	-
Digging/Burying	90.63	30.04	78.95	13.67
Rearing	55.49	23.61	61.58	14.66
Propping	60.94	23.70	53.36	12.54
Displacement	60.49	21.33	63.20	7.7
Bar-related behaviour	54.71	20.32	55.97	23.02
Sniff object	63.10	29.11	no objects present	no objects present
Sniff & Touch object	60.22	20.33		
Chew/Bite object	46.61	21.18		
Jump at lid	-	12.79	72.49	10.44

Note. There were no objects present during the schedule sessions for the FIOE or VIOE groups. A dash (-) indicates that no instances of the behaviour were observed.

Duration measures

With respect to the duration measures, ***Hypothesis 1 was supported***. As predicted, the percentage of total duration occurring during the PRPs was markedly higher in both ***fixed-interval*** groups for all behavioural categories (Table 6.4).

6.3.1.2 HYPOTHESIS TWO: EFFECT OF NOVEL STIMULUS OBJECTS ON PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s AND VI60-s SCHEDULES

*It is predicted that the presence or absence of novel stimulus objects during **fixed-interval** and **variable-interval** running may have some effect on the proportions of behaviours occurring during the PRPs. Thus, it is expected that there will be a difference between the "OS" groups with objects present, and the "OE" groups with objects absent during **fixed-interval** and **variable-interval** sessions (**FIOS** compared to **FIOE** & **VIOS** compared to **VIOE**).*

The *fixed-interval* groups

There was ***partial support for Hypothesis 2***, with respect to the frequency and duration measures. The presence or absence of objects during ***fixed-interval*** sessions had an effect on the proportion of frequency and duration of some of the behaviours that occurred during PRPs, as shown in Table 6.4.

When objects were absent (FIOE group), the proportions were lower for the frequency of ***pica***, ***digging/burying***, ***propping*** and ***bar-related behaviour***. ***Jump at lid*** only occurred if objects were absent. The proportions were very similar (<5% difference) irrespective of presence or absence of objects for the frequency of ***rearing*** and ***displacement*** (Table 6.4).

When objects were absent (FIOE group), the proportions were lower for the duration of ***digging/burying*** and ***propping***. For this same group, the proportion was higher (by about 7%) for the duration of ***rearing***. ***Jump at lid*** only occurred if objects were absent. The proportions were very similar (<5% difference) irrespective of presence or absence of objects for the duration of ***pica***, ***displacement*** and ***bar-related behaviour*** (Table 6.4).

The *variable-interval* groups

Hypothesis 2 was supported. That is, the presence or absence of objects during ***variable-interval*** sessions had an effect on the proportion of frequency and duration of all behaviours that occurred during PRPs (Table 6.4).

When objects were absent (VIOE group), the proportions were lower for the frequency and duration of every category of "non-object directed" behaviour (Table 6.4).

6.3.2 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE DURING THE PRPs, OVER SESSIONS, AND BETWEEN GROUPS

The changes in each behavioural measure (frequency & duration) occurring during the PRPs over the three schedule sessions are presented graphically in Figures 6.11 – 6.14 (inclusive). The scores for all four groups are plotted on each graph (except for ***object-directed behaviours***, since only two groups had objects present), allowing some comparison in trends across the sessions. It should be stressed that this section only covers the patterns of change during the PRPs. The patterns of change for each session in full (not just during the PRPs) are provided in section 6.3.6.

No firm expectations are held with respect to patterns of change within PRPs over the three sessions. If PRPs are stable over sessions, then the proportion of frequency and duration of behaviour should remain constant over sessions.

6.3.2.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

The mean frequency and duration scores of ***bar-related behaviour*** during the PRPs were markedly higher for the ***fixed-interval*** groups across all sessions (Figure 6.11). For the FIOS group, an overall decline in the frequency measure was observed, but the duration measure increased. Thus, there were fewer instances during the PRPs, but they were of longer duration across the three sessions. For the FIOE group, a decline in the frequency measure was seen, but the duration measure remained almost constant across sessions (a very small increase). A gradual increase in the frequency and duration measures was observed for the VIOS group. For the VIOE group there was an overall increase in both the frequency and duration of this behaviour during the PRPs.

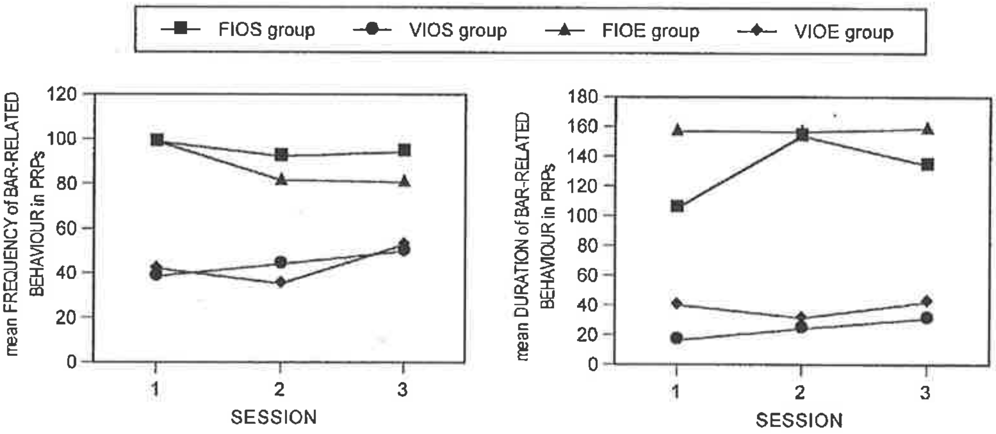


Figure 6.11. Mean frequency (left) and duration (right) scores of ***bar-related behaviour*** during the PRPs for all four groups in Experiment 1

6.3.2.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

All three ***object-directed*** behavioural categories showed noticeably higher frequency and duration scores for the ***fixed-interval*** group (FIOS), during the PRPs (Figure 6.12). The frequency and duration of ***sniff object*** and ***sniff and touch object*** scores during the PRPs showed an overall decline (not always linear) over the three sessions for both the FIOS and VIOS groups. Not all rats engaged in ***chew/bite object*** during the PRPs. In fact, only one rat in the VIOS group was observed to ***chew/bite object*** during the PRPs. An overall decrease across sessions in the frequency and duration scores of this behaviour during PRPs was observed in the FIOS group.

6.3.2.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

The mean frequency and duration scores of ***propping*** during the PRPs were higher for the ***fixed-interval*** groups across all sessions (Figure 6.13). For the FIOS group, a slight increase in both frequency and duration occurred over the three sessions, whilst a decline in these measures was seen for the FIOE group. A slight overall decrease was observed for the frequency and duration measures of ***propping*** scores over the three sessions, for both ***variable-interval*** groups.

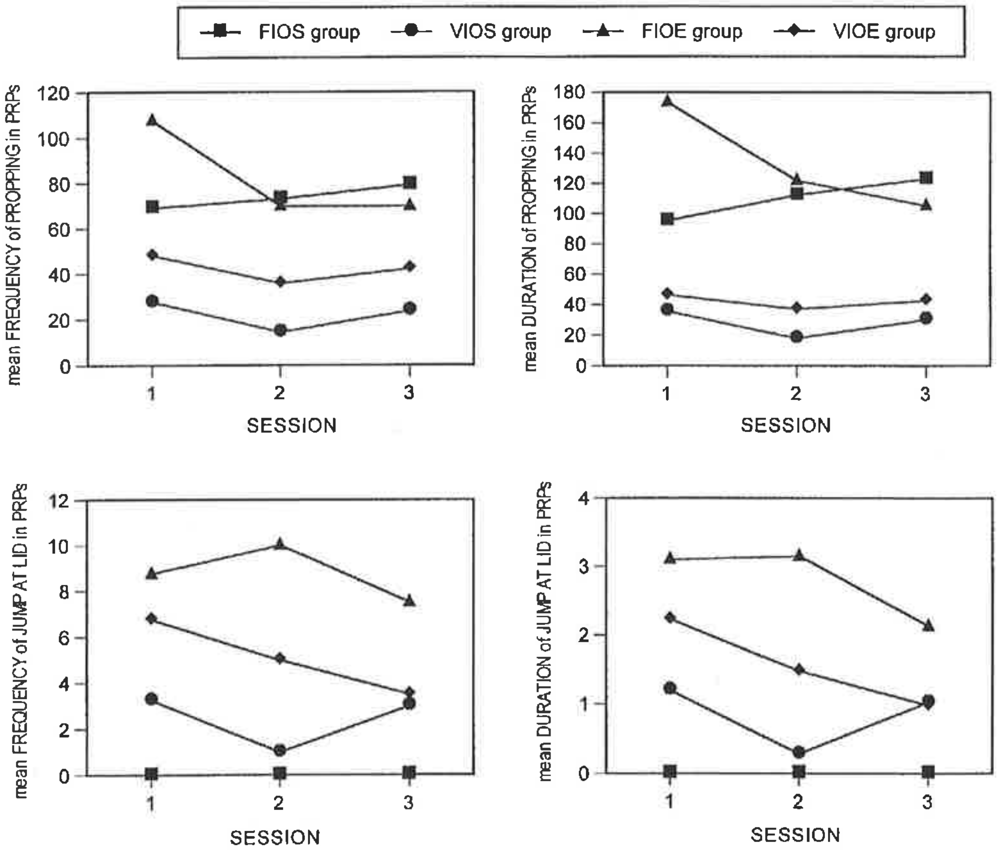


Figure 6.13. Mean frequency (left) and duration (right) scores of ***behaviour directed at the peripheral areas of the box*** during the PRPs, for all four groups in Experiment 1 (top- ***propping***, & bottom- ***jump at lid***)

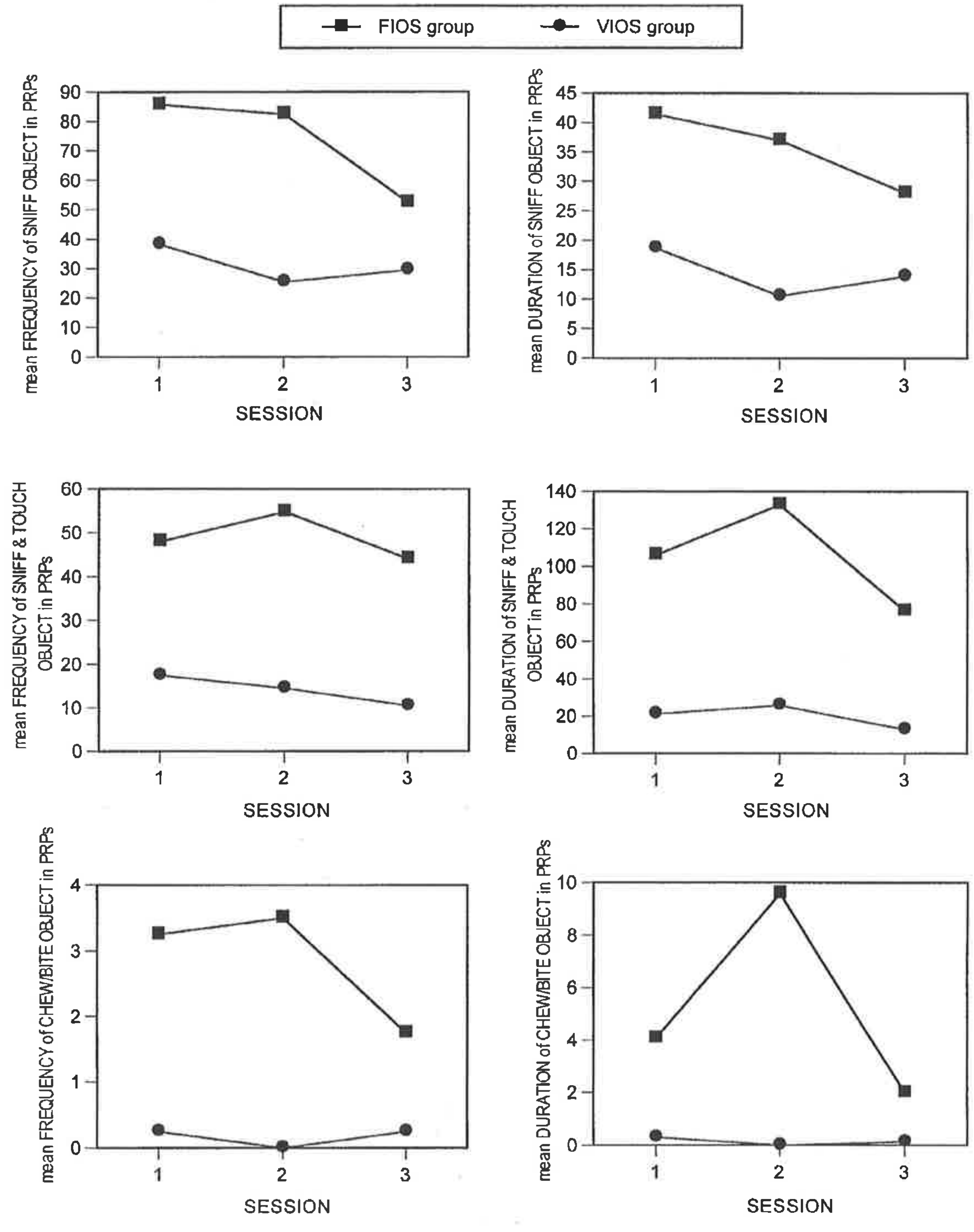


Figure 6.12. Mean frequency (left) and duration (right) scores of ***behaviour directed at the stimulus objects*** during the PRPs for the FIOS and VIOS groups in Experiment 1 (top- ***sniff object***, middle- ***sniff & touch object***, & bottom- ***chew/bite object***)

For the ***jump at lid*** category, the patterns were all different (see Figure 6.13). No instances of this behaviour were observed for the FIOS group. By contrast, the FIOE group obtained the highest scores, with an overall decrease in both frequency and duration during PRPs across sessions. Both ***variable-interval*** groups showed an overall decrease across sessions (almost linear for the VIOE group).

6.3.2.4 OTHER BEHAVIOURAL CATEGORIES

Figure 6.14 (I) indicates that the mean frequency and duration scores of ***displacement*** during the PRPs were higher for the ***fixed-interval*** groups across all sessions. Slight increases in the frequency of ***displacement*** during PRPs over the three sessions were evident for all four groups. For the duration measures, a steady increase was observed for the ***fixed-interval*** groups, with only a slight overall increase during PRPs shown for the ***variable-interval*** groups.

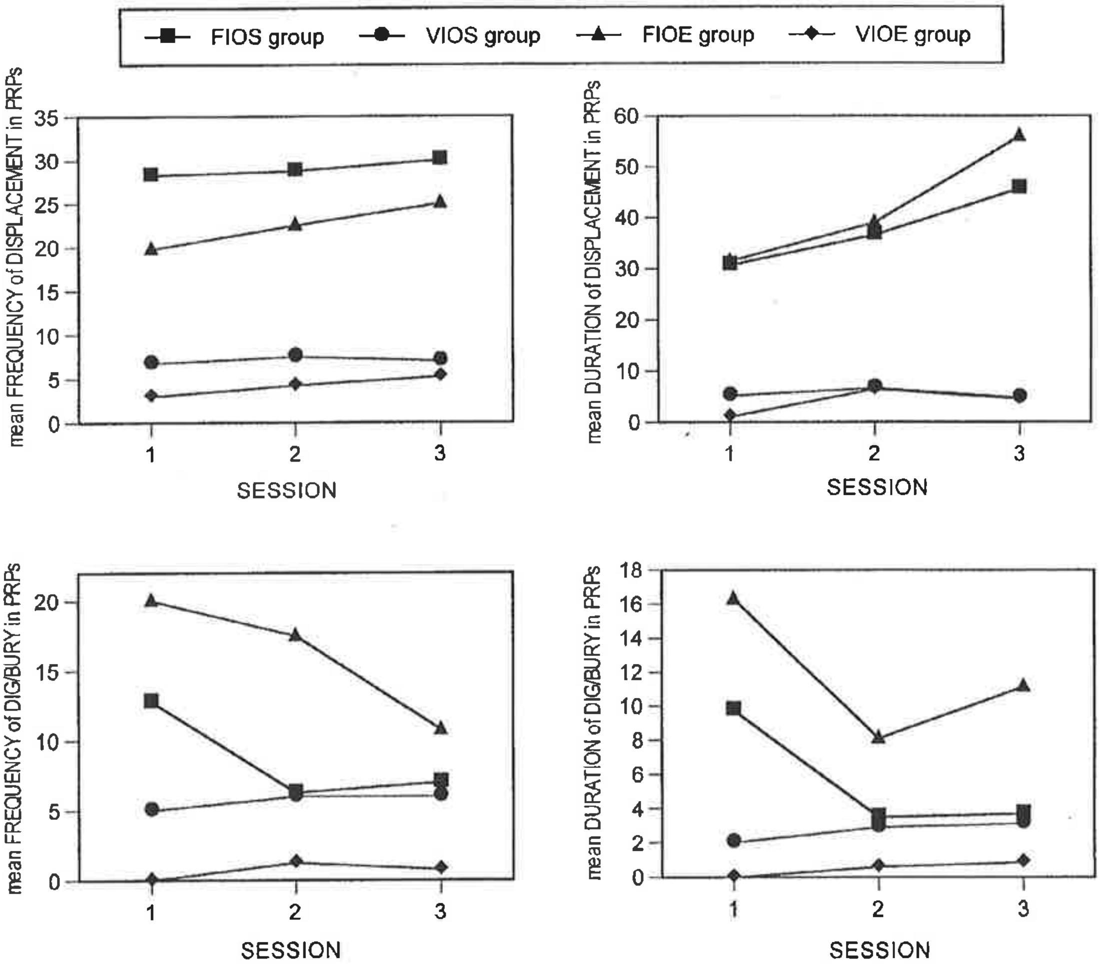


Figure 6.14 (I). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** during the PRPs, for all four groups in Experiment 1 (top- ***displacement***, & bottom- ***digging/burying***)

For ***digging/burying***, the mean frequency and duration scores during the PRPs were again higher for the ***fixed-interval*** groups across all sessions (Figure 6.14:I). An overall decrease in these measures during the PRPs was evident for both ***fixed-interval*** groups, whereas a slight increase was observed for the ***variable-interval*** groups. The raw data indicate that only one rat in the VIOE group engaged in ***digging/burying*** during the PRPs.

The mean frequency and duration scores of ***rearing*** during the PRPs were higher for the ***fixed-interval*** groups across all sessions (Figure 6.14:II). An overall tendency to increase was evident for the frequency and duration measures over the three sessions, for all four groups. The increase was more marked for the two ***fixed-interval*** groups.

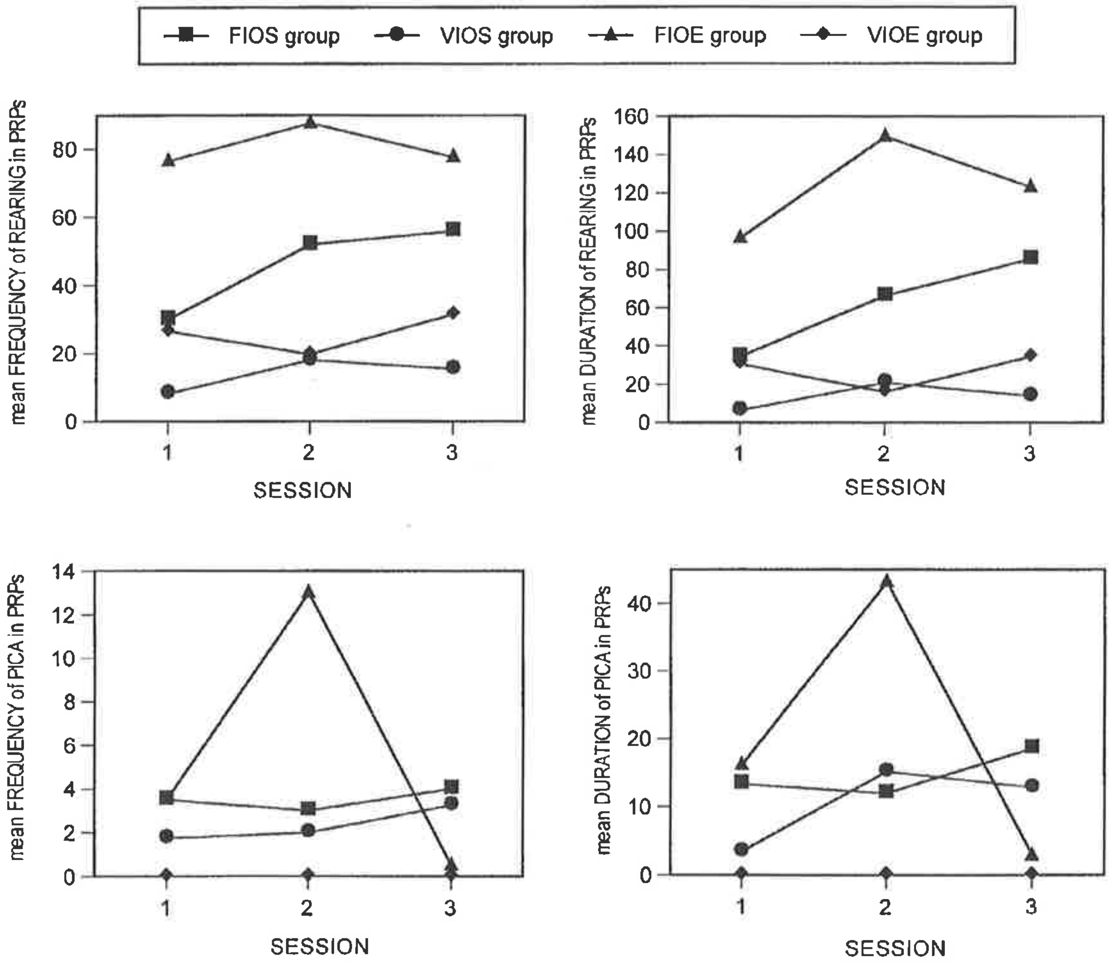


Figure 6.14 (II). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** during the PRPs, for all four groups in Experiment 1 (top- ***rearing***, & bottom- ***pica***)

Figure 6.14(II) shows that there were no instances of ***pica*** during the PRPs for the VIOE group. For the FIOE group, there was a marked increase in session 2, followed by an overall decline. For the two groups with objects present during the schedule sessions (FIOS & VIOS), there was a slight increase over the three sessions, in both the frequency and duration of ***pica*** during PRPs.

6.3.3 CHANGES IN BEHAVIOURS DURING PRPs OVER SCHEDULE SESSIONS, BETWEEN SCHEDULES AND BETWEEN OBJECT CONDITIONS

The previous section presented the mean frequency and duration of the scored behaviours exhibited by the four groups of rats graphically. Since the sample sizes were small, the data have been primarily analysed by description. Bearing this in mind, the data are now analysed by means of statistical testing. A multivariate analysis of variance (MANOVA) was performed for each of the frequency and duration measures, occurring during the PRPs. For each MANOVA there were three independent (or grouping) variables: object (present or absent), schedule (***fixed-interval*** or ***variable-interval***) and session. In each case there was one dependent variable: the frequency or duration measure of a particular behavioural category.

The *F* value associated with the independent/grouping variable (object, schedule or session) in each instance tested the hypothesis that the independent variable had no main effect on the frequency or duration measure being examined (Norusis, 1983). A statistically non-significant *F* value meant that the group means being compared were not significantly different. A statistically significant interaction implied that the dependent variable was *jointly* affected by both grouping variables (Norusis, 1983). Such interactions suggest that there is no point in looking at the separate main effects of the grouping variables, since both affect the behavioural measure.

It should be noted, that there were no objects present in two of the four groups (FIOE & VIOE) during schedule sessions. Therefore, the grouping variable "object" has an obvious effect on ***object-directed behaviours***. If the other independent variables (schedule or session) have a main effect on the frequency or duration of ***object-directed behaviours***, it is only relevant for the two groups with objects present during schedule sessions (FIOS & VIOS).

MANOVA's were not performed on three of the behavioural categories (both frequency & duration measures), since these behaviours occurred too infrequently in the four groups. The behaviours were ***pica***, ***jump at lid*** and ***chew/bite object***. However, there were some instances, and it is worth looking for any possible patterns in these behaviours in the graphs (Figures 6.12, 6.13 & 6.14:II) and tables (Appendix A). The remaining categories of behaviour included in this statistical analysis are: ***bar-related behaviour***, ***sniff object***, ***sniff and touch object***, ***propping***, ***displacement***, ***digging/burying*** and ***rearing***.

Main effect of *schedule*

As can be seen from Table 6.5, the differences between the schedules (***fixed-interval*** or ***variable-interval***) were statistically significant for the frequency and duration measures of all seven behavioural categories. Visual inspection of Figures 6.15 (I-III) indicates that for every behavioural category that demonstrated a main effect of ***schedule***, the mean frequency or duration scores during the PRPs were noticeably higher for the ***fixed-interval*** groups in every session. That is, the frequency and duration of ***digging/burying***, ***rearing***, ***propping***, ***displacement***, ***bar-related behaviour***, ***sniff object*** and ***sniff and touch object*** occurring during the PRPs was higher for rats run on the FI60-s schedule.

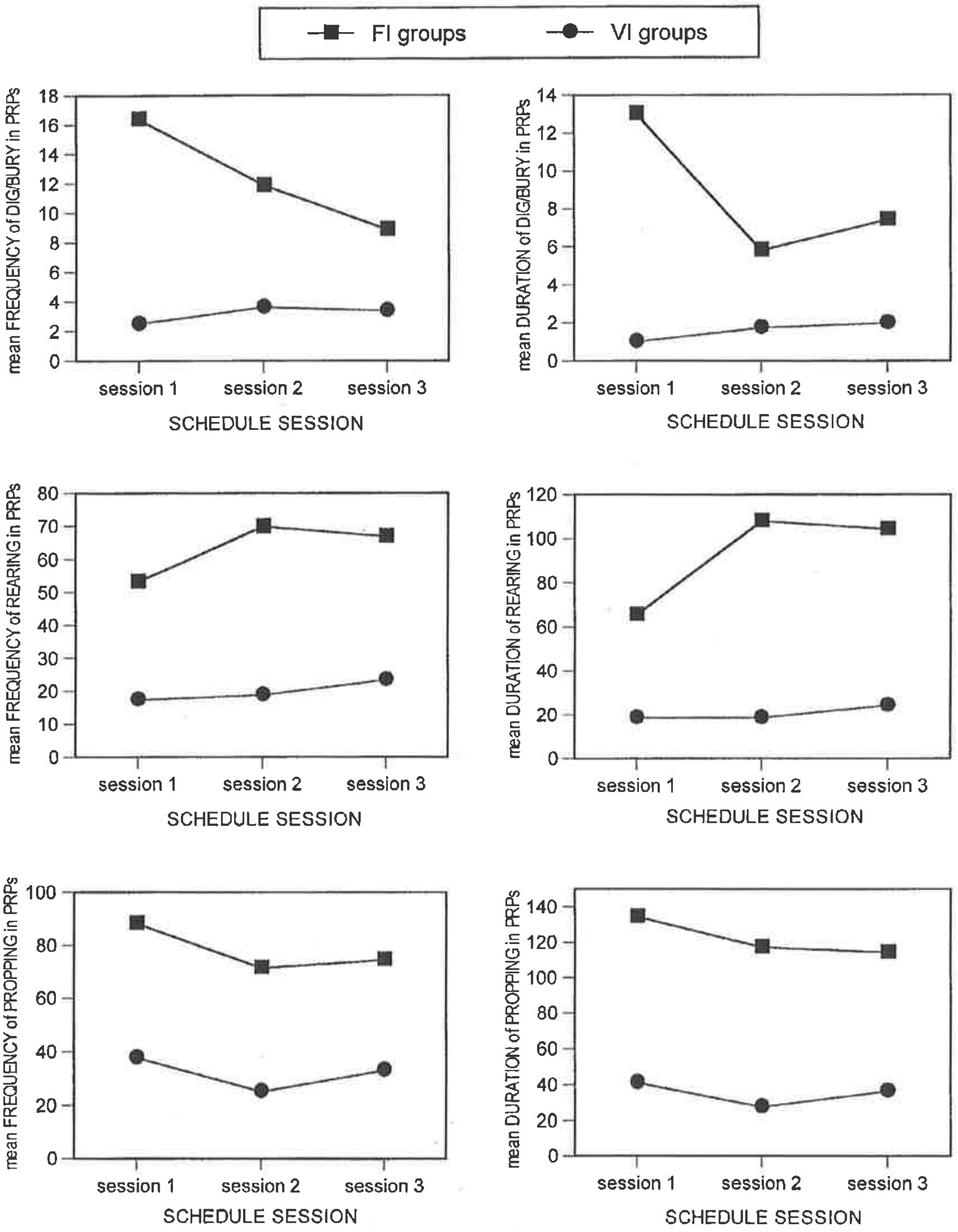


Figure 6.15 (I). Mean frequency (left) and duration (right) of behaviours during the PRPs for the "schedule" grouping variable (top- ***digging/burying***, middle- ***rearing***, & bottom- ***propping***)

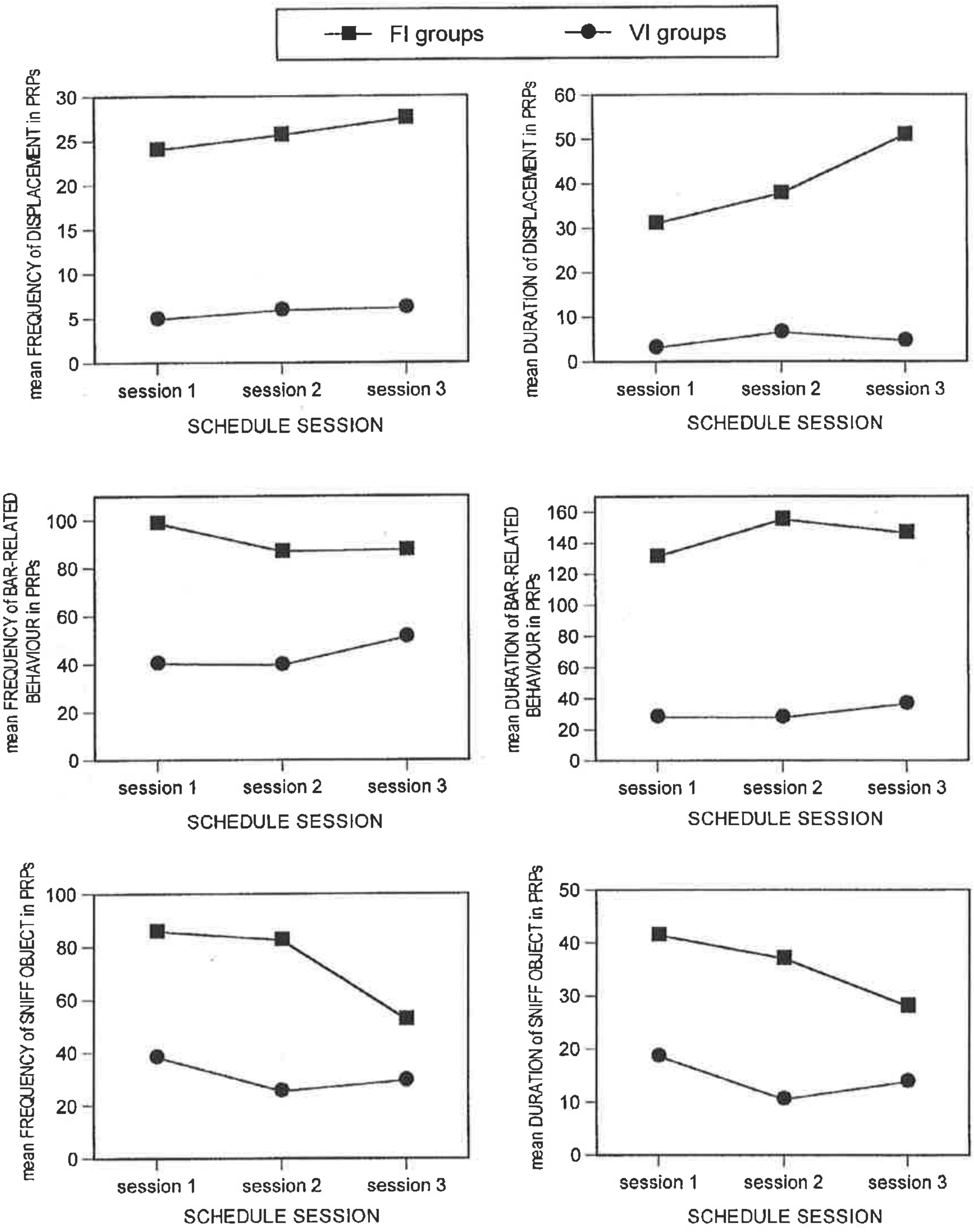


Figure 6.15 (II). Mean frequency (left) and duration (right) of behaviours during the PRPs for the "schedule" grouping variable (top- ***displacement***, middle- ***bar-related behaviour***, & bottom- ***sniff object***)

Table 6.5
Experiment 1 significance levels obtained for measures of behavioural categories during PRPs (*schedule* main effect).

Variable	*F*(1,12)	Significance level (*p*)
Frequency of ***digging/burying****	6.84	<.05
Duration of ***digging/burying****	5.81	<.05
Frequency of ***rearing***	12.11	<.01
Duration of ***rearing***	9.58	<.01
Frequency of ***propping***	7.85	<.05
Duration of ***propping***	13.74	<.005
Frequency of ***displacement***	23.14	<.001
Duration of ***displacement***	28.24	<.001
Frequency of ***sniff and touch object***	7.89	<.05
Duration of ***sniff and touch object***	12.33	<.005
Frequency of ***sniff object***	22.07	<.005
Duration of ***sniff object***	35.88	<.001
Frequency of ***bar-related behaviour***	23.87	<.001
Duration of ***bar-related behaviour***	8.20	<.05

Note. Objects were only present in the FIOS and VIOS groups. (*) indicates that only two instances of this behaviour were observed in the VIOE group during the PRPs. Thus it may be more appropriate to look at possible patterns in Figure 6.14(I), than to use statistical analysis.

Figures 6.15 (I) and (II) show that the mean frequency and duration of ***digging/burying*** and frequency of ***bar-related behaviour*** during the PRPs increased slightly over ***variable-interval*** sessions, whereas these measures decreased over ***fixed-interval*** sessions. Overall increases over sessions were observed for both schedules (***fixed-interval*** **&** ***variable-interval***) for the frequency and duration of ***rearing***, ***displacement***, and duration of ***bar-related behaviour*** during PRPs. An overall decrease in the frequency and duration of ***propping***, ***sniff object*** and ***sniff and touch object*** (Figure 6.15:III) during the PRPs occurred for both schedule types.

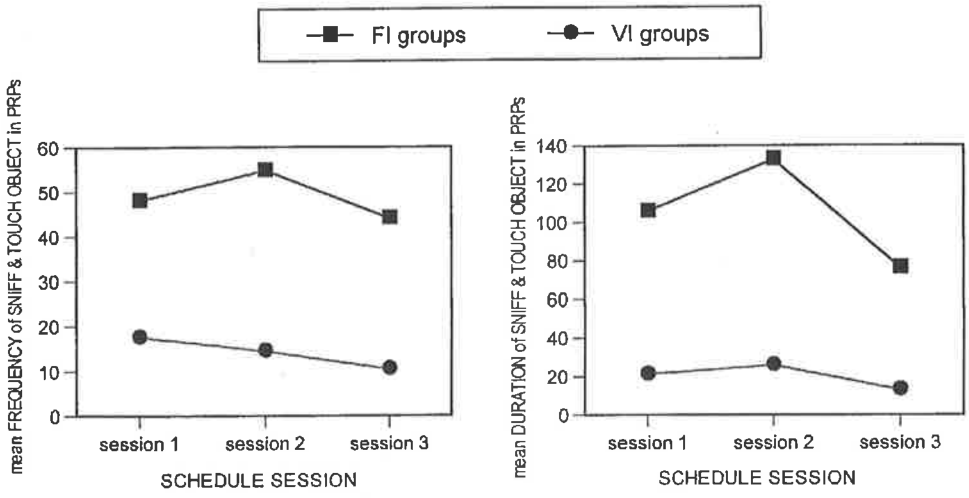


Figure 6.15 (III). Mean frequency (left) and duration (right) of ***sniff and touch object*** during the PRPs for the "schedule" grouping variable

Main effect of *session*

Statistically significant differences over the three schedule sessions (*i.e.*, a ***session*** main effect) were only reflected in the frequency of ***sniff object*** [*F* (2,24)=3.51, *p*<.05] and the duration of ***sniff and touch object*** [*F* (2,24)=3.58, *p*<.05] during the PRPs. Again, it should be noted that objects were only present in the FIOS and VIOS groups. Figure 6.15(IV) shows that the frequency of ***sniff object*** decreased in every session, whilst the duration of ***sniff and touch object*** increased in the second session and then decreased (with an overall decrease over the three sessions).

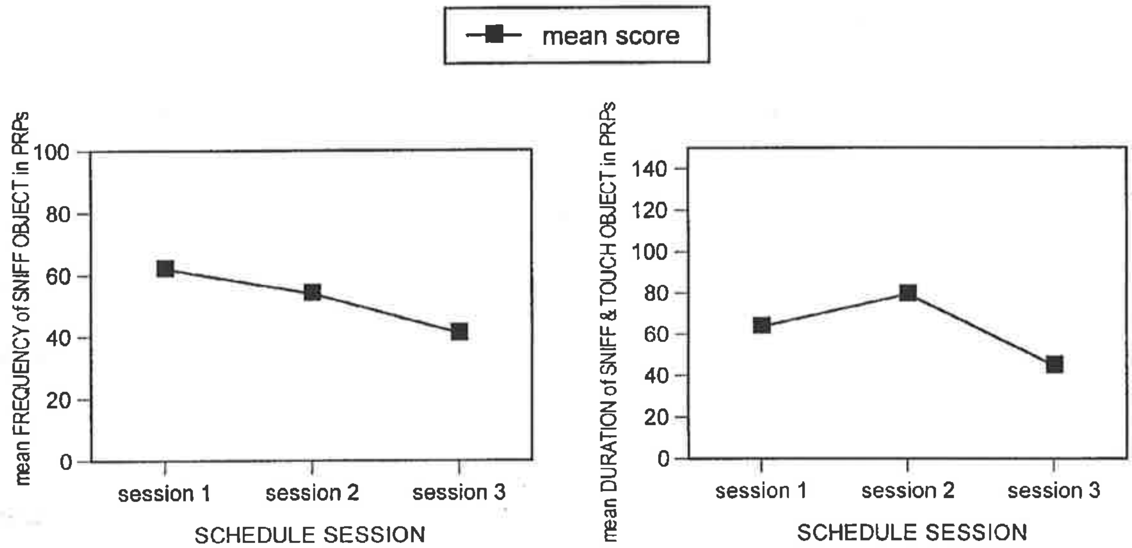


Figure 6.15 (IV). Mean frequency of ***sniff object*** (left) and duration of ***sniff and touch object*** (right) during the PRPs for the "session" grouping variable (***Note*:** objects were only present in two of the four groups)

6.3.4 THE MOST FREQUENTLY OCCURRING BEHAVIOURS, AND ONES OF LONGEST DURATION IN SCHEDULE AND EXTINCTION SESSIONS

In order to test Hypotheses 3 - 6, it was necessary to determine which behavioural events occurred most frequently in each group, for the ***schedule*** (***fixed-interval*** or ***variable-interval***) and ***extinction*** sessions (separately). The mean values for each frequency measure were summed over the three ***schedule*** sessions, and summed over the three ***extinction*** sessions (separately). Similarly, the mean values for each duration measure were summed over the three ***schedule*** and ***extinction*** sessions (separately), and then used to determine which behavioural measures were of longest duration in each group during ***schedule*** and ***extinction*** sessions. These values are presented in separate tables for the ***fixed-interval*** and ***variable-interval*** groups, in the current section. The raw data can be found in Appendix A.

6.3.4.1 HYPOTHESIS THREE: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING FI60-s AND VI60-S SCHEDULES

If objects are <u>*absent*</u> *during* ***fixed-interval*** *and* ***variable-interval*** *sessions, more time and effort can be devoted to behaviours that are* <u>*not*</u> *object-directed. Thus, it is expected that* <u>*higher*</u> *frequencies and durations of non-object behaviours will be observed in the* ***FIOE*** *and* ***VIOE*** *groups during schedule sessions, when compared to their same schedule counterparts. In addition, without objects present to "distract" them during schedule sessions, the frequency and duration of* ***bar pressing*** *scores is expected to be* <u>*higher*</u> *in the* ***FIOE*** *and* ***VIOE*** *groups (****FIOE*** *compared to* ***FIOS*** *&* ***VIOE*** *compared to* ***VIOS****).*

<u>The frequency measures for the *fixed-interval* groups</u>

The mean frequency of each behavioural category for the FIOS group (summed over the three ***fixed-interval*** sessions) in increasing order was: ***pica***; ***chew/bite object***; ***digging/burying***; ***displacement***; ***sniff and touch object***; ***rearing***; ***sniff object***; ***propping***; ***bar-related behaviour***; and ***bar pressing*** (Table 6.6). These values ranged from 13.25 to 2494.25. The behaviour to occur most frequently (apart from ***bar pressing***) was ***bar-related behaviour***, followed by ***propping***. Few instances (<35) of ***pica***, ***chew/bite object*** and ***digging/burying*** were observed. No instances of ***jump at the lid*** were observed.

Using the mean values for each frequency measure summed over the three ***fixed-interval*** sessions (given in Table 6.6), the behavioural events that occurred most frequently in the FIOE group were: ***pica***; ***jump at lid***; ***digging/burying***; ***displacement***; ***rearing***; ***propping***; ***bar-related behaviour***; and ***bar pressing*** (in increasing order). The values ranged from 25.5 to 3427.25. After ***bar pressing***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***propping***. The least frequent behaviours (<40) were ***pica*** and ***jump at lid***.

<u>The duration measures for the *fixed-interval* groups</u>

In increasing order of duration for the FIOS group for the ***fixed-interval*** sessions, these measures were: ***digging/burying***; ***chew/bite object***; ***pica***; ***sniff object***; ***displacement***; ***rearing***; ***bar pressing***; ***sniff and touch object***; ***propping***; and ***bar-related behaviour*** (Table 6.6). These values ranged from 18.68 seconds to 718.91 seconds. Most time was spent engaged in ***bar-related behaviour***, followed by ***propping*** and ***sniff and touch object***. These three behaviours took up more time than ***bar pressing***. Least time (<60 seconds) was spent engaged in ***digging/burying***, ***chew/bite object***, and ***pica***.

Table 6.6
The mean frequency and duration of behaviours for the FIOS and FIOE groups, summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR SCHEDULE SESSIONS * FIOS GROUP**	**SUM OF MEANS FOR SCHEDULE SESSIONS * FIOE GROUP**
FREQUENCIES		
Pica	13.25	25.5
Digging/Burying	31.25	64
Rearing	259.5	439.75
Propping	433.5	612.5
Displacement	178.75	129.5
Bar-related Behaviour	1196.25	1551.5
Sniff object	368.75	no
Sniff & Touch object	250.75	objects
Chew/Bite object	16.25	present
Jump at Lid	0	35.75
Bar pressing	2494.25	3427.25
DURATIONS (in seconds)		
Pica	55.71	80.73
Digging/Burying	18.68	45.03
Rearing	335.88	599.31
Propping	543.03	751.16
Displacement	186.78	200.1
Bar-related Behaviour	718.91	843.73
Sniff object	168.78	no
Sniff & Touch object	523.28	objects
Chew/Bite object	33.6	present
Jump at Lid	0	11.56
Bar pressing	459.79	517.78

For the FIOE group, in increasing order of duration, these measures summed over the three ***fixed-interval*** sessions were: ***jump at lid***; ***digging/burying***; ***pica***; ***displacement***; ***bar pressing***; ***rearing***; ***propping***; and ***bar-related behaviour*** (Table 6.6). These values ranged from 11.56 seconds to 843.73 seconds. Most time was spent engaged in ***bar-related behaviour***, followed by ***propping*** and ***rearing***. These three behaviours took up more time than ***bar pressing***. Least time (<60 seconds) was spent engaged in *jump at lid* and ***digging/burying***.

The frequency measures for the *variable-interval* groups

In increasing order, the mean frequency of each behavioural category for the VIOS group, summed over the three ***variable-interval*** sessions was: ***chew/bite object***; ***pica***; ***jump at lid***; ***digging/burying***; ***displacement***; ***rearing***; ***sniff and touch object***; ***propping***; ***sniff object***; ***bar-related behaviour***; and ***bar pressing*** (Table 6.7). These values ranged from 0.75 to 2894.75. ***Bar-related behaviour*** was the most frequently occurring behaviour (apart from ***bar pressing***), followed by ***sniff object*** and ***propping***. Few instances (<25) of ***chew/bite object*** and ***pica*** were observed. The frequency of ***digging/burying*** and ***jump at lid*** was strikingly similar.

Table 6.7 provides the mean values for each frequency measure summed over the three ***variable-interval*** sessions for the VIOE group. In increasing order, the behavioural measures were: ***digging/burying***; ***jump at lid***; ***displacement***; ***rearing***; ***propping***; ***bar-related behaviour***; and ***bar pressing***. These values ranged from 14 to 3184. Apart from ***bar pressing***, the most frequently occurring behaviour was ***bar-related behaviour*** followed by ***propping***. No instances of ***pica*** and few instances (<15) of ***digging/burying*** were observed.

Table 6.7
The mean frequency and duration of behaviours for the VIOS and VIOE groups, summed over the three ***variable-interval*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR SCHEDULE SESSIONS * VIOS GROUP**	**SUM OF MEANS FOR SCHEDULE SESSIONS * VIOE GROUP**
FREQUENCIES		
Pica	22.75	0
Digging/Burying	54	14
Rearing	175.25	607.25
Propping	334	1196
Displacement	95.5	160.25
Bar-related Behaviour	973.5	1204
Sniff object	367.75	no
Sniff & Touch object	200	objects
Chew/Bite object	0.75	present
Jump at Lid	53.75	150.5
Bar pressing	2894.75	3184
DURATIONS (in seconds)		
Pica	90.03	0
Digging/Burying	26.83	10.46
Rearing	175.2	555.46
Propping	353.76	1006.69
Displacement	78.03	156.43
Bar-related Behaviour	351.79	493.76
Sniff object	147.98	no
Sniff & Touch object	296.36	objects
Chew/Bite object	2.03	present
Jump at Lid	19.63	44.93
Bar pressing	543.18	592.88

The duration measures for the *variable-interval* groups

For the VIOS group, in increasing order of duration (summed over the three ***variable-interval*** sessions), the measures were: ***chew/bite object***; ***jump at lid***; ***digging/burying***; ***displacement***; ***pica***; ***sniff object***; ***rearing***; ***sniff and touch object***; ***bar-related behaviour***; ***propping***; and ***bar pressing*** (Table 6.7). These values ranged from 2.03 seconds to 543.18 seconds. Apart from ***bar pressing***, most time was spent engaged in ***propping***, followed by ***bar-related behaviour***. The rats spent little time (<30 seconds) engaged in ***chew/bite object***, ***jump at lid*** and ***digging/burying***.

In increasing order of duration, the mean values for each duration measure summed over the three ***variable-interval*** sessions for the VIOE group were: ***digging/burying***; ***jump at lid***; ***displacement***; ***bar-related behaviour***; ***rearing***; ***bar pressing***; and ***propping*** (Table 6.7). These values ranged from 10.46 seconds to 1006.69 seconds. Most time was spent engaged in ***propping***, followed by ***bar pressing*** and ***rearing***. Least time (<50 seconds) was spent engaged in ***digging/burying*** and ***jump at lid***.

Summary

Hypothesis 3 was supported, with respect to the frequency and duration measures for the ***fixed-interval*** and ***variable-interval*** groups (with a couple of exceptions). Without objects to "distract" them during ***fixed-interval*** and ***variable-interval*** sessions, the FIOE and VIOE rats were able to engage in more ***bar pressing*** and other non-object behaviours (than the FIOS & VIOS rats).

The frequency of non object-directed behaviours was markedly higher in the group without objects (FIOE group) during ***fixed-interval*** sessions, especially frequency of ***bar pressing*** and ***bar-related behaviour***. The only exception was frequency of ***displacement***. The duration of non object-directed behaviours (including ***bar pressing***) was also markedly higher in the FIOE group during ***fixed-interval*** sessions (Table 6.6).

The frequency of non object-directed behaviours (including ***bar pressing***) was markedly higher in the group without objects (VIOE group) during ***variable-interval*** sessions, with the exception of ***digging/burying***. In addition, there were no instances of ***pica***. The duration of non object-directed behaviours was also markedly higher in the VIOE group during ***variable-interval*** sessions, with the exception of ***digging/burying*** (Table 6.7).

6.3.4.2 HYPOTHESIS FOUR: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

*For rats previously run on a **fixed-interval** schedule, when objects are first encountered during extinction, it is expected that higher frequencies and durations of object-directed behaviours will be observed. That is, the **FIOE** group will direct more behaviour towards novel stimulus objects during extinction sessions than the **FIOS** group. No firm expectations are held for the other behavioural categories.*

*Since extinction is less readily discriminated after a **variable-interval** schedule, and the VIOE group are more likely to be under the "control of the schedule", less behaviour will be directed towards novel stimulus objects (lower frequencies & durations) during extinction sessions (than for the **VIOS** group). No firm expectations are held for the other behavioural categories.*

The frequency measures for the *fixed-interval* groups

Table 6.8 provides the mean values for each frequency measure summed over the three ***extinction*** sessions, for the FIOS group. In increasing order, these categories were: ***jump at lid***; ***chew/bite object***; ***pica***; ***digging/burying***; ***displacement***; ***sniff and touch object***; ***sniff object***; ***propping***; ***rearing***; ***bar-related behaviour***; and ***bar pressing***. These values ranged from 3 to 1990.75. Apart from ***bar pressing***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***rearing*** and ***propping***. The least frequently occurring behaviours (<20) were: ***jump at lid*** and ***chew/bite object***.

For the FIOE group, in increasing order, the mean frequency of each behavioural category summed over the ***extinction*** sessions was: ***chew/bite object***; ***jump at lid***; ***pica***; *digging/burying*; ***displacement***; ***sniff and touch object***; ***sniff object***; ***rearing***; ***propping***; ***bar-related behaviour***; and ***bar pressing*** (Table 6.8). These values ranged from 5.5 to 2969. Apart from ***bar pressing***, the most frequently occurring behaviour was ***bar-related behaviour***, followed by ***propping***, and ***rearing***. Few instances (<30) of ***chew/bite object***, ***jump at lid***, and ***pica*** were observed.

The duration measures for the *fixed-interval* groups

In increasing order of duration for the FIOS group during the ***extinction*** sessions, the behavioural measures were: ***jump at lid***; ***digging/burying***; ***chew/bite object***; ***sniff object***; ***displacement***; ***bar pressing***; ***pica***; ***sniff and touch object***; ***bar-related behaviour***; ***propping*** and ***rearing*** (Table 6.8). These values ranged from 0.88 seconds to 779.38 seconds. Most time was spent engaged in ***rearing***, followed by ***propping*** and ***bar-related behaviour***. In addition, ***sniff***

and touch object and ***pica*** took up more time than ***bar pressing***. Least amount of time (<60 seconds) was spent engaged in ***jump at lid***, ***digging/burying*** and ***chew/bite object***.

Table 6.8

The mean frequency and duration of behaviours for the FIOS and FIOE groups, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR EXTINCTION SESSIONS * FIOS GROUP	SUM OF MEANS FOR EXTINCTION SESSIONS * FIOE GROUP
FREQUENCIES		
Pica	40.5	28
Digging/Burying	41.25	61.5
Rearing	497	491
Propping	484.5	530.25
Displacement	161.25	133
Bar-related Behaviour	1120.25	1046.25
Sniff object	308.5	320.25
Sniff & Touch object	207.5	229.75
Chew/Bite object	16.75	5.5
Jump at Lid	3	9.25
Bar pressing	1990.75	2969
DURATIONS (in seconds)		
Pica	344.11	116.91
Digging/Burying	42.16	41.41
Rearing	779.38	812.73
Propping	744.81	656.86
Displacement	224.1	327.43
Bar-related Behaviour	605.71	438.09
Sniff object	144.06	138.43
Sniff & Touch object	408.41	652.73
Chew/Bite object	50.36	15.36
Jump at Lid	0.88	2.86
Bar pressing	315.06	368.46

In increasing order of duration for the FIOE group during the ***extinction*** sessions, the behavioural measures were: ***jump at lid***; ***chew/bite object***; ***digging/burying***; ***pica***; ***sniff object***; ***displacement***; ***bar pressing***; ***bar-related behaviour***; ***sniff and touch object***; ***propping***; and ***rearing*** (Table 6.8). These values ranged from 2.86 seconds to 812.73 seconds. Most time was spent engaged in ***rearing***, followed by ***propping*** and ***sniff and touch object***. In addition, ***bar-related behaviour*** took up more time than ***bar pressing***. Least time (<60 seconds) was spent engaged in ***jump at lid***, ***chew/bite object*** and ***digging/burying***.

The frequency measures for the *variable-interval* groups

For the VIOS group, in increasing order, the mean frequency of each behavioural category summed over the ***extinction*** sessions was: ***chew/bite object***; ***pica***; ***jump at lid***; ***digging/burying***; ***displacement***; ***sniff and touch object***; ***rearing***; ***sniff object***; ***propping***; ***bar-related behaviour*** and ***bar pressing*** (Table 6.9). These values ranged from 19 to 1850.25. Apart from ***bar pressing***, the most frequently occurring behaviour was ***bar-related behaviour***, followed by ***propping***, ***sniff object***, and ***rearing***. Least frequently (<55) occurring behaviours were ***chew/bite object***, ***pica*** and ***jump at lid***.

Table 6.9
The mean frequency and duration of behaviours for the VIOS and VIOE groups, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR EXTINCTION SESSIONS * VIOS GROUP	SUM OF MEANS FOR EXTINCTION SESSIONS * VIOE GROUP
FREQUENCIES		
Pica	50.25	10.25
Digging/Burying	71.25	17.75
Rearing	328.25	582
Propping	452.25	1125
Displacement	118.25	141.75
Bar-related Behaviour	1041	633.5
Sniff object	382.75	332.5
Sniff & Touch object	282	262.5
Chew/Bite object	19	9
Jump at Lid	53.25	74.25
Bar pressing	1850.25	1631.25
DURATIONS (in seconds)		
Pica	265.86	86.7
Digging/Burying	20.88	8.36
Rearing	445.83	674.04
Propping	518.44	1290.48
Displacement	150.13	237.73
Bar-related Behaviour	536.11	351.83
Sniff object	146.38	120.65
Sniff & Touch object	598.25	634.26
Chew/Bite object	60.99	22.16
Jump at Lid	16.76	20.86
Bar pressing	308.35	260.46

For the VIOE group, in increasing order, the mean frequency of each behavioural category summed over the ***extinction*** sessions was: ***chew/bite object***; ***pica***; ***digging/burying***; ***jump at lid***; ***displacement***; ***sniff and touch object***; ***sniff object***; ***rearing***; ***bar-related behaviour***; ***propping***; and ***bar pressing*** (Table 6.9). These values ranged from 9 to 1631.25. Apart from *bar pressing*, the most frequently occurring behaviour was ***propping*** followed by ***bar-related behaviour*** and ***rearing***. Least frequently (<20) occurring behaviours were ***chew/bite object***, ***pica*** and ***digging/burying***.

The duration measures for the *variable-interval* groups

In increasing order of duration, the measures summed over the three ***extinction*** sessions for the VIOS group were: ***jump at lid***; ***digging/burying***; ***chew/bite object***; ***sniff object***; ***displacement***; ***pica***; ***bar pressing***; ***rearing***; ***propping***; ***bar-related behaviour***; and ***sniff and touch object*** (Table 6.9). These values ranged from 16.76 seconds to 598.25 seconds. Most time was spent engaged in ***sniff and touch object***, followed by ***bar-related behaviour***, and ***propping***. In addition, ***rearing*** took up more time than ***bar pressing***. Least time (<30 seconds) was spent engaged in ***jump at lid*** and ***digging/burying***.

In increasing order of duration for the VIOE group during the ***extinction*** sessions, the behavioural measures were: ***digging/burying***; ***jump at lid***; ***chew/bite object***; ***pica***; ***sniff object***; ***displacement***; ***bar pressing***; ***bar-related behaviour***; ***sniff and touch object***; ***rearing***; and ***propping*** (Table 6.9). These values ranged from 8.36 seconds to 1290.48 seconds. Most time was spent engaged in ***propping***, followed by ***rearing*** and ***sniff and touch object***. In addition, ***bar-related behaviour*** took up more time than ***bar pressing***. Least time (<25 seconds) was spent engaged in ***digging/burying***, ***jump at lid*** and ***chew/bite object***.

Summary

There was ***partial support for Hypothesis 4***, with respect to the frequency and duration measures during ***extinction***, for the rats previously run on the ***fixed-interval*** schedule (Table 6.8). Thus, there was some support for the prediction that the frequency and duration of ***object-directed behaviours*** would be higher in the FIOE group during ***extinction*** (when objects were first encountered). No firm expectations were held for the other non-object behaviours.

When objects were first encountered during ***extinction*** (FIOE group), frequency of ***sniff and touch object*** and ***sniff object*** were higher. The frequency of ***chew/bite object***, on the other hand, was noticeably less. With respect to the other behaviours, the frequency of ***pica***, ***bar-related behaviour***, ***rearing*** and ***displacement*** was lower for the FIOE group (Table 6.8).

When objects were first encountered during ***extinction*** (FIOE group), duration of ***sniff and touch object*** was higher. The duration of ***chew/bite object*** and ***sniff object***, however, was noticeably less. With respect to the other behaviours, the duration of ***pica***, ***bar-related behaviour***, ***digging/burying*** and ***propping*** were lower for the FIOE group (Table 6.8).

Hypothesis 4 was supported, with respect to the frequency and duration measures during ***extinction***, for the rats previously run on the ***variable-interval*** schedule (Table 6.9). That is, the frequency and duration of ***object-directed behaviours*** was lower in the VIOE group during ***extinction***, because they were more likely to have been "under control of the schedule" (without objects to "distract" them during ***variable-interval*** running). No firm expectations were held for the other non-object behaviours.

When objects were first encountered during ***extinction*** (VIOE group), less ***object-directed behaviour*** (in terms of frequency) was engaged in during ***extinction***. With respect to the other behaviours, the frequency of ***pica***, ***digging/burying***, ***bar-related behaviour*** and ***bar pressing*** were also lower for the VIOE group (Table 6.9).

When objects were first encountered during ***extinction*** (VIOE group), less time was spent engaged in ***object-directed behaviour*** during ***extinction***, with one exception. Only the duration of ***sniff and touch object*** was higher in this group. With respect to the other behaviours, the duration of ***pica***, ***digging/burying***, ***bar-related behaviour*** and ***bar pressing*** were lower for the VIOE group (Table 6.9).

6.3.4.3 HYPOTHESIS FIVE: FREQUENCY AND DURATION OF BEHAVIOURS DURING FI60-s AND VI60-s SCHEDULES

Rats run on the more predictable ***fixed-interval*** *schedule should demonstrate lower frequency and duration of* ***bar pressing*** *and higher frequency and duration of other behaviours than their counterpart rats run on the less predictable* ***variable-interval*** *schedule (****FIOS*** *compared to* ***VIOS*** *&* ***FIOE*** *compared to* ***VIOE****).*

Table 6.10 provides a summary of the mean frequency and duration of behaviours for all groups summed over the three schedule sessions (Table 6.6 & Table 6.7 combined).

The frequency measures

With respect to the frequency measures, there was ***partial support for Hypothesis 5***. It was predicted that lower frequency of ***bar pressing*** would be observed in the ***fixed-interval*** groups. However, this was only the case when objects were present (FIOS group).

It was further predicted that higher frequency of other behaviours would be observed in the ***fixed-interval*** groups. This was indeed the case for the frequency of ***bar-related behaviour*** (both groups), and the three ***object-directed behaviours*** were higher in the FIOS group (although ***sniff object*** was almost the same). However, frequency of ***jump at lid*** was either nonexistent (FIOS group) or much lower for the ***fixed-interval*** groups (Table 6.10).

Table 6.10
The mean frequency and duration of behaviours for all groups summed over the three schedule sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR SCHEDULE SESSIONS * FIOS GROUP**	**SUM OF MEANS FOR SCHEDULE SESSIONS * VIOS GROUP**	**SUM OF MEANS FOR SCHEDULE SESSIONS * FIOE GROUP**	**SUM OF MEANS FOR SCHEDULE SESSIONS * VIOE GROUP**
FREQUENCIES				
Pica	13.25	22.75	25.5	0
Digging/Burying	31.25	54	64	14
Rearing	259.5	175.25	439.75	607.25
Propping	433.5	334	612.5	1196
Displacement	178.75	95.5	129.5	160.25
Bar-related Behaviour	1196.25	973.5	1551.5	1204
Sniff object	368.75	367.75	no	no
Sniff & Touch object	250.75	200	objects	objects
Chew/Bite object	16.25	0.75	present	present
Jump at Lid	0	53.75	35.75	150.5
Bar pressing	2494.25	2894.75	3427.25	3184
DURATIONS (in seconds)				
Pica	55.71	90.03	80.73	0
Digging/Burying	18.68	26.83	45.03	10.46
Rearing	335.88	175.2	599.31	555.46
Propping	543.03	353.76	751.16	1006.69
Displacement	186.78	78.03	200.1	156.43
Bar-related Behaviour	718.91	351.79	843.73	493.76
Sniff object	168.78	147.98	no	no
Sniff & Touch object	523.28	296.36	objects	objects
Chew/Bite object	33.6	2.03	present	present
Jump at Lid	0	19.63	11.56	44.93
Bar pressing	459.79	543.18	517.78	592.88

If objects were present (FIOS group), the frequency scores of ***rearing***, ***propping***, ***displacement*** were higher for the ***fixed-interval*** rats (***support for Hypothesis 6***), whereas the frequency of ***pica*** and ***digging/burying*** was lower. However, if objects were absent, this trend was the exact opposite (Table 6.10).

Thus, the presence or absence of objects as well as the predictability or unpredictability of the schedule appeared to have an effect upon the frequency measures.

The duration measures

With respect to the duration measures, there was ***partial support for Hypothesis 5***. It was predicted that lower duration of ***bar pressing*** would be observed in the ***fixed-interval*** groups. Indeed, this was found to be the case.

It was also predicted that higher duration of other behaviours would be observed in the ***fixed-interval*** groups. For rats run on the ***fixed-interval*** schedule, the duration of ***rearing***, ***displacement*** and the three ***object-directed behaviours*** were higher, as expected. In addition, the duration of ***bar-related behaviour*** was markedly higher in these groups (Table 6.10).

However, if objects were present, the duration scores of ***pica***, and ***digging/burying*** were lower for ***fixed-interval*** rats, whereas the duration of ***propping*** was higher. If objects were absent, the reverse was true for these behaviours (Table 6.10).

Again, the presence or absence of objects as well as the predictability or unpredictability of the schedule appeared to have an effect upon the duration measures.

6.3.4.4 HYPOTHESIS SIX: FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

During extinction, the ***fixed-interval*** *rats should more readily discriminate between the previous* ***fixed-interval*** *schedule and new extinction sessions, than their counterpart rats previously run on the* ***variable-interval*** *schedule (**FIOS** compared to **VIOS** & **FIOE** compared to **VIOE**). Thus,* ***fixed-interval*** *groups should demonstrate lower frequency and duration of* ***bar pressing*** *and higher frequency and duration of other behaviours.*

Table 6.11 provides a summary of the mean frequency and duration of behaviours for all groups summed over the three ***extinction*** sessions (Table 6.8 & Table 6.9 combined).

The frequency measures

With respect to the frequency measures, there was ***partial support for Hypothesis 6***. It was predicted that lower frequency of ***bar pressing*** would be observed in the ***fixed-interval*** groups. In fact, the opposite was found to be the case. The frequency of ***bar pressing*** was higher for rats in the ***fixed-interval*** groups, especially for the group with objects first present during ***extinction*** (FIOE group).

Table 6.11
The mean frequency and duration of behaviours for all groups summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR EXTINCTION SESSIONS * FIOS GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS * VIOS GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS * FIOE GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS * VIOE GROUP**
FREQUENCIES				
Pica	40.5	50.25	28	10.25
Digging/Burying	41.25	71.25	61.5	17.75
Rearing	497	328.25	491	582
Propping	484.5	452.25	530.25	1125
Displacement	161.25	118.25	133	141.75
Bar-related Behaviour	1120.25	1041	1046.25	633.5
Sniff object	308.5	382.75	320.25	332.5
Sniff & Touch object	207.5	282	229.75	262.5
Chew/Bite object	16.75	19	5.5	9
Jump at Lid	3	53.25	9.25	74.25
Bar pressing	1990.75	1850.25	2969	1631.25
DURATIONS (in seconds)				
Pica	344.11	265.86	116.91	86.7
Digging/Burying	42.16	20.88	41.41	8.36
Rearing	779.38	445.83	812.73	674.04
Propping	744.81	518.44	656.86	1290.48
Displacement	224.1	150.13	327.43	237.73
Bar-related Behaviour	605.71	536.11	438.09	351.83
Sniff object	144.06	146.38	138.43	120.65
Sniff & Touch object	408.41	598.25	652.73	634.26
Chew/Bite object	50.36	60.99	15.36	22.16
Jump at Lid	0.88	16.76	2.86	20.86
Bar pressing	315.06	308.35	368.46	260.46

Hypothesis 6 also predicted that higher frequency of other behaviours would be observed in the ***fixed-interval*** groups. Indeed, the frequency of ***bar-related behaviour*** was higher for the ***fixed-interval*** groups. However, the frequency of the three ***object-directed behaviours*** was lower for rats previously run on the ***fixed-interval*** schedule, and the frequency of ***jump at lid*** was much lower for these groups (Table 6.11).

If objects were present during schedule sessions (***fixed-interval*** or ***variable-interval***), the frequency scores of ***pica*** and ***digging/burying*** were lower for the ***fixed-interval*** group (FIOS), whilst the frequency scores of ***rearing***, ***propping*** and ***displacement*** were higher. If objects were first present during ***extinction*** sessions, the reverse was the case for these behaviours in the ***fixed-interval*** group (FIOE).

Thus, whether objects were first present during ***schedule*** sessions or ***extinction***, as well as the ease or difficulty of the discrimination between the previous ***schedule*** and new ***extinction*** conditions appeared to have an effect upon the frequency measures.

The duration measures

With respect to the duration measures, there was ***partial support for Hypothesis 6***. It was predicted that lower frequency of ***bar pressing*** would be observed in the ***fixed-interval*** groups. Instead, the duration of ***bar pressing*** was higher for the ***fixed-interval*** groups.

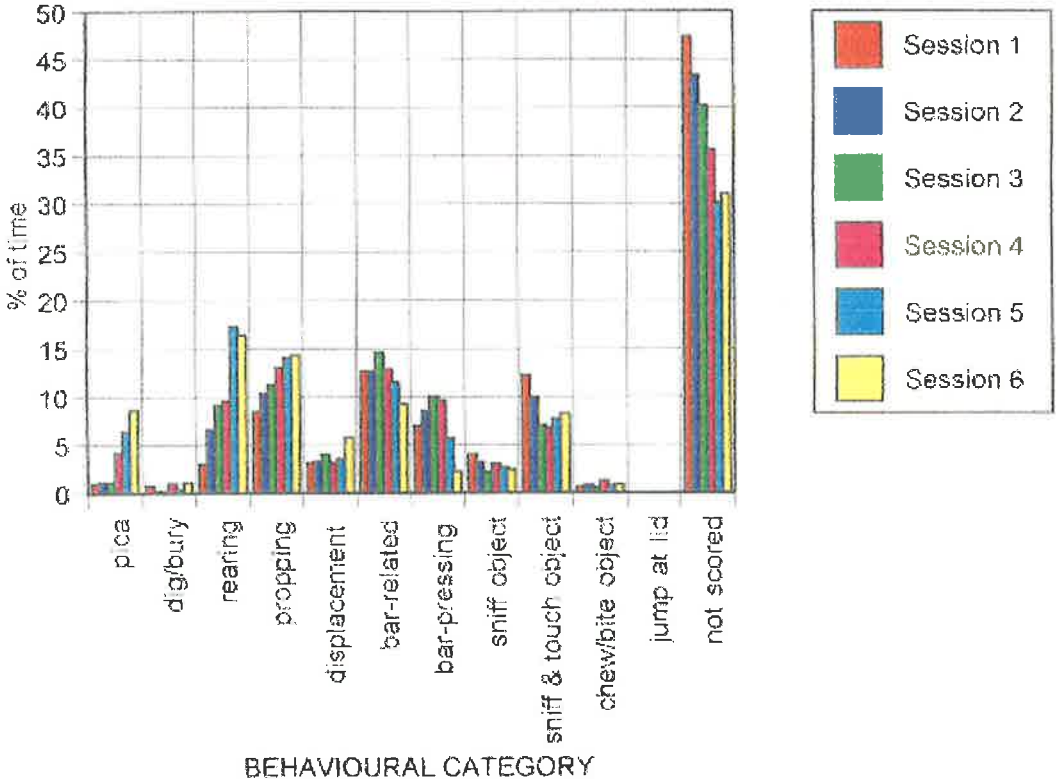
Hypothesis 6 also predicted that higher frequency of other behaviours would be observed in the ***fixed-interval*** groups. As predicted, the duration of ***bar-related behaviour***, ***pica***, ***digging/burying***, ***rearing***, and ***displacement*** were higher for the ***fixed-interval*** groups. However, the duration scores for ***chew/bite object*** and ***jump at lid*** were lower (Table 6.11).

If objects were present during schedule sessions, the duration scores of ***sniff object*** and ***sniff and touch object*** were lower for the ***fixed-interval*** group (FIOS), whilst the duration scores of ***propping*** were higher. If objects were first present during ***extinction*** sessions, the reverse was the case for these behaviours in the ***fixed-interval*** group (FIOE).

Again, whether objects were first present during ***schedule*** sessions or ***extinction***, as well as whether the ease or difficulty of the discrimination between the previous ***schedule*** and new ***extinction*** conditions appeared to have an effect upon the duration measures.

6.3.5 PERCENTAGE OF TOTAL SESSION TIME SPENT ENGAGED IN EACH BEHAVIOURAL CATEGORY, OVER SESSIONS, AND BETWEEN GROUPS

Graphical representations for the mean percentage of time spent engaged in each behavioural category are provided in Figures 6.16 (I) and (II). It should be noted that a substantial percentage of "not scored" exists for each group. As Table 6.12 indicates, between 25% and 70% of session time was spent engaged in behavioural categories that were not scored despite the wide range of behavioural categories included (eleven in all). Most of this ***not scored*** category is likely to



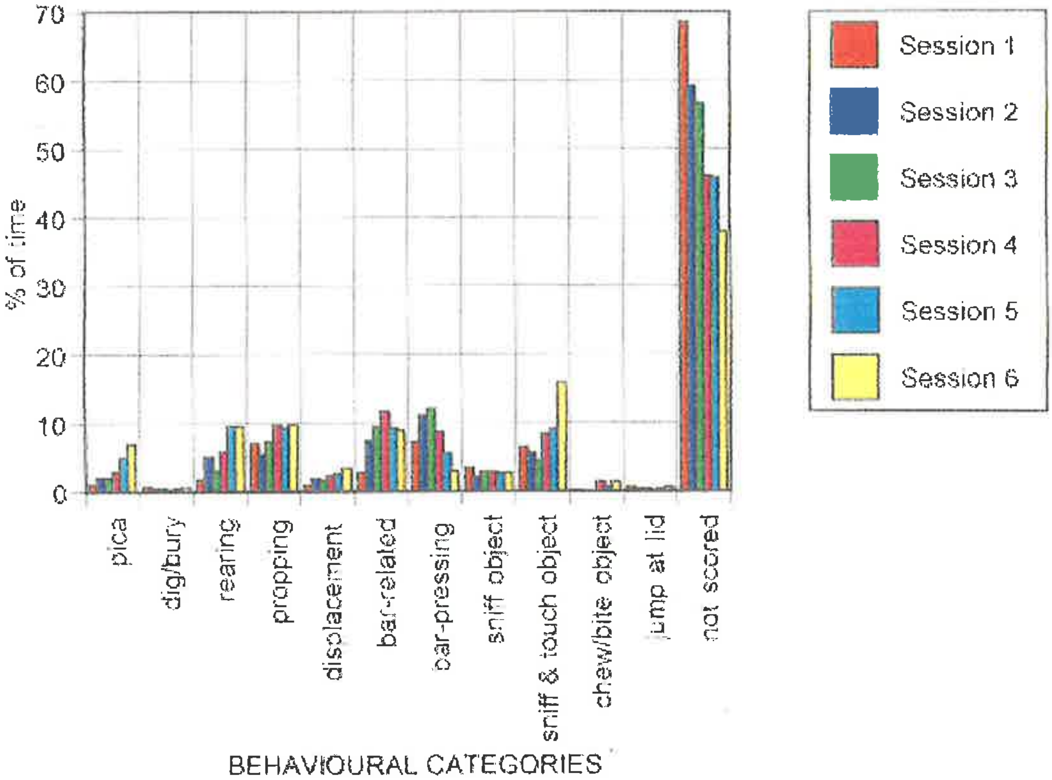
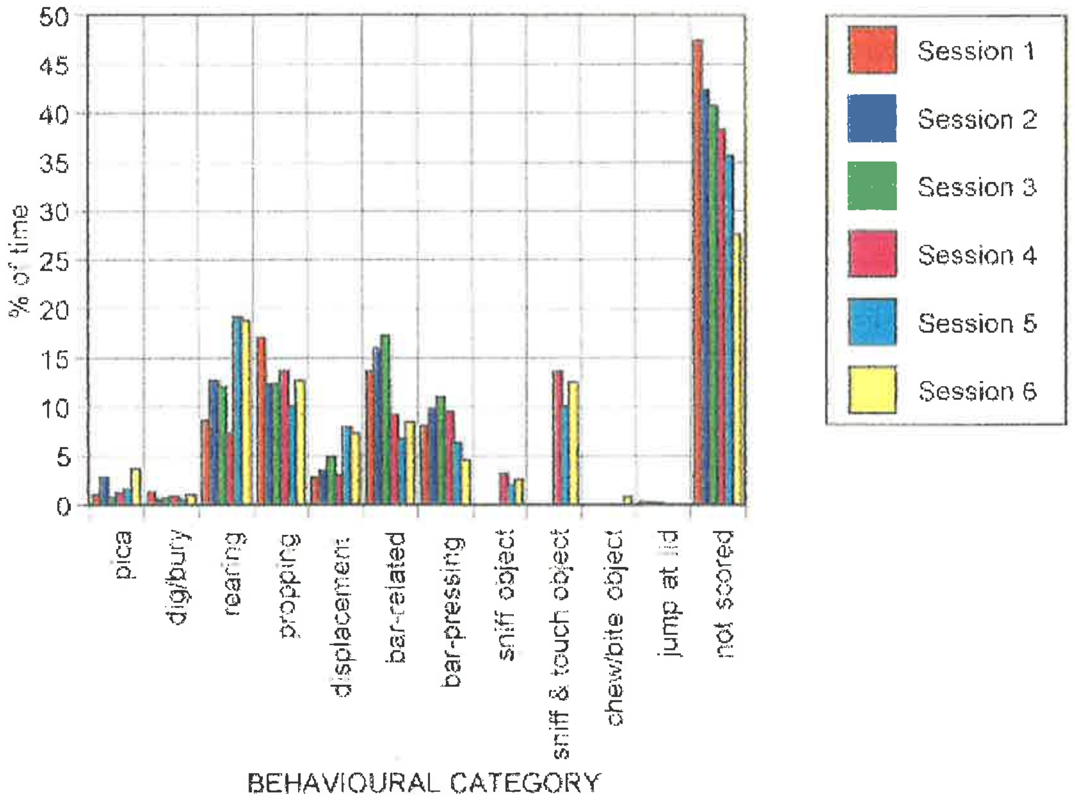


Figure 6.16 (I). Mean percentage of time spent engaged in each behavioural category, for the FIOS (top) and VIOS (bottom) groups in Experiment 1, for each session. (Calculated as mean time in seconds spent engaged in behaviour, as a percentage of total session time, i.e., 1800 seconds).



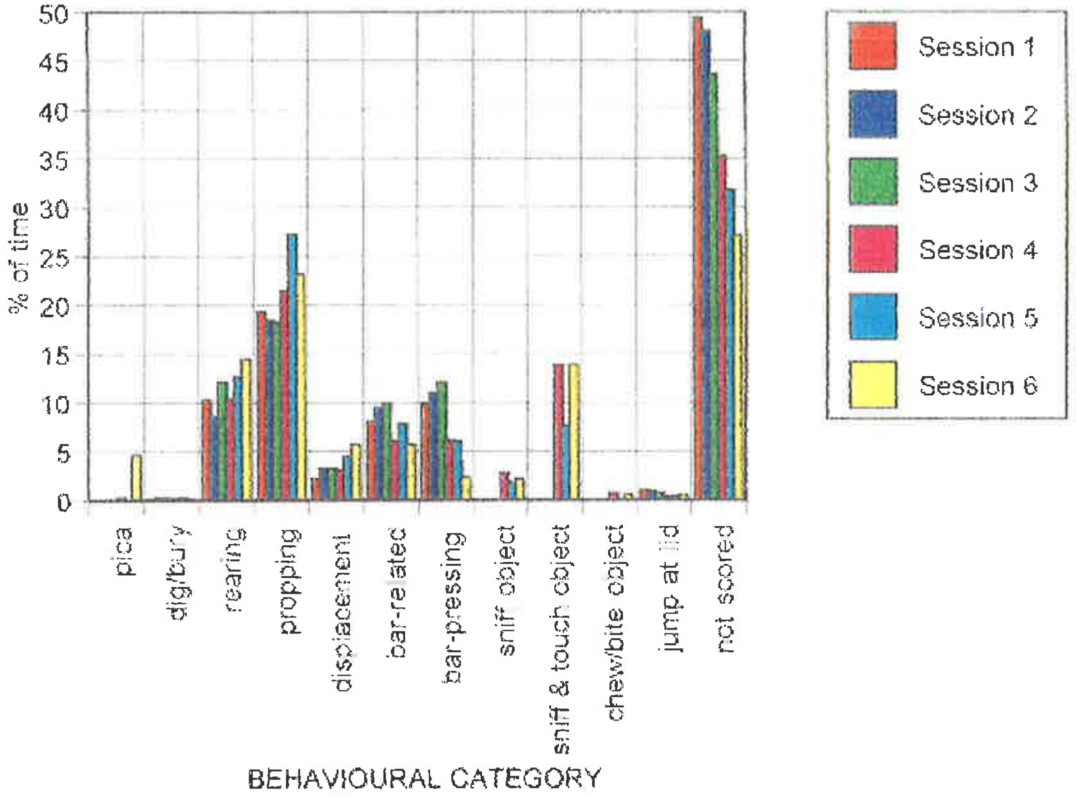


Figure 6.16 (II). Mean percentage of time spent engaged in each behavioural category, for the FIOE (top) and VIOE (bottom) groups in Experiment 1, for each session. (Calculated as mean time in seconds spent engaged in behaviour, as a percentage of total session time, i.e., 1800 seconds).

represent ***general ambulatory behaviour***. That is, the rats' movement between the bar area, objects, and peripheral areas of the box.

Table 6.12
The percentage of total session time (1800 seconds) spent engaged in behaviour that was ***not scored***.

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS	47.41 %	43.38 %	40.14 %	35.6 %	30.09 %	31.03 %
VIOS	68.43 %	59.14 %	56.6 %	46.06 %	45.72 %	37.78 %
FIOE	47.41 %	42.39 %	40.79 %	38.38 %	35.62 %	27.6 %
VIOE	49.36 %	48.06 %	43.65 %	35.24 %	31.73 %	27.05 %

The percentage of total session time spent engaged in behaviours that were ***not scored*** decreased over both ***schedule*** and ***extinction*** sessions for all groups. These percentages were strikingly similar in the ***fixed-interval*** groups in every session, irrespective of whether objects were present or not. For the ***variable-interval*** groups, the percentages were higher in every session, if objects were first present during ***schedule*** sessions (VIOS group). Overall, the percentages were higher for both ***variable-interval*** groups during ***schedule*** sessions, whereas only the VIOS group was noticeably higher during ***extinction*** sessions.

6.3.5.1 BEHAVIOURS DIRECTED AT THE BAR AND FOOD-TROUGH AREA

During ***schedule*** sessions, the ***fixed-interval*** groups engaged in ***behaviour directed at the bar and food-trough area*** spent between 19.63% and 28.25% of total session time engaged in ***behaviour directed at the bar and food-trough area*** (Table 6.13). By contrast, these behaviours represented between 9.85% and 21.97% of total session time for the ***variable-interval*** groups. Thus, ***behaviour directed at the bar and food-trough area*** took up less than 29% of total session time in all cases, but never represented less than 9% of total session time during ***schedule*** sessions. The percentages were higher in every session for groups with objects absent during ***schedule*** sessions (FIOE & VIOE).

During ***extinction*** sessions, the ***fixed-interval*** groups engaged in ***behaviour directed at the bar and food-trough area*** for between 11.42% and 22.48% of total session time (Table 6.13). The

variable-interval groups spent between 8.04% and 20.35% of ***extinction*** sessions engaged in these behaviours. ***Behaviour directed at the bar and food-trough area*** took up less than 23% of total session time, but never represented less than 8% of total session time during ***extinction***. The percentages were higher for groups with objects first present during ***schedule*** sessions (FIOS & VIOS), except in session 6 for the ***fixed-interval*** groups.

Table 6.13
The percentage of total session time (1800 seconds) spent engaged in ***behaviour directed at the bar and food-trough area*** (***bar-pressing*** + ***bar-related behaviour***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS	19.63 %	21.22 %	24.63 %	22.48 %	17.26 %	11.42 %
VIOS	9.85 %	18.41 %	21.46 %	20.35 %	14.76 %	11.81 %
FIOE	21.71 %	25.69 %	28.25 %	18.73 %	13.10 %	12.98 %
VIOE	17.87 %	20.53 %	21.97 %	12.14 %	13.84 %	8.04 %

The overall pattern for all four groups was similar (except session 5 for the VIOE group). The percentages gradually increased over the three ***schedule*** sessions, then decreased in the first ***extinction*** session and continued to gradually decrease. The score for the VIOS group in the first ***schedule*** session was substantially lower than the other groups. Similarly, the score for the VIOE group in the first ***extinction*** session was substantially lower (Table 6.13).

6.3.5.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

During ***schedule*** sessions, the FIOS group spent between 9.66% and 16.81% of total session time engaged in ***behaviour directed at the stimulus objects*** (Table 6.14). These percentages were lower for the VIOS group (between 7.23% & 9.91%). Thus, between 7% and 17% of total session time was spent engaged in ***object-directed behaviours*** in all cases.

During ***extinction*** sessions, between 10.98% and 11.47% of the FIOS group's time was spent engaged in these behaviours, whereas the percentages were higher for the FIOE group, ranging from 12.06% to 16.9% (Table 6.14). The VIOS group spent between 12.42% and 19.87% of its total session time engaged in ***object-directed behaviours*** during ***extinction***. For the VIOE group the percentages ranged from 9.46% to 17.19% during these sessions. In ***extinction***, between 9% and 20% of total session time was spent engaged in ***object-directed behaviours*** in all instances.

Table 6.14
The percentage of total session time (1800 seconds) spent engaged in ***object-directed behaviours*** (***sniff object*** + ***sniff and touch object*** + ***chew/bite object***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS	16.81 %	13.85 %	9.66 %	11.03 %	10.98 %	11.47 %
VIOS	9.91 %	7.66 %	7.23 %	12.47 %	12.42 %	19.87 %
FIOE	no objects present	no objects present	no objects present	16.90 %	12.06 %	15.85 %
VIOE	no objects present	no objects present	no objects present	7.19 %	9.46 %	16.52 %

Overall, the percentage of session time spent engaged in ***object-directed behaviours*** never exceeded 20%. For groups with objects present during ***schedule*** sessions (FIOS & VIOS), the time spent engaged in these behaviours was highest for the ***variable-interval*** group over the three ***schedule*** sessions (substantially higher in the first two sessions). During the ***extinction*** sessions, the VIOS group again spent more time engaged in ***object-directed behaviours*** than the FIOS group. For the VIOS group, the ***extinction*** scores were much higher than those obtained during the ***schedule*** sessions. For the FIOS group, the scores were similar during ***extinction***. For both of these groups, the highest ***schedule*** session score was obtained in the first session (suggesting that habituation to the novel objects was taking place). The highest ***extinction*** session score was obtained in the last session (suggesting that more ***object-directed exploratory behaviour*** occurred as the ***bar pressing*** response extinguished).

For groups with objects first present during ***extinction*** sessions (FIOE & VIOE), the highest score was obtained in the first ***extinction*** session, but the score in the last ***extinction*** session was not much lower. The score in these two sessions was slightly higher for the VIOE group. The scores for the FIOE and VIOE groups in the first ***extinction*** session (their first encounter with novel objects) were higher than for the other two groups, but not so for the later ***extinction*** sessions (Table 6.14).

The ***chew/bite object*** category, which might be ***object-directed aggression***, took up less than 1.5% of total session time in all cases (see Tables A.12-A.14 in Appendix A for more information & raw data).

6.3.5.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

The ***jump at lid*** category took up less than 1% of total session time in all cases (see Appendix A). The percentages were slightly higher for the VIOE group in all but the last ***extinction*** session (where it was marginally lower than the VIOS group). No instances of the behaviour were observed in the FIOS group for the first four sessions. Thus, most of the ***behaviour directed at the peripheral areas of the box*** was comprised of ***propping*** (Table 6.15).

During ***schedule*** sessions, the ***fixed-interval*** groups spent between 8.54% and 17.28% of total session time engaged in ***behaviour directed at the peripheral areas of the box*** (Table 6.15). The range was greater for the ***variable-interval*** groups, between 5.71% and 20.27%. If objects were present, the percentages were higher for the ***fixed-interval*** group (FIOS), whereas if objects were absent, the percentages were lower for the ***fixed-interval*** group (FIOE). The percentages were higher in every session, for groups with objects absent during ***schedule*** sessions (FIOE & VIOE groups).

During ***extinction***, the percentages ranged from 10.15% to 14.34% for the ***fixed-interval*** groups and between 9.64% and 27.63% for the ***variable-interval*** groups (Table 6.15). When objects were first present during ***schedule*** sessions, the percentages were higher for the ***fixed-interval*** group (FIOS). With objects first present during ***extinction***, the percentages were higher in the ***variable-interval*** group (VIOE).

Table 6.15
The percentage of total session time (1800 seconds) spent engaged in ***behaviour directed at the peripheral areas of the box (propping + jump at lid).***

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS	8.54 %	10.36 %	11.27 %	13.02 %	14.07 %	14.34 %
VIOS	7.47 %	5.71 %	7.56 %	9.84 %	9.64 %	10.25 %
FIOE	17.28 %	12.53 %	12.56 %	13.70 %	10.15 %	12.80 %
VIOE	20.27 %	19.30 %	18.85 %	21.66 %	27.63 %	23.55 %

Overall, the percentages increased over ***schedule*** sessions for groups with objects present, whereas a decrease was observed if objects were absent (Table 6.15). In the first ***extinction*** session, the percentage of total session spent engaged in ***behaviours directed at the peripheral areas*** increased in all groups. An overall increase across ***extinction*** sessions occurred in all but the FIOE group. Further, an overall increase across all six sessions was observed in all but the FIOE group.

6.3.5.4 OTHER BEHAVIOURAL CATEGORIES

During ***schedule*** sessions, the ***fixed-interval*** groups spent between 2.75% and 4.9% of total session time engaged in ***displacement***, whereas the percentages were lower for the ***variable-interval*** groups, ranging from 0.92% to 3.26% (Table 6.16). The ***fixed-interval*** group percentages were higher in every session. If objects were present (FIOS & VIOS groups), the percentages were lower (except for the FIOS group in session 1). During ***extinction*** sessions, between 2.94% and 7.93% of the ***fixed-interval*** groups' session was spent in ***displacement***. For the ***variable-interval*** groups, the percentages ranged from 2.34% to 5.7%. If objects were first present during ***extinction*** (VIOE & FIOE groups), the percentages were higher than for their counterpart groups.

The percentage of total session spent engaged in ***displacement*** increased across ***schedule*** sessions for all groups (Table 6.16). The percentages decreased in the first ***extinction*** session for all but the VIOS group. For all groups there was an overall increase across ***extinction*** sessions. There was also an overall increase across all six sessions for all four groups.

Comparatively little session time was spent engaged in ***digging/burying*** (Table 6.16). Less than 1.3% of any session was taken up by this behaviour by any group. Overall, there was a decrease across ***schedule*** sessions and an increase over ***extinction*** sessions for all but the VIOE group (in both cases).

During ***schedule*** sessions, the ***variable-interval*** groups spent between 1.74% and 12.03% of total session time engaged in ***rearing***, whilst the percentages ranged from 2.96% to 12.66% for the ***fixed-interval*** groups (Table 6.16). If objects were present (FIOS and VIOS groups), less time was spent engaged in ***rearing***. The ***fixed-interval*** groups spent more time ***rearing*** than their counterparts (except FIOE group in session 1). During ***extinction***, between 7.27% and 19.11% of ***fixed-interval*** session time was spent ***rearing***. The ***variable-interval*** groups spent between 5.82% and 14.41% of sessions engaged in this behaviour. The ***fixed-interval*** groups spent more time ***rearing*** than their counterparts (except FIOE group in session 4). If objects were first present during ***extinction*** (FIOE & VIOE groups), the percentages were higher (except for the FIOE group in session 4).

Table 6.16
The percentage of total session time (1800 seconds) spent engaged in ***other behavioural categories*** (***displacement***, ***digging/burying***, ***rearing*** and ***pica***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS	***displacement*** 3.07 % ***dig/bury*** 0.69% ***rearing*** 2.96% ***pica*** 0.96%	***displacement*** 3.29 % ***dig/bury*** 0.21% ***rearing*** 6.61% ***pica*** 1.07%	***displacement*** 4.02 % ***dig/bury*** 0.14% ***rearing*** 9.09% ***pica*** 1.06%	***displacement*** 3.14 % ***dig/bury*** 0.97% ***rearing*** 9.61% ***pica*** 4.15%	***displacement*** 3.55% ***dig/bury*** 0.37% ***rearing*** 17.31% ***pica*** 6.37%	***displacement*** 5.76 % ***dig/bury*** 1.01% ***rearing*** 16.38% ***pica*** 8.59%
VIOS	***displacement*** 0.92 % ***dig/bury*** 0.59% ***rearing*** 1.74% ***pica*** 1.08%	***displacement*** 1.77 % ***dig/bury*** 0.43% ***rearing*** 4.98% ***pica*** 1.9%	***displacement*** 1.64 % ***dig/bury*** 0.48% ***rearing*** 3.01% ***pica*** 2.02%	***displacement*** 2.34 % ***dig/bury*** 0.24% ***rearing*** 5.82% ***pica*** 2.89%	***displacement*** 2.64 % ***dig/bury*** 0.39% ***rearing*** 9.51% ***pica*** 4.93%	***displacement*** 3.36 % ***dig/bury*** 0.53% ***rearing*** 9.45% ***pica*** 6.95%
FIOE	***displacement*** 2.75 % ***dig/bury*** 1.29% ***rearing*** 8.59% ***pica*** 0.98%	***displacement*** 3.47 % ***dig/bury*** 0.51% ***rearing*** 12.66% ***pica*** 2.75%	***displacement*** 4.9 % ***dig/bury*** 0.7% ***rearing*** 12.05% ***pica*** 0.76%	***displacement*** 2.94 % ***dig/bury*** 0.89% ***rearing*** 7.27% ***pica*** 1.2%	***displacement*** 7.93 % ***dig/bury*** 0.42% ***rearing*** 19.11% ***pica*** 1.6%	***displacement*** 7.31 % ***dig/bury*** 0.99% ***rearing*** 18.77% ***pica*** 3.7%
VIOE	***displacement*** 2.18 % ***dig/bury*** 0.1% ***rearing*** 10.21% ***pica*** 0	***displacement*** 3.24 % ***dig/bury*** 0.25% ***rearing*** 8.62% ***pica*** 0	***displacement*** 3.26 % ***dig/bury*** 0.23% ***rearing*** 12.03% ***pica*** 0	***displacement*** 3.06 % ***dig/bury*** 0.14% ***rearing*** 10.35% ***pica*** 0.22%	***displacement*** 4.45 % ***dig/bury*** 0.2% ***rearing*** 12.69% ***pica*** 0	***displacement*** 5.7 % ***dig/bury*** 0.12% ***rearing*** 14.41% ***pica*** 4.6%

For all groups, the percentage of total session time spent engaged in ***rearing*** showed an overall increase across the six sessions (Table 6.16). Overall, the percentages increased over ***schedule*** sessions, and increased over ***extinction***. If objects were first present during ***extinction***, a decrease in ***rearing*** was observed in the first ***extinction*** session. That is, when objects were first encountered, ***rearing*** decreased. The percentage was lowest when objects were first encountered during ***schedule*** sessions (FIOS & VIOS groups).

The percentage of total session spent engaged in ***pica*** was zero (VIOE group) or low (<3%) during ***schedule*** sessions for all groups (Table 6.16). During ***extinction***, the percentages were higher in all groups. When objects were first encountered during ***extinction*** (FIOE & VIOE group), the percentages were lower in every session. The ***fixed-interval*** group percentages were higher than their counterparts (except FIOE group in session 6). Overall, the percentage of total session time spent in ***pica*** increased over the six sessions for all groups. If objects were first present during ***schedule*** sessions, the percentages increased over ***schedule*** sessions. The percentages increased over ***extinction*** for all groups.

6.3.6 PATTERNS OF CHANGE IN BEHAVIOURAL MEASURES OVER SESSIONS, AND BETWEEN GROUPS

The changes in each behavioural measure (frequency & duration) over the three ***schedule*** sessions (sessions 1 - 3), and three ***extinction*** sessions (sessions 4 - 6) are presented graphically in Figures 6.17 - 6.20: II (inclusive). The scores for all four groups are plotted on each graph, allowing a visual comparison of trends across the six sessions.

6.3.6.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

For ***bar pressing***, a similar trend was observed across the ***schedule*** sessions for all four groups (Figure 6.17). Both the frequency and duration measures increased steadily over the three ***schedule*** sessions, with the highest frequency and duration scores recorded in session 3 for all four groups (except the FIOS group frequency). The frequency measure increased in session 4 for the FIOS group, but decreased in the other three groups (very sharply for the VIOE group). An overall dramatic decrease was observed in both the frequency and duration measures over the three ***extinction*** sessions. Similar values in both frequency and duration scores were found for the FIOS, VIOS and VIOE groups in the last session. These values were higher for the FIOE group.

Steady increases in the frequency and duration of ***bar-related behaviour*** scores were observed for the VIOS, FIOE and VIOE groups over the three ***schedule*** sessions (Figure 6.17). An overall increase in frequency and duration measures was also observed for the FIOS group over the same sessions. An overall decline in frequency of ***bar-related behaviour*** was observed for all four groups over the three ***extinction*** sessions, following a decrease in scores between session 3 and session 4 in all but the FIOS group. Similarly, an overall decrease in the duration measure was seen in all four groups over the three ***extinction*** sessions, following a decrease in scores between session 3 and session 4 in all but the VIOS group. The highest frequency score was seen in session 3 for the FIOE, VIOS and VIOE groups, and in session 4 for the FIOS group. The highest duration score was seen in session 3 for the FIOE, FIOS and VIOE groups, and in session 4 for the VIOS group.

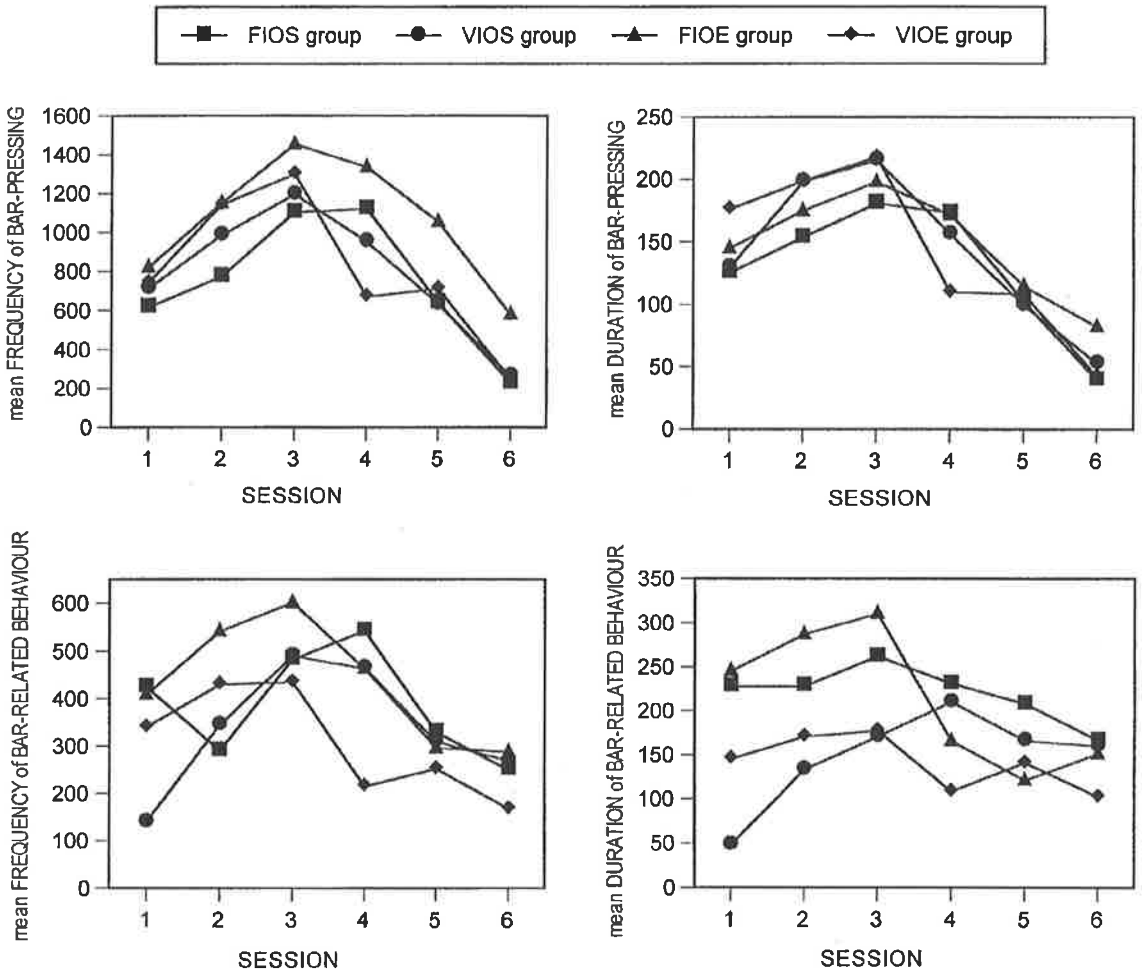


Figure 6.17. Mean frequency (left) and duration (right) scores of ***behaviour directed at the bar and food-trough area*** for all four groups in Experiment 1 (top- ***bar pressing***, & bottom- ***bar-related behaviour***)

6.3.6.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

For the ***sniff object*** category, the FIOS group frequency and duration scores decreased steadily (linear), whilst the VIOS group measures showed an overall decrease over the three ***schedule*** sessions, with lowest scores obtained in the second session (Figure 6.18). Higher frequency and duration measures were seen for the FIOS group in the first two sessions, before dropping to a value that was lower than in the VIOS group. The frequency and duration scores showed an overall decrease over the ***extinction*** sessions for all four groups, with lowest scores observed in the second ***extinction*** session in all but the FIOS group. Highest frequency and duration scores were observed in the VIOS group during ***extinction***. The pattern and value of scores was very similar for the FIOE and VIOE groups.

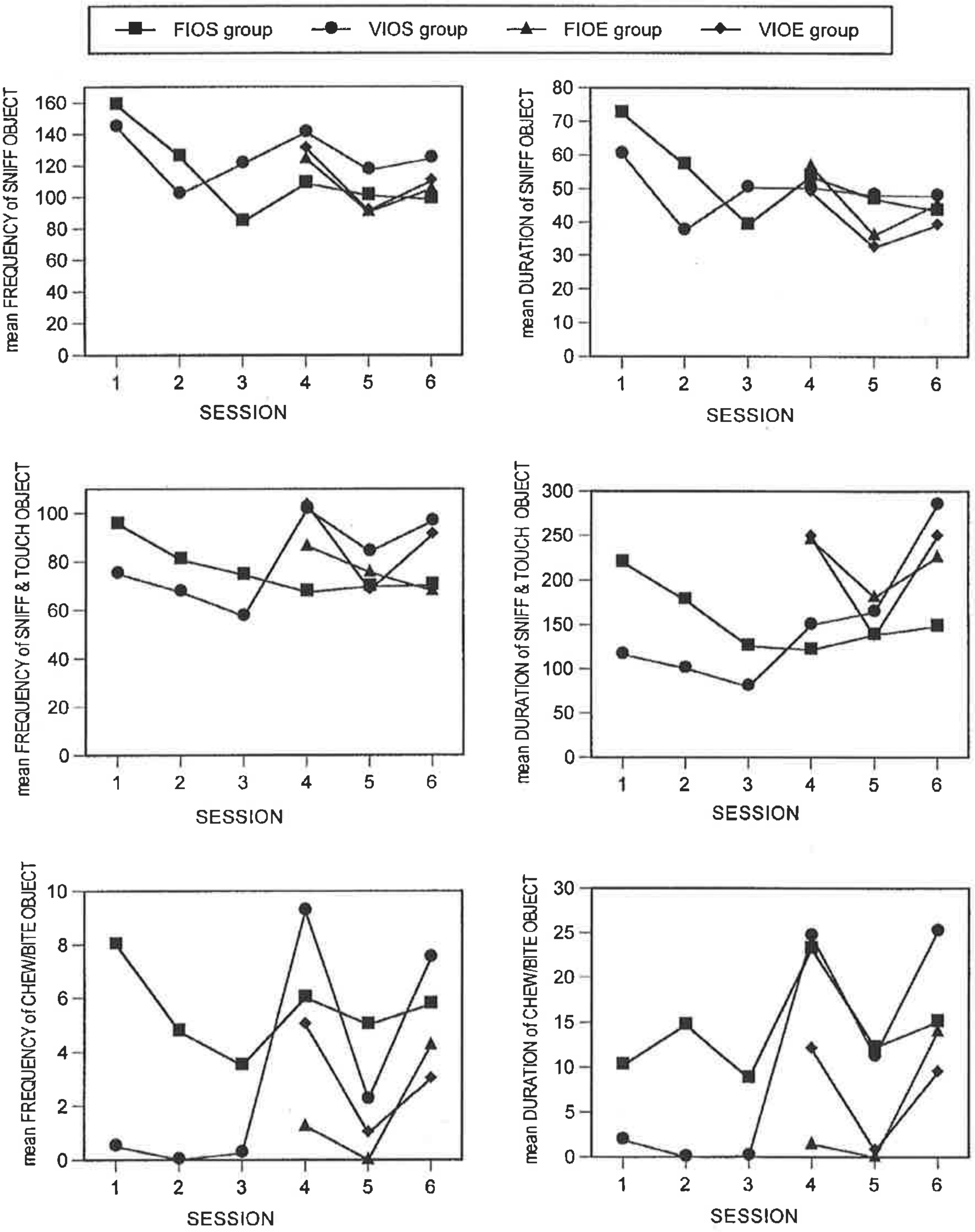


Figure 6.18. Mean frequency (left) and duration (right) scores of ***behaviour directed at the stimulus objects*** for all four groups in Experiment 1 (top- ***sniff object***, middle- ***sniff & touch object*** & bottom- ***chew/bite object***)

The frequency and duration of ***sniff and touch object*** scores decreased steadily over the ***schedule*** sessions for the FIOS and VIOS groups, but the FIOS scores were higher in every session (Figure 6.18). For the FIOS group, the frequency and duration scores dropped slightly in the first ***extinction*** session before increasing gradually over the last two sessions. For the VIOS group, the frequency and duration scores increased noticeably in the first ***extinction*** session, but the frequency then showed an overall decrease whilst the duration increased markedly over the ***extinction*** sessions. The frequency scores decreased over ***extinction*** for the FIOE and VIOE groups. The duration scores dropped sharply in the second ***extinction*** session for these groups, but with a slight decrease overall for the FIOE group and little overall change for the VIOE group.

For ***chew/bite object***, the frequency and duration scores indicate an overall decrease across the ***schedule*** sessions for the FIOS and VIOS groups, with the FIOS scores higher in each session (Figure 6.18). The frequency and duration scores plummeted in the second ***extinction*** session for all four groups. Only the FIOE group showed an overall increase in frequency scores over ***extinction***, whilst the VIOS and FIOE showed an overall increase in duration scores over ***extinction***.

6.3.6.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

The highest frequency and duration measures of ***propping*** in every session were observed for the VIOE group (Figures 6.19). Both measures showed a slight decrease over the three ***schedule*** sessions for this group. The frequency measure showed an overall decrease over the three ***extinction*** sessions, whilst the duration measure increased over these sessions for the VIOE group. A sharp peak in duration was seen in session 5 for this group. For the FIOS group, there was a steady increase in the duration and overall increase in the frequency of ***propping*** over the six sessions. For the VIOS group, there was little overall change in frequency and duration scores over ***schedule*** or ***extinction*** sessions, but with a noticeable increase in the first ***extinction*** session. For the FIOE group, the frequency and duration scores indicate an overall decrease over ***schedule*** sessions (dropping in session 2) and a similar pattern over ***extinction*** sessions. There was a slight decrease in frequency and a slight increase in duration in the first ***extinction*** session. In summary, the highest frequency of ***propping*** score was seen in session 1 for the FIOE and VIOE groups, in session 4 for the VIOS group, and in session 5 for the FIOS group. The highest duration scores for this behaviour were observed in session 1 for the FIOE group, session 5 for the VIOE group, and in session 6 for the FIOS and VIOS groups.

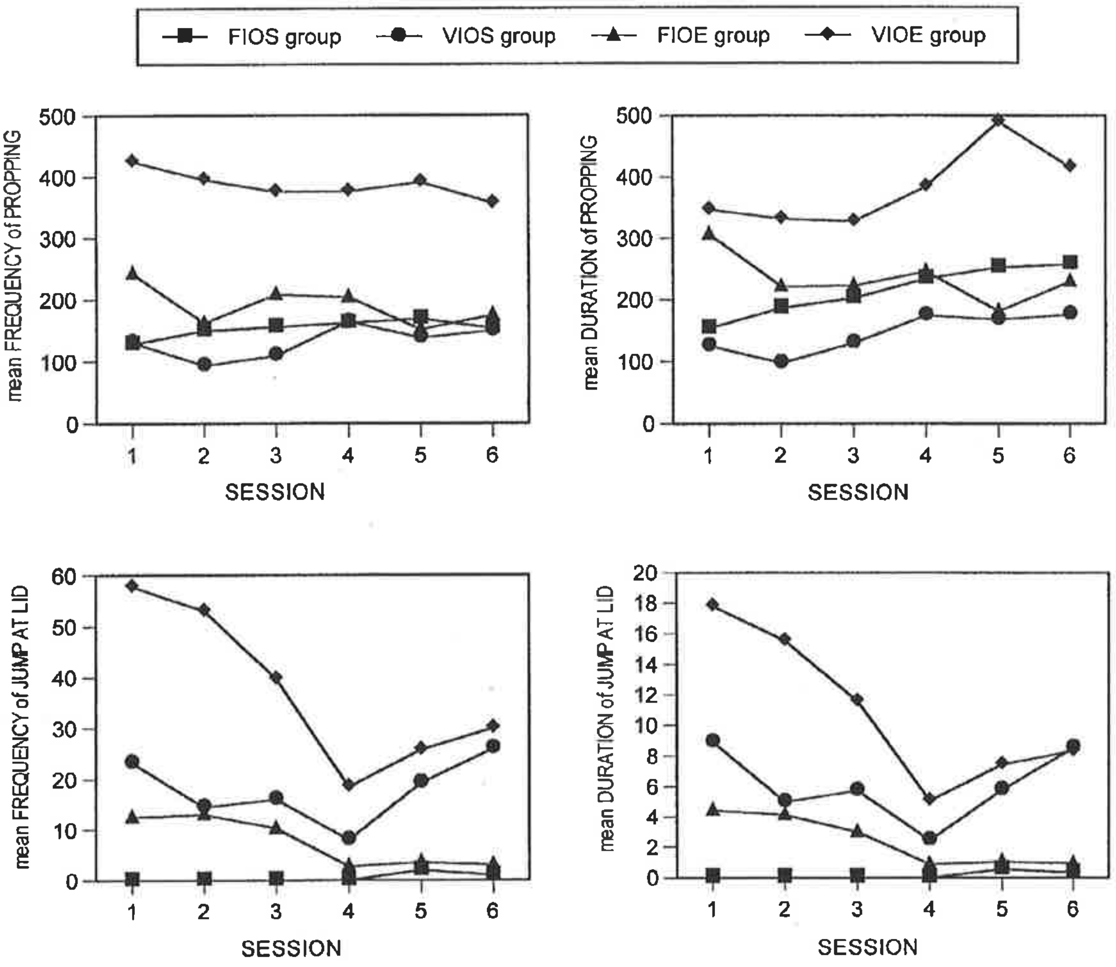


Figure 6.19. Mean frequency (left) and duration (right) scores of ***behaviour directed at the peripheral areas of the box*** for all four groups in Experiment 1 (top- ***propping***, & bottom- ***jump at lid***)

Jump at lid (Figure 6.19) frequency and duration scores were highest for the VIOE group in every session (except duration was slightly less than the VIOS score in session 6). The next highest scores were seen in the VIOS group. Only a few instances of ***jump at lid*** occurred in session 5 and 6 for the FIOS group. The frequency and duration scores showed an overall decrease over ***schedule*** sessions for all groups. These measures then dropped further in the first ***extinction*** session, before increasing over ***extinction*** in the VIOE and VIOS groups and remaining almost constant (& minimal) in the FIOS group.

6.3.6.4 OTHER BEHAVIOURAL CATEGORIES

As Figure 6.20 (I) indicates, for the ***displacement*** category, the lowest frequency and duration scores were observed in the VIOS group (except frequency in session 4). The highest frequency scores were observed in the FIOS group, whilst the highest duration scores were found for the FIOE group in four of the six sessions. An overall increase in the frequency and duration scores was observed in the VIOS, FIOE and VIOE groups over the six sessions. For the FIOS group, there was a slight overall decrease in frequency scores, but an overall increase in duration scores. Whilst the highest frequency scores were observed during ***schedule*** sessions for all but the VIOS group, the highest duration scores were during ***extinction*** for all groups.

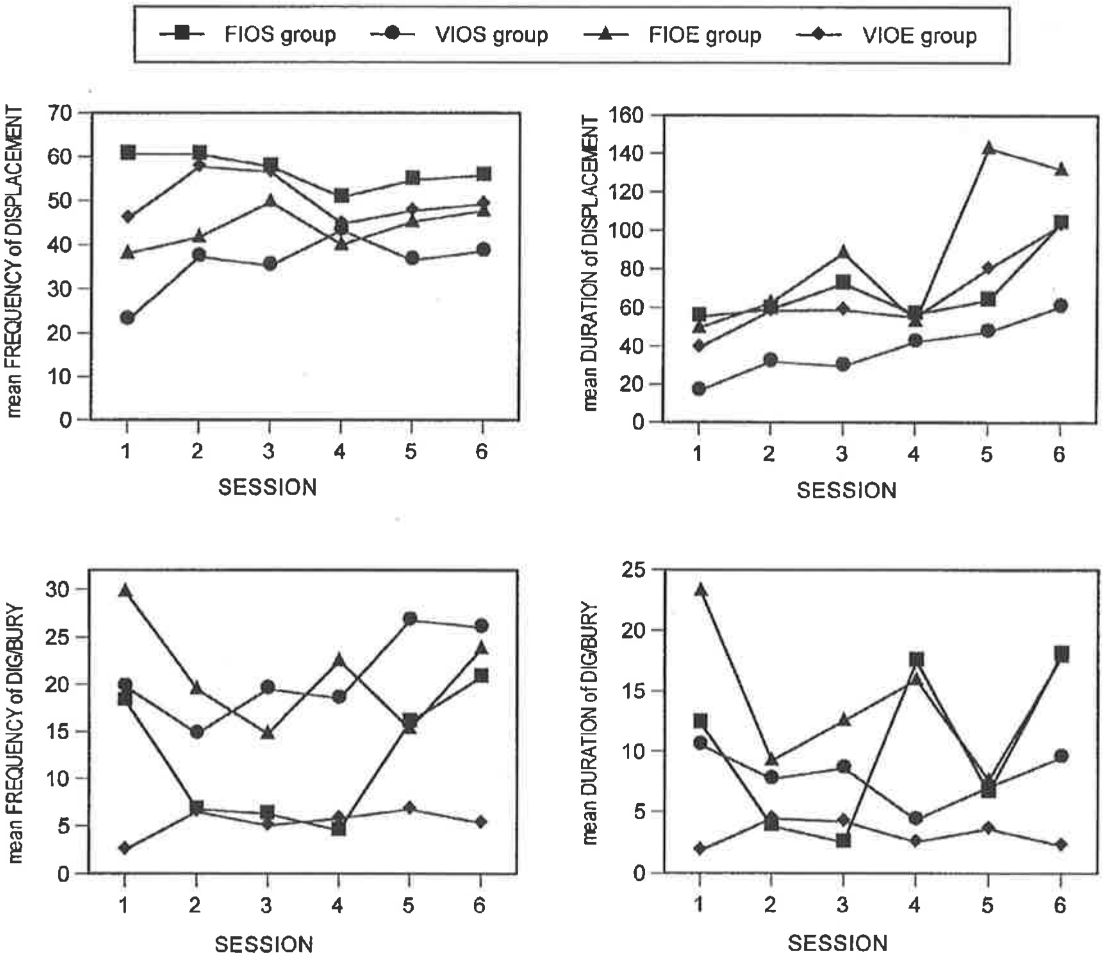


Figure 6.20 (I). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** for all four groups in Experiment 1 (top- ***displacement***, & bottom- ***digging/burying***)

For the ***digging/burying*** category, the frequency and duration scores were low and showed little change (slight overall increase) for the VIOE group over the six sessions (Figure 6.20:I). For the FIOS group, the measures decreased over the ***schedule*** sessions, and then increased to their highest scores over ***extinction***. The frequency and duration scores indicate an overall decrease across the six sessions for the FIOE group, whilst the frequency scores increased overall and the duration scores decreased slightly overall for the VIOS group. The highest frequency scores were seen in ***extinction*** for all but the FIOE group, whereas the highest duration scores were observed in ***schedule*** sessions for the FIOE and VIOS groups.

Figure 6.20 (II) indicates that the frequency and duration of ***rearing*** scores showed an overall increase for all four groups over all six sessions, with a decrease in measures during the first

extinction session for the FIOE and VIOE groups and an increase for the FIOS and VIOS groups. The highest frequency scores were seen in ***extinction*** for all but the VIOE group, and the highest duration scores were seen in ***extinction*** for all groups.

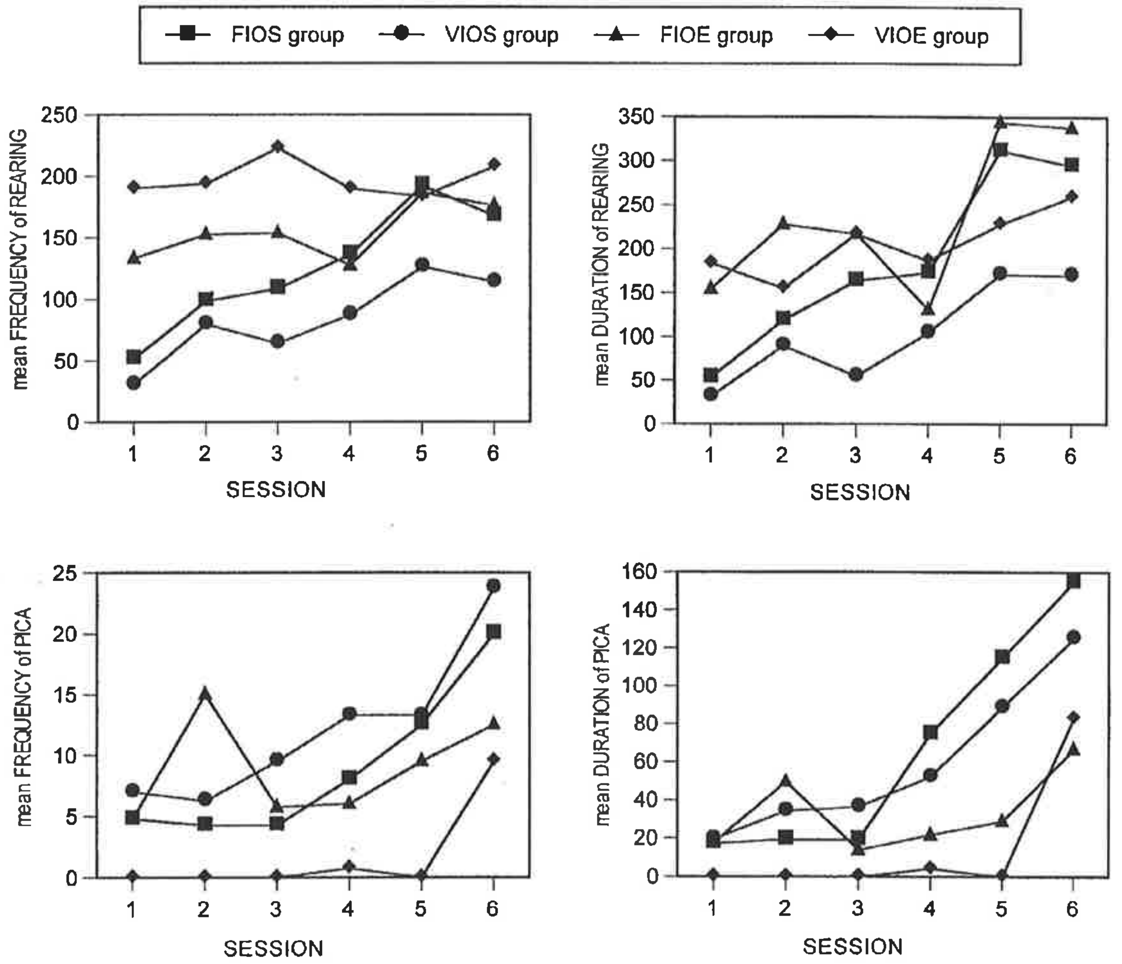


Figure 6.20 (II). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** for all four groups in Experiment 1 (top- ***rearing***, & bottom- ***pica***)

For the VIOE group, no instances of ***pica*** were observed in the three ***schedule*** sessions or the second ***extinction*** session (Figure 6.20:II). In session 4, some ***pica*** was observed, and the frequency and duration measures increased markedly in session 6. For the VIOS group, there was a steady increase in the frequency and duration scores over the six sessions, with a more dramatic increase evident over the ***extinction*** sessions. Very little change was seen in the frequency and duration scores for the FIOS group over the three ***schedule*** sessions. This was followed by a dramatic linear increase in ***pica*** over the three ***extinction*** sessions. For the FIOE group, there was an overall increase in both measures over the six sessions. The highest frequency and duration scores were observed in session 6 for all groups (except frequency for the FIOE group, which was highest in session 2).

6.3.7 CHANGES IN BEHAVIOURS OVER SESSIONS, BETWEEN SCHEDULES, AND BETWEEN OBJECT CONDITIONS

The previous section presented the mean frequency and duration of the scored behaviours exhibited by the four groups of rats graphically. Since the sample sizes were small, the data have been primarily analysed by description. Bearing this in mind, the data are now analysed by means of statistical testing. A multivariate analysis of variance (MANOVA) was performed for each of the frequency and duration measures, during the three ***schedule*** sessions (section 6.3.7.1), the three ***extinction*** sessions (section 6.3.7.2), and all six sessions (section 6.3.7.3). For each MANOVA there were three independent (or grouping) variables: object (objects first present during ***schedule*** or ***extinction***), schedule (***fixed-interval*** or ***variable-interval***) and session. In each case there was one dependent variable: the frequency or duration measure of a particular behavioural category.

The *F* value associated with the independent/grouping variable (object, schedule or session) in each instance tested the hypothesis that the independent variable had no main effect on the frequency or duration measure being examined (Norusis, 1983). A statistically non-significant *F* value meant that the group means being compared were not significantly different. A statistically significant interaction implied that the dependent variable was *jointly* affected by both grouping variables (Norusis, 1983). Such interactions suggest that there is no point in looking at the separate main effects of the grouping variables, since both affect the behavioural measure.

It should be noted, that objects were absent in two of the four groups (FIOE & VIOE) during ***schedule*** sessions. Therefore, the grouping variable "object" has an obvious effect on ***object-directed behaviours*** in those three sessions. If the other independent variables (schedule or session) have a main effect on the frequency or duration of ***object-directed behaviours***, it is only relevant for the two groups with objects present during ***schedule*** sessions (FIOS & VIOS).

MANOVA's were not performed on three of the behavioural categories (both frequency & duration measures), since these behaviours occurred too infrequently in the four groups. The behaviours were ***pica***, ***jump at lid*** and ***chew/bite object***. However, there were some instances, and it is worth looking for any possible patterns in these behaviours in the graphs (Figures 6.18, 6.19 & 6.20:II) and tables (Appendix A). The remaining seven categories of behaviour included in this statistical analysis are: ***bar-related behaviour***, ***sniff object***, ***sniff and touch object***, ***propping***, ***displacement***, ***digging/burying*** and ***rearing***.

6.3.7.1 SCHEDULE SESSIONS

Main effect of *schedule*

The differences between the schedules (***fixed-interval*** or ***variable-interval***) were statistically significant for only one measure. The schedule that rats were run on affected the duration of ***bar-related behaviour*** [*F* (1,12)=5.01, *p*<.05] during schedule sessions. Specifically, the mean duration of this behaviour was much higher in every session for rats run on the ***fixed-interval*** schedule (Figure 6.21:I).

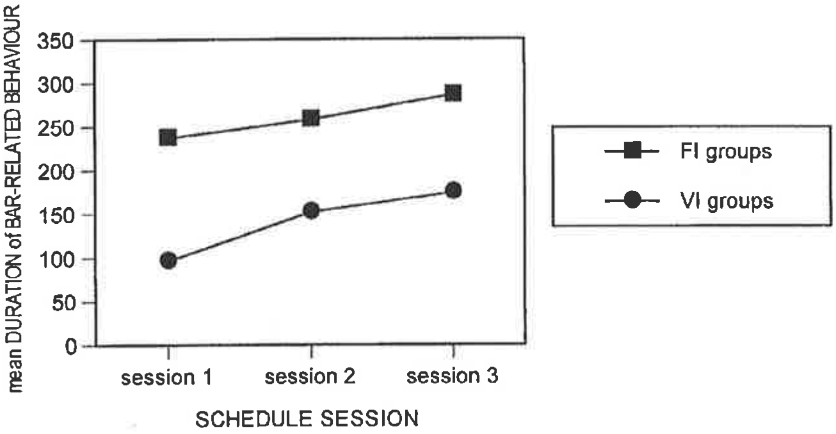


Figure 6.21 (I). Mean duration of ***bar-related behaviour*** for the "schedule" grouping variable during the ***schedule*** sessions

Main effect of *object*

A statistically significant main effect of ***object*** was found for the frequency of ***rearing*** [*F* (1,12)=5.5, *p*<.05], the duration of ***rearing*** [*F* (1,12)=4.9, *p*<.05] and the duration of ***propping*** [*F* (1,12)=5.57, *p*<.05] during schedule sessions. Thus, the presence or absence of objects affected three measures of behaviour. As Figure 6.21(II) indicates, the mean frequency and duration of ***rearing*** and the duration of ***propping*** scores were much higher in every session if objects were absent (FIOE & VIOE groups).

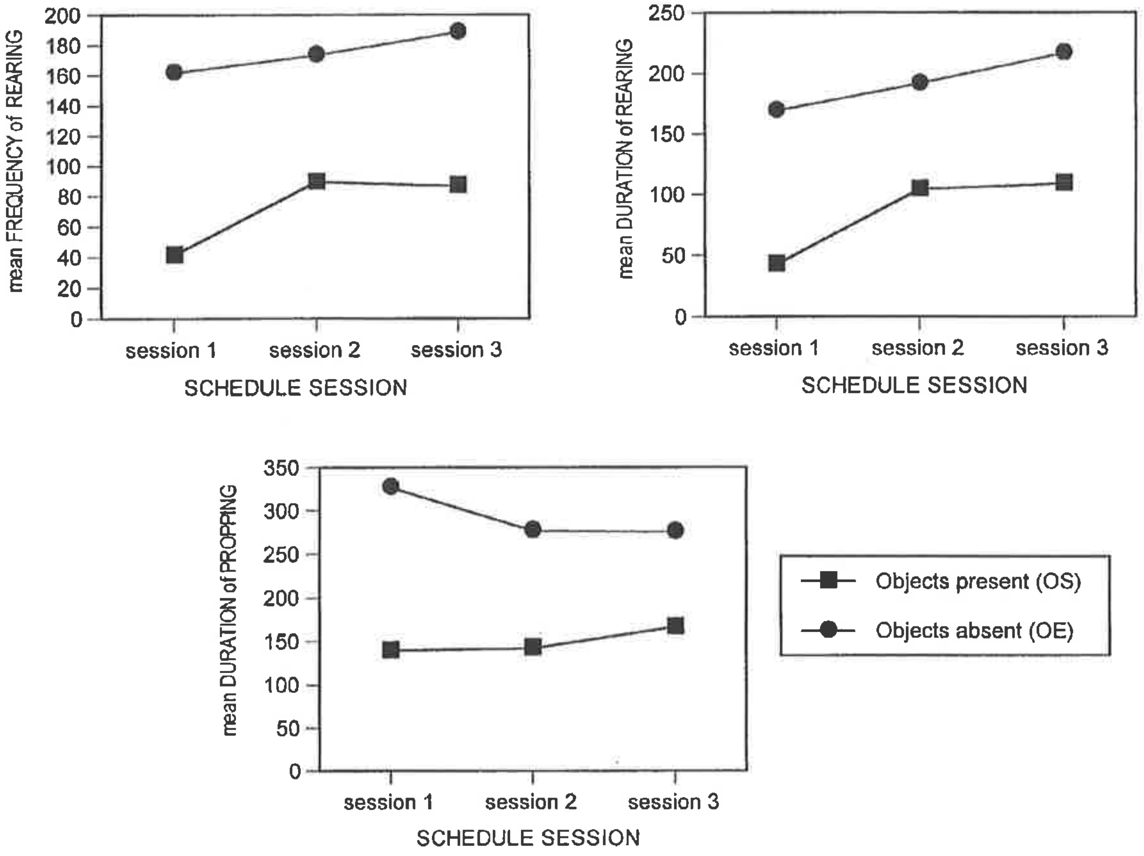


Figure 6.21 (II). Mean frequency of ***rearing*** (top left), duration of ***rearing*** (top right) and duration of ***propping*** (bottom) for the "object" grouping variable during ***schedule*** sessions

Main effect of *session*

As can be seen from Table 6.17, the differences between sessions were statistically significant for most of the frequency and duration measures. That is, the session number clearly affected the frequency and duration of most of the behaviours (except both measures of ***digging/burying*** & ***propping***, & the frequency of ***bar-related behaviour***). The mean frequency and duration of ***rearing***, ***displacement***, ***bar pressing*** and the duration of ***bar-related behaviour*** increased in every session (Figures 6.21:III & IV). By contrast, the frequency and duration of ***sniff and touch object*** and ***sniff object*** decreased over the three sessions for the two groups with objects present (Figures 6.21:III & IV).

Table 6.17
Experiment 1 significance levels obtained for measures of behavioural categories during the three schedule sessions (*session* effect).

Variable	***F*(2,24)**	**Significance level (*p*)**
Frequency of ***rearing***	4.4	<.05
Duration of ***rearing***	3.51	<.05
Frequency of ***displacement***	3.78	<.05
Duration of ***displacement***	10.56	<.01
Frequency of ***sniff and touch object***	4.0	<.05
Duration of ***sniff and touch object***	7.38	<.01
Frequency of ***sniff object***	7.86	<.01
Duration of ***sniff object***	5.43	<.05
Duration of ***bar-related behaviour***	7.12	<.01
Frequency of ***bar pressing***	28.03	<.001
Duration of ***bar pressing***	12.72	<.001

Note. Objects were only present in two of the four groups

Schedule x session **interaction effect**

The MANOVA for the duration of ***digging/burying*** yielded a statistically significant ***schedule*** x ***session*** interaction [*F* (2,24)=4.11, *p*<.05]. This means that the duration of ***digging/burying*** was *jointly* affected by the schedule (***fixed-interval*** or ***variable-interval***) *and* session grouping variables during schedule sessions. As can be seen in Figure 6.21(V), the mean duration of ***digging/burying*** decreased over the three sessions (mean for all four groups), but in actual fact, this pattern was only reflected in the ***fixed-interval*** groups. For the ***variable-interval*** rats there was virtually no change over the three sessions.

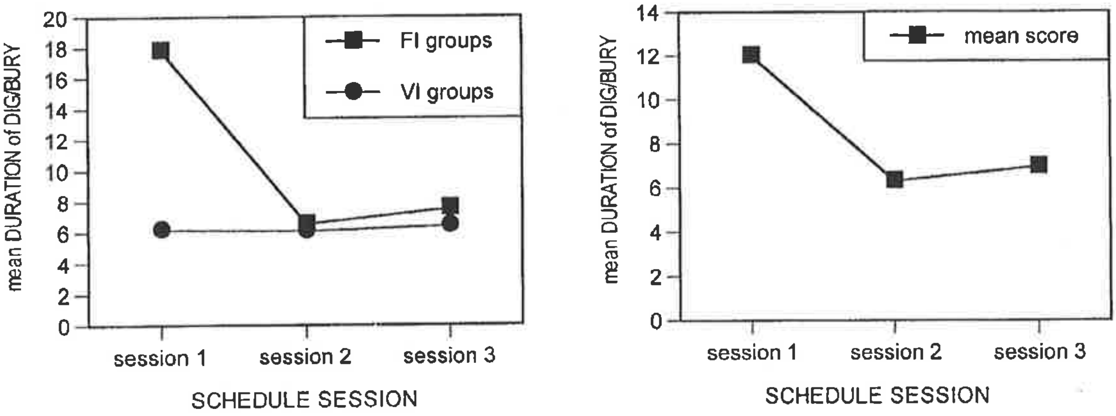


Figure 6.21 (V). Duration of ***digging/burying*** was jointly affected by the "schedule" and "session" grouping variables (left- "schedule" grouping variable means, & right- "session" grouping variable means)

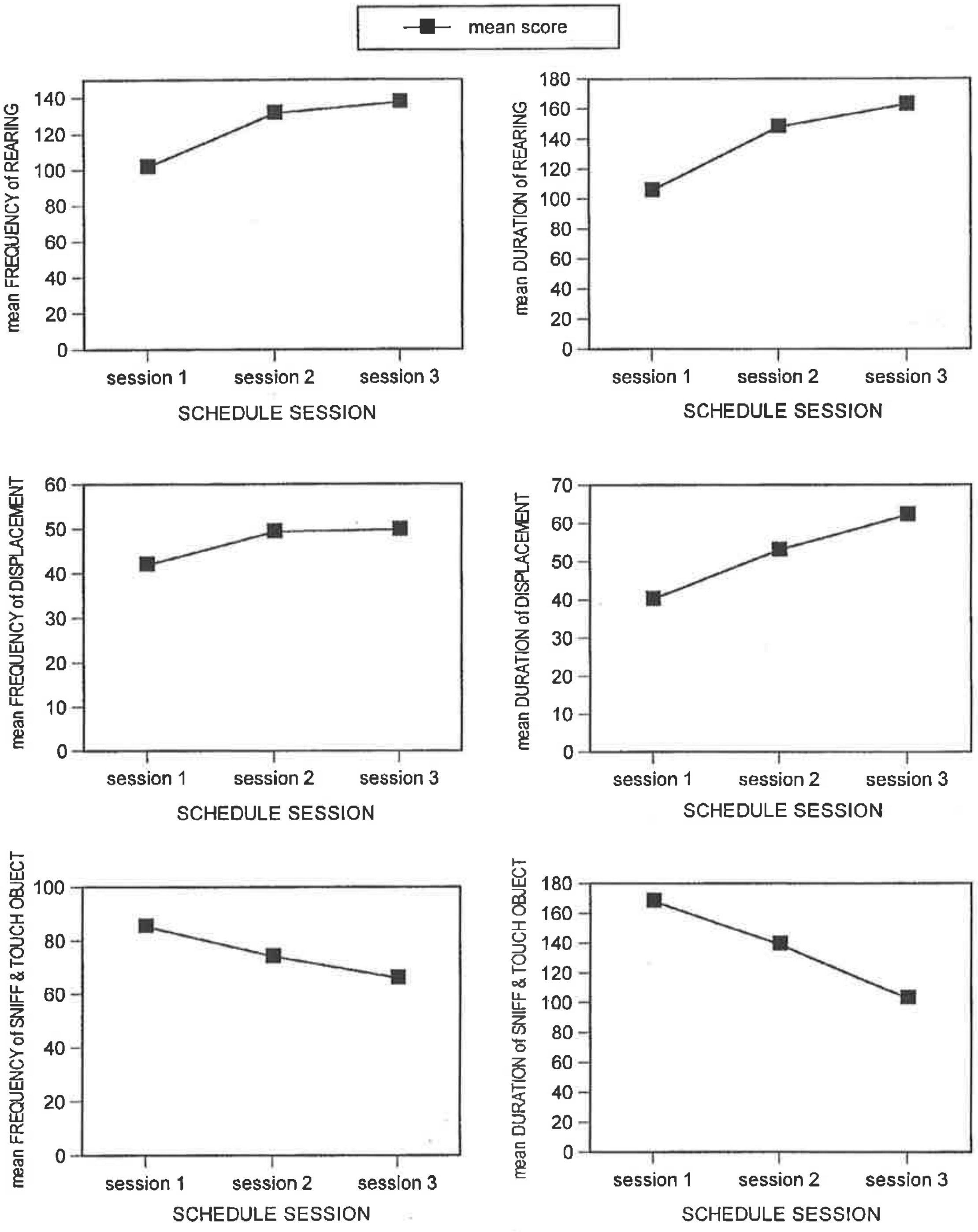


Figure 6.21 (III). Mean frequency (left) and duration (right) scores of behaviours for the "session" grouping variable during schedule sessions (top- ***rearing***, middle- ***displacement***, & bottom- ***sniff & touch object***)

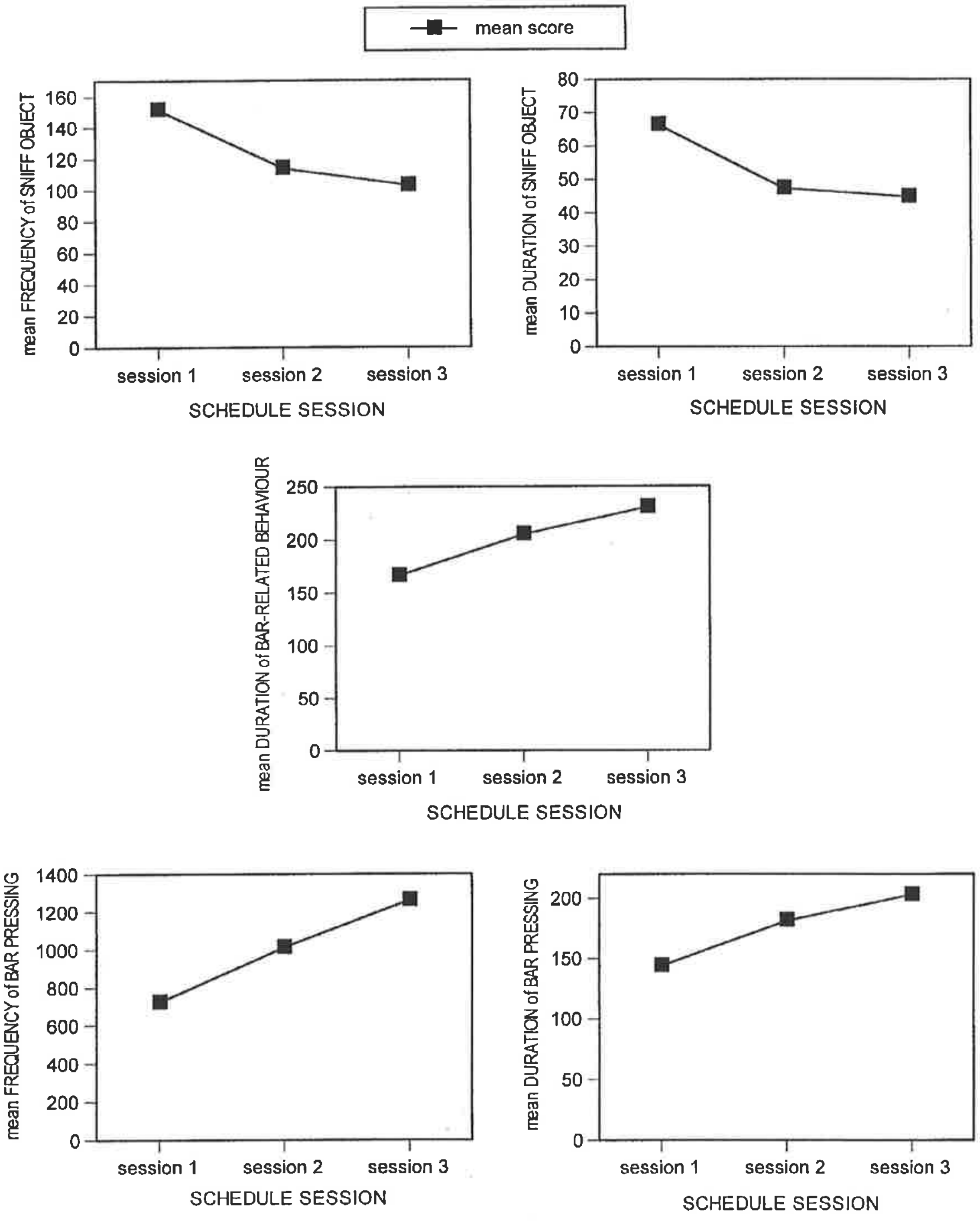


Figure 6.21 (IV). Mean frequency (left) and duration (right) scores of behaviours for the "session" grouping variable during schedule sessions (top- ***sniff object***, middle- ***bar-related behaviour***, & bottom- ***bar pressing***)

Object x schedule x session interaction effect

A statistically significant ***object*** x ***schedule*** x ***session*** interaction was found for the frequency of ***bar-related behaviour*** [*F* (2,24)=5.28, *p*<.05]. In this instance, the frequency of ***bar-related behaviour*** was affected by all three grouping variables during ***schedule*** sessions. Figure 6.21(VI) indicates that the mean frequency of ***bar-related behaviour*** increased over the three sessions. The scores were higher in every session for rats run on the ***fixed-interval*** schedule and also for rats with objects absent during these sessions.

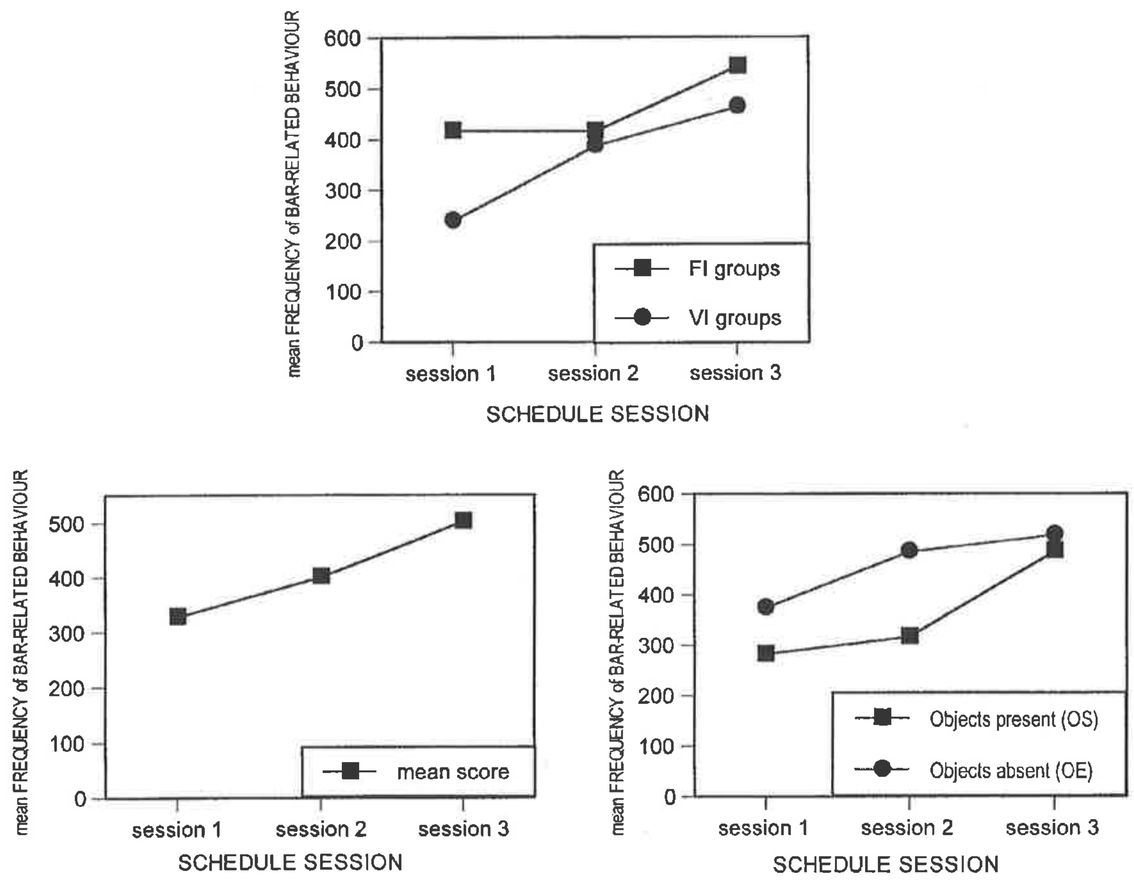


Figure 6.21 (VI). Frequency of ***bar-related behaviour*** was affected by all three grouping variables during schedule sessions (top- “schedule” grouping variable, bottom left- “session” grouping variable & bottom right- “object” grouping variable)

6.3.7.2 EXTINCTION SESSIONS

Main effect of *session*

The differences between ***extinction*** sessions were statistically significant for many of the frequency and duration measures (Table 6.18). That is, the session number clearly affected the frequency and duration of most of the behaviours (except ***digging/burying***, ***propping***, frequency of ***displacement*** & ***sniff & touch object***, & duration of ***bar-related behaviour***). In particular, the frequency and duration of ***rearing*** and ***displacement*** showed an overall increase across

extinction (Figure 6.22:I), whereas the frequency and duration of ***sniff object***, ***bar pressing*** and the frequency of ***bar-related behaviour*** decreased over the three ***extinction*** sessions (Figures 6.22:I & II).

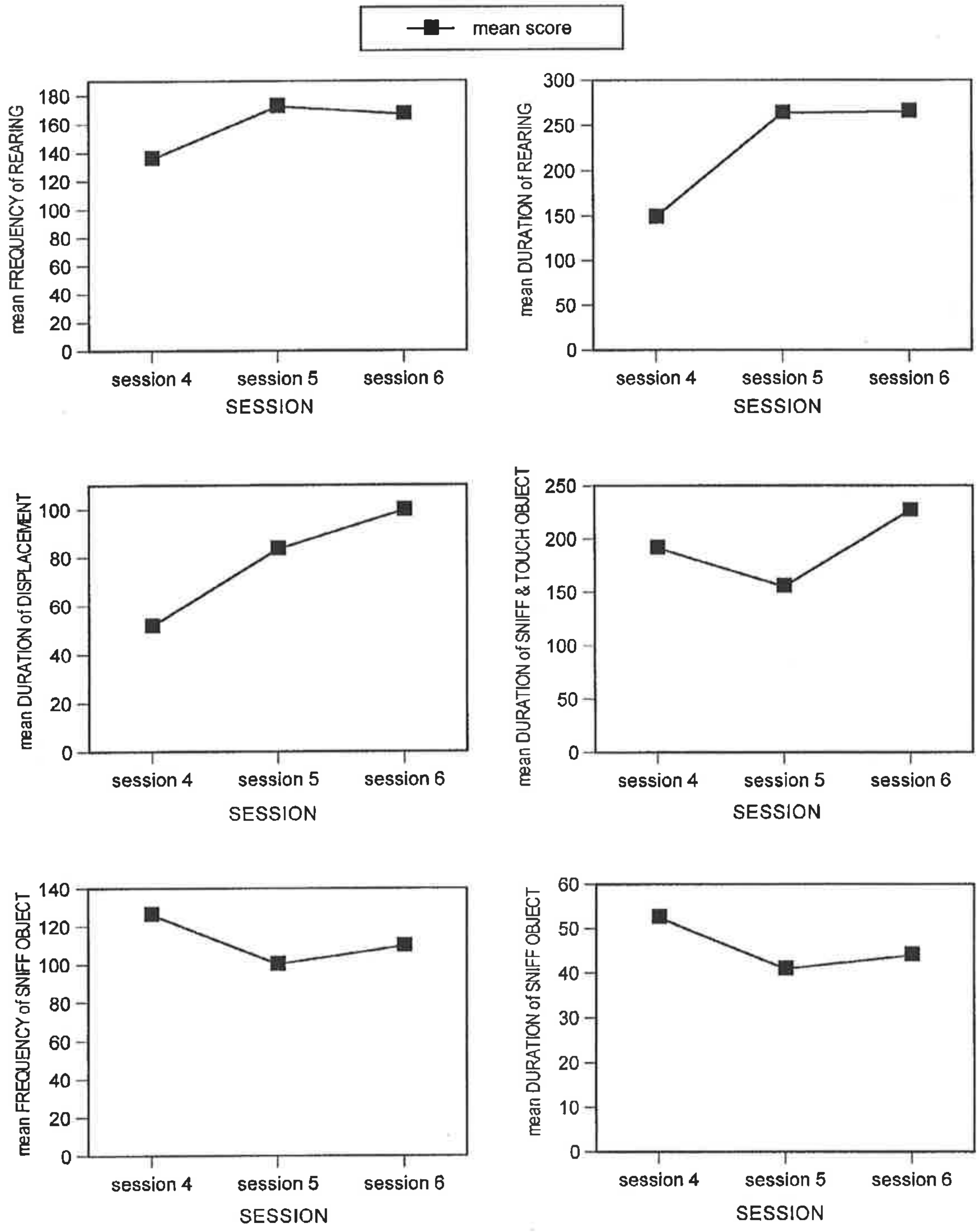


Figure 6.22 (I). Mean frequency and duration of behaviours for the "session" grouping variable during ***extinction*** (top- frequency & duration of ***rearing***, middle- duration of ***displacement*** & ***sniff & touch object***, & bottom- frequency & duration of ***sniff object***)

Table 6.18
Experiment 1 significance levels obtained for measures of behavioural categories during the three extinction sessions (***session*** effect).

Variable	$F(2,24)$	Significance level (p)
Frequency of ***rearing***	4.32	<.05
Duration of ***rearing***	8.95	<.01
Duration of ***displacement***	6.97	<.01
Duration of ***sniff and touch object***	4.19	<.05
Frequency of ***sniff object***	9.80	<.01
Duration of ***sniff object***	7.47	<.01
Frequency of ***bar-related behaviour***	21.87	<.001
Frequency of ***bar pressing***	48.37	<.001
Duration of ***bar pressing***	59.36	<.001

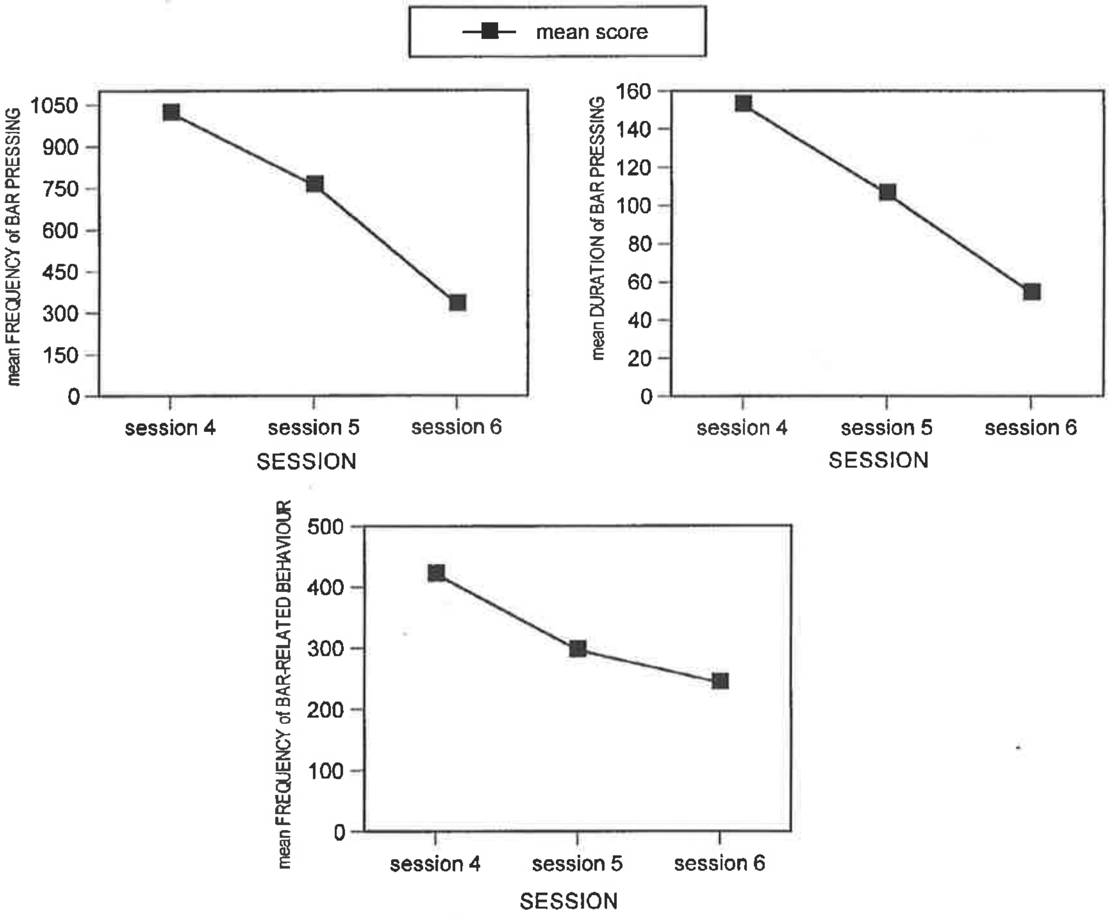


Figure 6.22 (II). Mean frequency and duration of behaviours for the "session" grouping variable during *extinction* (top- frequency & duration of *bar pressing*, & bottom- frequency of *bar-related behaviour*)

Object x schedule interaction effect

The MANOVA for the frequency of ***digging/burying*** yielded a statistically significant ***object*** x ***schedule*** interaction [*F* (1,12)=8.57, *p*<.05]. Thus, the frequency of ***digging/burying*** was *jointly* affected by the object (first present during ***schedule*** or ***extinction*** sessions) *and* schedule (***fixed-interval*** or ***variable-interval***) grouping variables during ***extinction*** sessions. Visual inspection of Figure 6.22(III) shows that the frequency of ***digging/burying*** increased most noticeably over ***extinction*** for rats that were previously run on the ***fixed-interval*** schedule and for rats that had first encountered objects during the ***schedule*** sessions (FIOS & VIOS groups). There was little change over ***extinction*** for rats that first encountered objects during ***extinction*** sessions and a less noticeable increase for rats previously run on the ***variable-interval*** schedule.

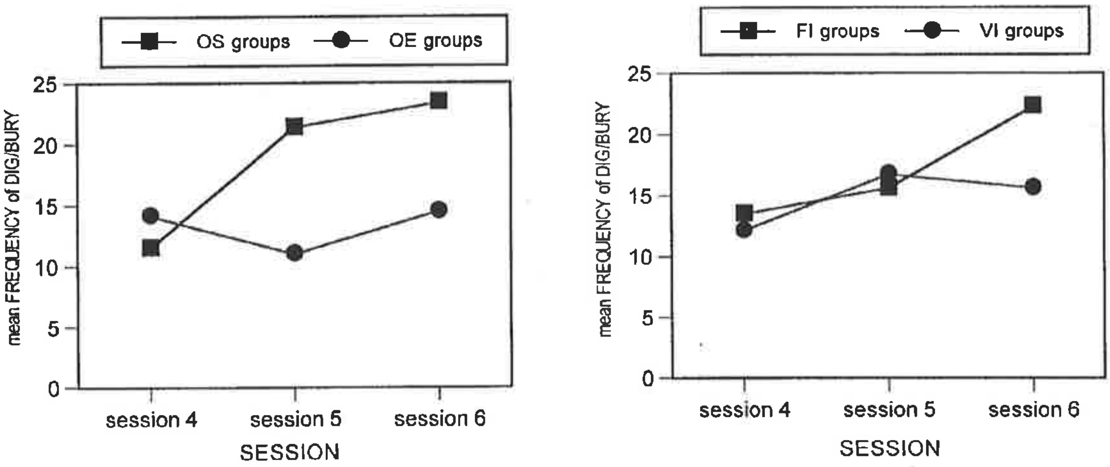
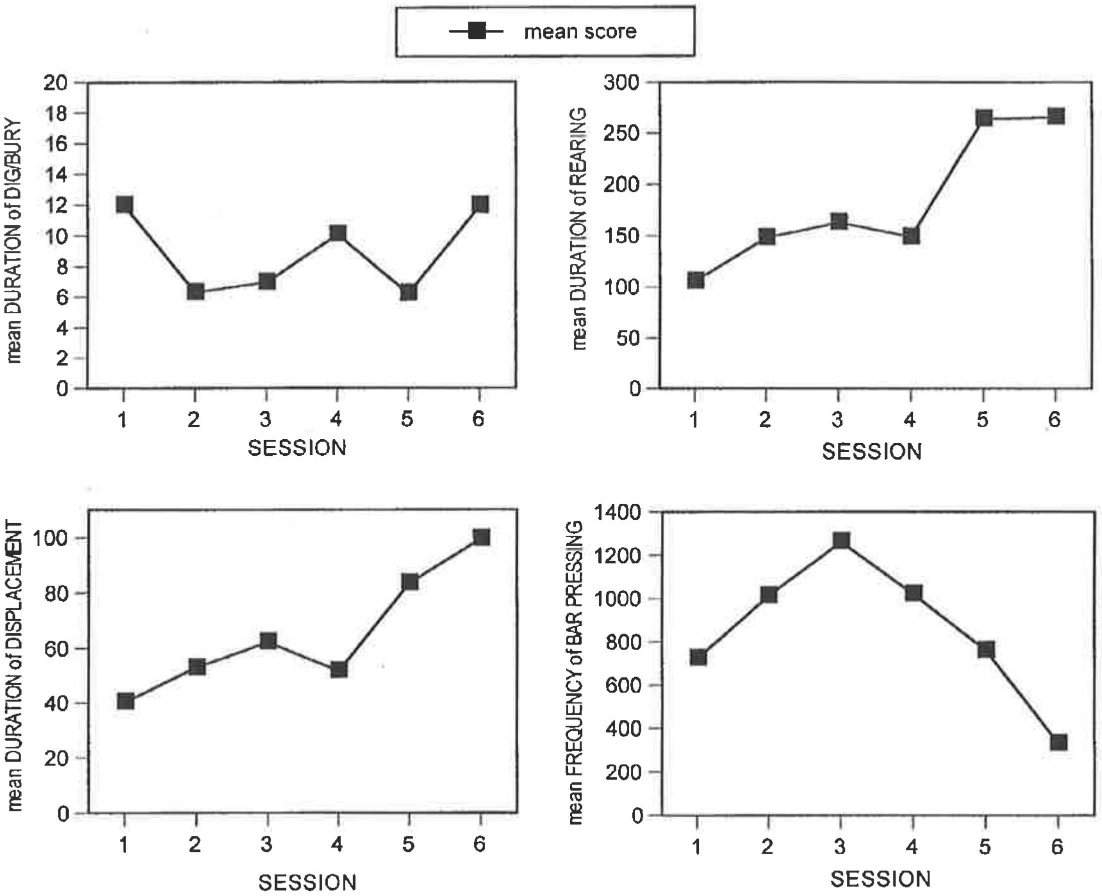


Figure 6.22 (III). Mean frequency of ***digging/burying*** was jointly affected by the "object" and "schedule" grouping variables during ***extinction***

6.3.7.3 ALL SIX SESSIONS

Main effect of *session*

The differences between sessions were statistically significant for four measures of behaviour. That is, the session number affected the duration of ***digging/burying*** [*F* (5,60)=2.66, *p*<.05], duration of ***rearing*** [*F* (5,60)=9.65, *p*<.001], duration of ***displacement*** [*F* (5,60)=8.03, *p*<.001], and the frequency of ***bar pressing*** [*F* (5,60)=26.79, *p*<.001]. It should be noted that for the ***digging/burying*** category, there were five instances where this behaviour was not observed during a session (three in the VIOE group, & one each in the FIOE & FIOS groups). Figure 6.23(I) indicates that the duration of ***digging/burying*** decreased over ***schedule*** sessions, increased in the first ***extinction*** session, and then showed a slight overall increase across ***extinction***. The mean duration of ***rearing*** and ***displacement*** increased over ***schedule*** sessions, decreased slightly in the first ***extinction*** session and then increased sharply over ***extinction*** (Figure 6.23:I). The frequency of ***bar pressing*** increased markedly over the first three sessions, dropped noticeably in the first ***extinction*** session and then continued to decrease sharply over ***extinction*** (Figure 6.23:I).



<u>Figure 6.23 (I).</u> Mean frequency and duration of behaviours for the "session" grouping variable for all six sessions (top- duration of ***digging/burying*** & ***rearing***, & bottom- duration of ***displacement*** & frequency of ***bar pressing***)

Object x session interaction effect

A statistically significant ***object*** x ***session*** interaction was found for the frequency of ***rearing***, and the frequency and duration of ***sniff and touch object***, ***sniff object*** and ***bar-related behaviour*** (Table 6.19). That is, these measures were *jointly* affected by the object (objects first present during ***schedule*** or ***extinction***) *and* session grouping variables over the six sessions.

Visual inspection of Figure 6.23 (I) shows that the frequency of ***rearing*** increased over the six sessions, with an increase over ***schedule*** sessions, slight decrease in the first ***extinction*** session and a noticeable increase over the remaining ***extinction*** sessions. Although this measure increased over the six sessions for "OS" and "OE" groups, the increase was most pronounced for the "OS" groups, but the highest scores in every session were observed in the "OE" groups. That is, more bouts of ***rearing*** took place for groups of rats that only encountered objects during

extinction. A marked increase over sessions took place if rats first encountered objects during ***schedule*** sessions.

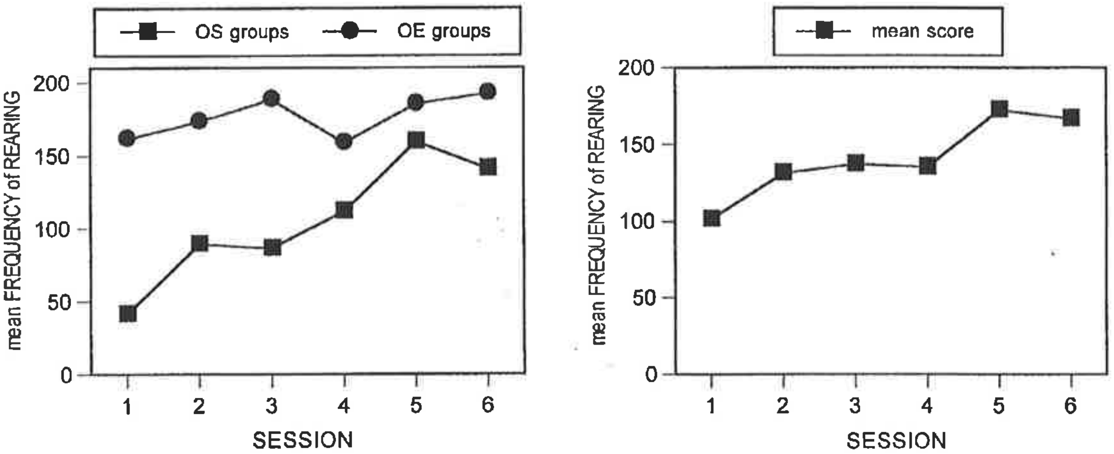


Figure 6.23 (II). Mean frequency of ***rearing*** was jointly affected by the "object" and "session" grouping variables over the six sessions

Table 6.19
Experiment 1 significance levels obtained for measures of behavioural categories during all six sessions (***object* x *session*** interaction effect).

Variable	***F*(5,60)**	**Significance level (*p*)**
Frequency of ***rearing***	2.47	<.05
Frequency of ***sniff and touch object***	15.63	<.001
Duration of ***sniff and touch object***	9.14	<.001
Frequency of ***sniff object***	26.69	<.001
Duration of ***sniff object***	22.32	<.001
Frequency of ***bar-related behaviour***	5.13	<.005
Duration of ***bar-related behaviour***	3.10	<.05

As shown in Figure 6.23 (III & IV), the frequency and duration of ***sniff object*** and ***sniff and touch object*** decreased over ***schedule*** sessions for the "OS" rats. During ***extinction***, the frequency and duration of ***sniff object*** and frequency of ***sniff and touch object*** decreased, but the duration of ***sniff and touch object*** increased. That is, the number of bouts of this behaviour dropped, but the time spent engaged in this form of ***exploration*** actually increased. The scores for these four measures were highest in the "OE" groups during the first ***extinction*** session (first encounter with objects), but only the duration of ***sniff and touch object*** was higher for these groups during the later ***extinction*** sessions. Overall, the duration of ***sniff and touch object*** decreased slightly over ***extinction*** for the "OE" groups, whereas the scores increased noticeably for the "OS" groups. Thus, when objects were first encountered appeared to most greatly affect the amount of time spent ***sniffing and touching objects*** during ***extinction*** and the pattern observed over these sessions.

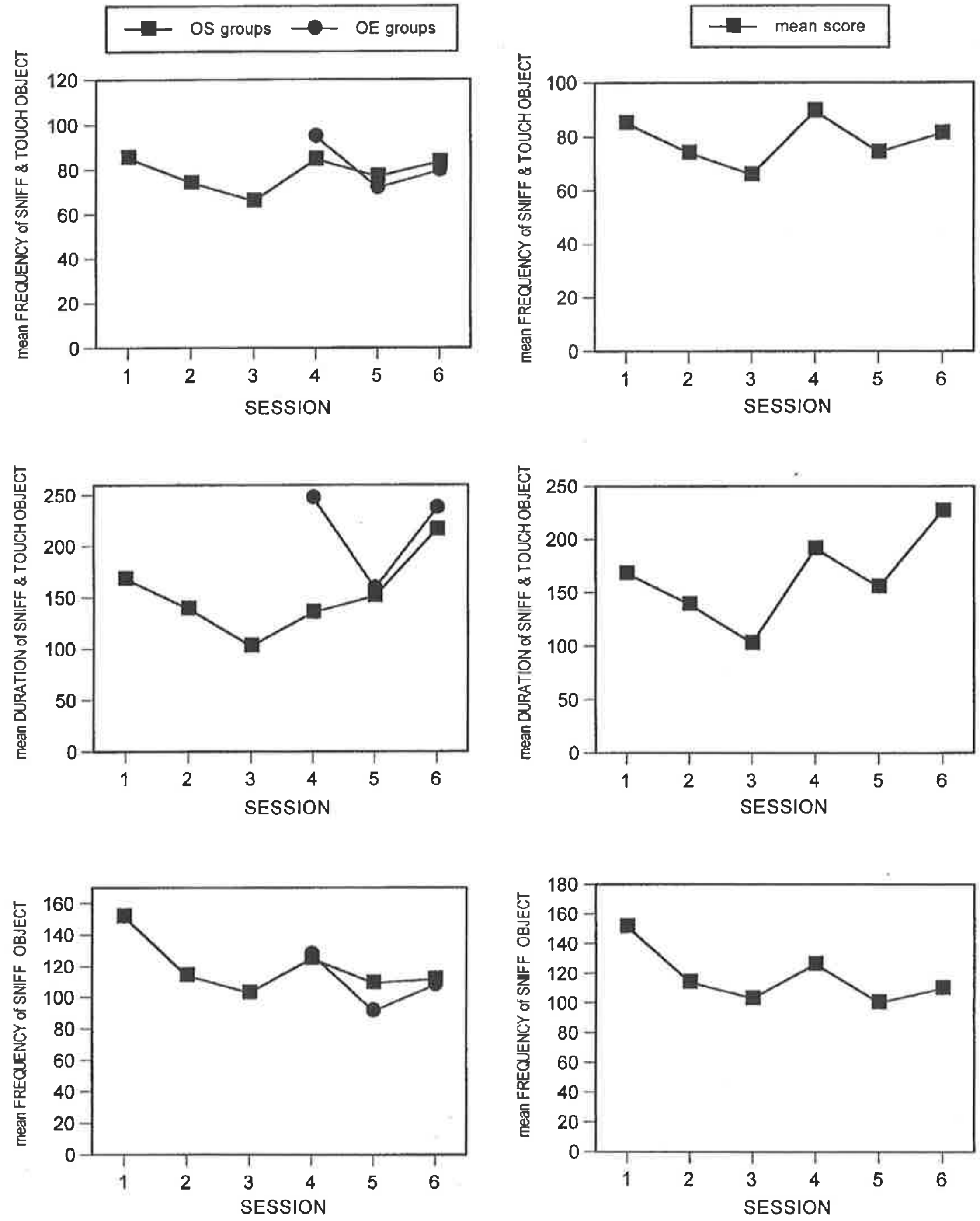


Figure 6.23 (III). Mean frequency and duration of behaviours jointly affected by the "object" (left) and "session" (right) grouping variables over the six sessions (top- frequency of ***sniff & touch object***, middle- duration of ***sniff & touch object***, & bottom- frequency of ***sniff object***)

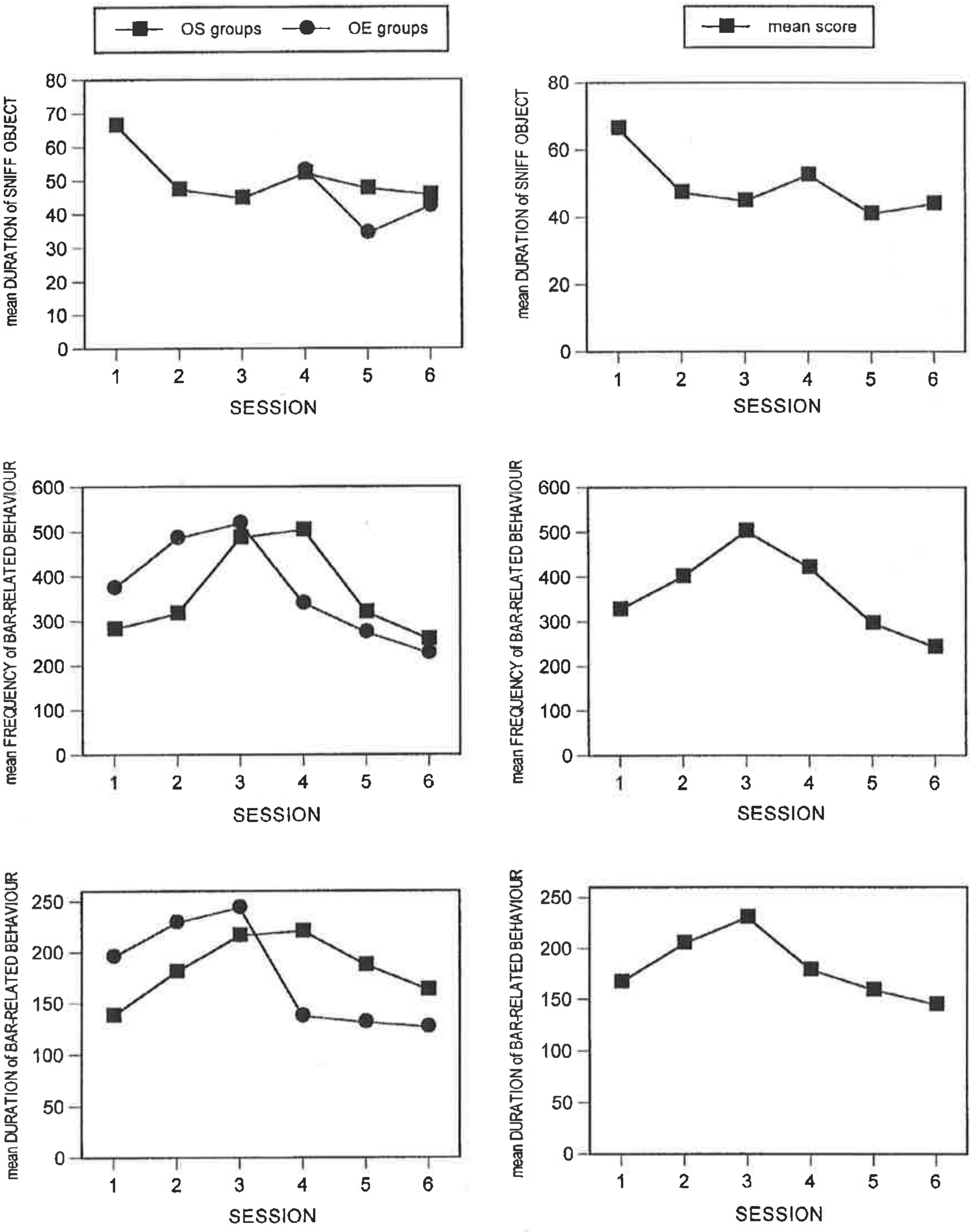


Figure 6.23 (IV). Mean frequency and duration of behaviours jointly affected by the "object" (left) and "session" (right) grouping variables over the six sessions (top- duration of ***sniff object***, middle- frequency of ***bar-related behaviour***, & bottom- duration of ***bar-related behaviour***)

Bar-related behaviour increased steadily over ***schedule*** sessions, dropped in the first ***extinction*** session and then continued to decrease over the remaining ***extinction*** sessions (Figure 6.23:IV). The scores for both measures of ***bar-related behaviour*** were highest in every ***schedule*** session for the "OE" groups, whereas during ***extinction*** the scores were noticeably lower for these groups. That is, if objects were absent during ***schedule*** sessions, more bouts of ***bar-related behaviour*** took place and more time was allocated to this behaviour. If objects were first encountered during ***extinction*** (the same "OE" groups), then the reverse pattern was observed during ***extinction***. Thus when objects were first encountered clearly had an affect on this behaviour.

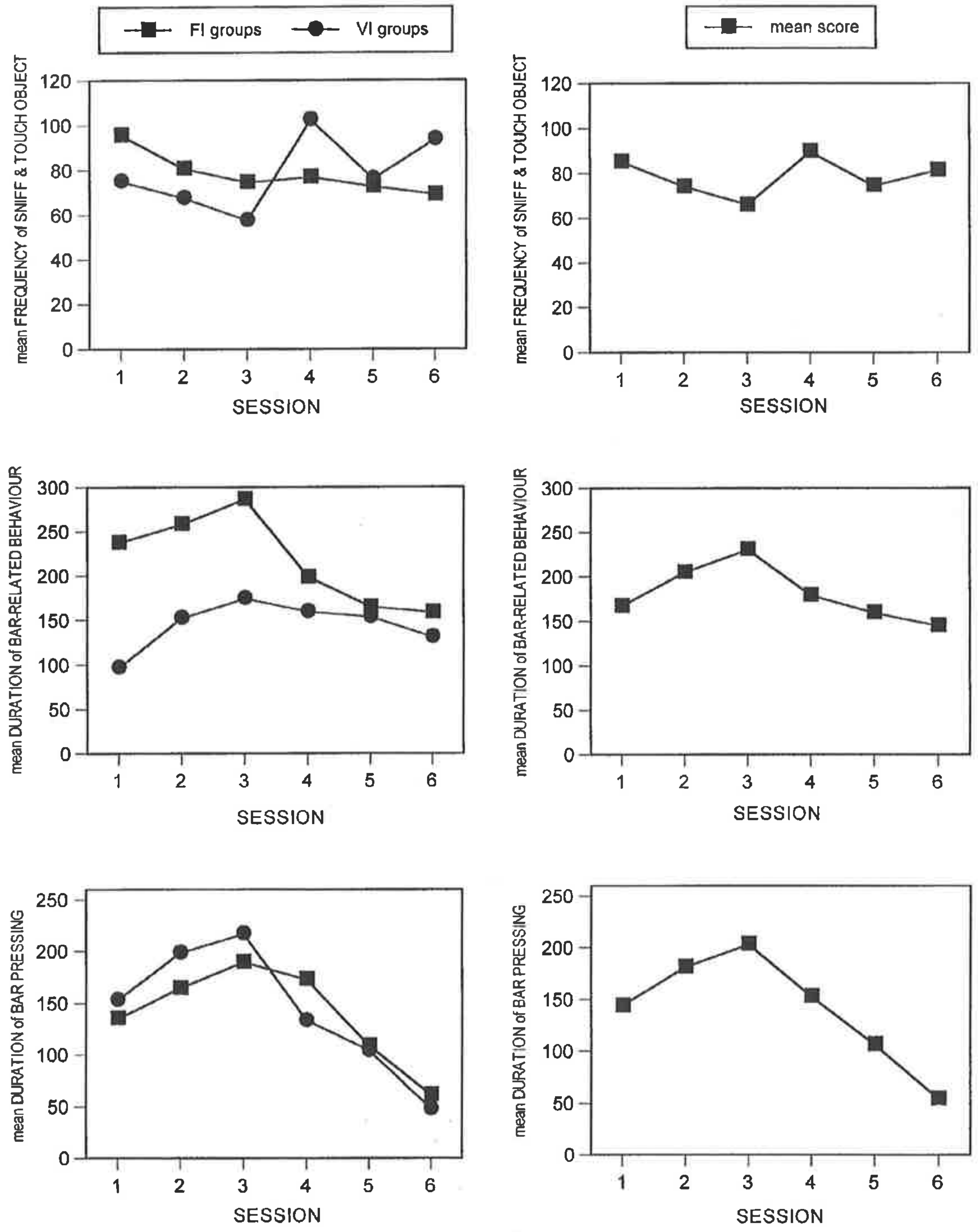


Figure 6.23 (V). Mean frequency and duration of behaviours jointly affected by the "schedule" (left) and "session" (right) grouping variables over the six sessions (top- frequency of ***sniff & touch object***, middle- duration of ***bar-related behaviour***, & bottom- duration of ***bar pressing***)

Schedule x session interaction effect

The MANOVAs for the frequency of ***sniff and touch object*** [*F* (5,60)=2.38, *p*<.05], duration of ***bar-related behaviour*** [*F* (5,60)=2.51, *p*<.05], and duration of ***bar pressing*** [*F* (5,60)=2.53, *p*<.05] yielded statistically significant ***schedule*** x ***session*** interactions. This means that these measures were *jointly* affected by the schedule (***fixed-interval*** or ***variable-interval***) *and* session grouping variables over the six sessions.

Visual inspection of Figure 6.23 (V) indicates that the duration of ***bar pressing*** and ***bar-related behaviour*** increased steadily over ***schedule*** sessions, decreased in the first ***extinction*** session and continued to decrease over the remaining sessions. The duration of ***bar-related behaviour*** scores were much higher for the ***fixed-interval*** groups during ***schedule*** sessions. During ***extinction***, these scores were still higher for the ***fixed-interval*** groups, but less noticeably so. The duration of ***bar pressing*** scores, by contrast, were higher for the ***variable-interval*** groups during ***schedule*** sessions, but also slightly lower during ***extinction***.

Frequency of ***sniff and touch object*** decreased over ***schedule*** sessions, increased in the first ***extinction*** session, but showed a slight decrease over ***extinction*** overall. These scores were higher in every ***schedule*** session for the ***fixed-interval*** groups, whereas the scores were lower in every ***extinction*** session for the same groups.

Object x schedule interaction effect

A statistically significant ***object*** x ***schedule*** interaction was found for the frequency of ***digging/burying*** [*F* (1,12)=7.62, *p*<.05]. Thus, frequency of ***digging/burying*** was *jointly* affected by the object (objects first present during ***schedule*** or ***extinction*** sessions) and schedule (***fixed-interval*** or ***variable-interval***) grouping variables.

As shown in Figure 6.23 (VI), frequency of ***digging/burying*** scores decreased over ***schedule*** sessions for the "OS" and "OE" groups. The scores then decreased in the first ***extinction*** session for the "OS" rats, whereas the scores increased for the "OE" rats. Frequency of ***digging/burying*** then increased over ***extinction*** for the "OS" groups, whereas there was little change over these same sessions for the "OE" groups. Frequency of ***digging/burying*** was highest in four of the six sessions for the "OS" groups. That is, more bouts of this behaviour tended to occur for rats whose first encounter with objects occurred during ***schedule*** sessions.

Frequency of ***digging/burying*** decreased noticeably over ***schedule*** sessions in the ***fixed-interval*** groups, whereas a minimal increase occurred in the ***variable-interval*** groups. In the first

extinction session, there was an almost imperceptible decrease for the ***variable-interval*** groups, but a slight increase for the ***fixed-interval*** groups. Both ***fixed-interval*** and ***variable-interval*** groups showed an increase over ***extinction***. Frequency of ***digging/burying*** was noticeably higher in three of the six sessions for the ***fixed-interval*** groups.

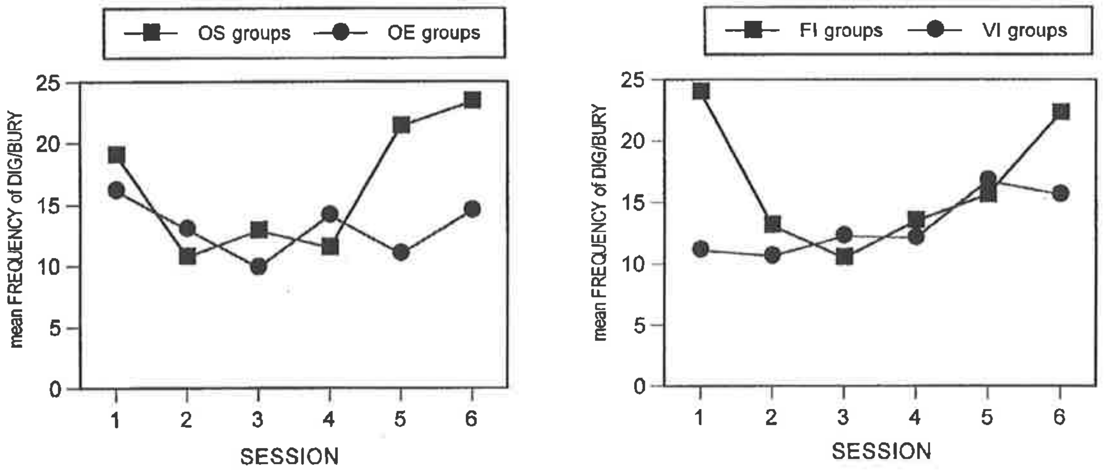


Figure 6.23 (VI). Mean frequency of ***digging/burying*** was jointly affected by the "object" and "schedule" grouping variables over the six sessions

6.3.7.4 INDEPENDENT JUDGING

Reliability of the experimenter's behavioural measurements and the behavioural criteria were tested via independent judging of an animal chosen at random. Two statistical procedures were followed in order to analyse the data obtained from the three independent judges.

The first statistical procedure involved the construction of two inter-correlation matrices: one for the frequency of behavioural events, and another for the duration of these events. The inter-correlation matrices were used to determine the degree of correlation between the three independent judges and the experimenter.

The probability values pertaining to the frequency of behavioural events were statistically significant for all judges:

	JUDGE 4 (Experimenter)	
JUDGE 1	r=.814	p<.01
JUDGE 2	r=.863	P<.01
JUDGE 3	r=.952	p<.001

The probability values for the duration measures were also statistically significant for all judges:

	JUDGE 4 (Experimenter)	
JUDGE 1	$r=.769$	$p<.05$
JUDGE 2	$r=.793$	$p<.05$
JUDGE 3	$r=.914$	$p<.01$

The second stage of statistical analysis involved the application of Kendall's W coefficient of concordance to the data. This program measured the agreement amongst the judges. A high degree of agreement was found to exist between the judges for the frequency and duration measures of all behavioural categories:

$W=.879$ $p<.001$.

6.4 DISCUSSION FOR EXPERIMENT 1

6.4.1 THE PRESENCE OF EXPLORATORY AND OTHER BEHAVIOURS DURING THE POST-REINFORCEMENT PAUSES

6.4.1.1 HYPOTHESIS ONE: PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s AND VI60-s SCHEDULES

Hypothesis one predicted that a larger proportion of each of the scored behaviours would occur during the PRPs for rats run on the ***fixed-interval*** schedule, when compared with the ***variable-interval*** counterpart (since only ***fixed-interval*** schedules are characterised by the existence of regular PRPs).

As expected, for the groups with objects present during ***schedule*** sessions (FIOS & VIOS), the percentage of total frequency occurring during the PRPs was much higher in the ***fixed-interval*** group for all behavioural categories, except ***chew/bite object*** and ***jump at lid***. ***Jump at lid*** was not observed in the FIOS group during ***schedule*** sessions. As predicted, the percentage of total duration occurring during the PRPs was markedly higher in the ***fixed-interval*** groups for all behavioural categories.

For the FIOS group, which had stimulus objects present during ***fixed-interval*** sessions, over 50% of each frequency measure (except ***bar-related behaviour*** & ***displacement***) and duration measure (except ***chew/bite object***) occurred during the PRPs. Over 75% of the frequency and duration of ***pica*** and ***digging/burying*** took place during the PRPs. The highest proportions were 83.2% (frequency) and 90.63% (duration). For the VIOS group, on the other hand, less than a third of each frequency (except ***chew/bite object***) and duration (except ***pica***) measure took place during the PRPs in the ***variable-interval*** sessions.

As predicted, for the groups with objects absent during ***schedule*** sessions (FIOE & VIOE), the percentage of total frequency occurring during the PRPs was markedly higher in the ***fixed-interval*** group for all behavioural categories. ***Pica*** was not observed in the VIOE group during ***schedule*** sessions. The percentage of total duration occurring during the PRPs was also markedly higher in the ***fixed-interval*** groups for all behavioural categories.

For the FIOE group (objects absent during ***fixed-interval*** sessions), over 50% of each frequency measure (except ***bar-related behaviour & propping***) and duration measure occurred during the PRPs in the ***fixed-interval*** sessions. Over 75% of the duration of ***pica*** and frequency and duration of ***digging/burying*** took place during the PRPs. For this group the highest percentages were 75.39% (frequency) and 78.95% (duration). By contrast, for the VIOE group, less than 15% of each frequency and duration (except ***bar-related behaviour***) measure took place during the PRPs in the ***variable-interval*** sessions.

Thus, the unpredictability of the ***variable-interval*** schedule did appear to prevent a regular PRP from developing.

Typically, these findings would be accounted for in part by the aversive nature of the PRPs (Dinsmoor, Lee & Brown, 1986). The stimuli present during PRPs are held to be negative predictors of food, and as such have aversive properties, which tend to suppress operant responding. The PRPs have been considered as aversive periods of "non-responding". If behaviours did take place during these pauses, they were purported to be excessive, maladaptive adjunctive behaviours. Certainly, PRPs were periods of zero instrumental responding, but that is as far as the inactivity or passivity went.

These findings demonstrate that a wide variety of behaviours were engaged in during the PRPs by all ***fixed-interval*** and ***variable-interval*** rats. These included: ***behaviour directed at the bar and food-trough area***, ***exploratory behaviour directed at the stimulus objects***, ***exploratory behaviour directed at the peripheral areas of the box***, ***displacement***, ***digging/burying***, ***rearing*** and ***pica***. When objects were absent the rats engaged in the other behaviours scored.

Litchfield (1987) found that rats were never passive during the PRPs or other periods of zero instrumental responding on ***fixed-ratio*** schedules. The results for Experiment 1 indicate that the same is true for rats run on a ***fixed-interval*** or ***variable-interval*** schedule. An increase in ***general activity*** (including ***ambulatory behaviour***, which was not scored) and all of the behaviours scored was observed in the PRPs of the more predictable schedule (***fixed-interval***). These behaviours need not be "maladaptive", "excessive", "irrelevant" or "out-of-context", as the ***adjunctive behaviours*** discussed by Falk (1971) appear to be. A number of the behaviours observed in this study were largely ***exploratory*** in nature, and as such can hardly be considered as irrelevant or out-of-context. Rats engaged in adaptive ***exploratory behaviours*** in a bid to discover alternative sources of food, or sources of novel stimulation.

Particularly high percentages (frequency & duration) of ***pica***, ***digging/burying*** and ***jump at lid*** (FIOE group only) took place during the PRPs. Litchfield (1987) suggests that the rather bizarre ***jump at lid*** behaviour may be ***escape-directed exploration***, which could also be considered adaptive in nature. The lid of the experimental box created a barrier to ***exploration***. Any behaviour directed at this area may have been an attempt to explore beyond the confines of the apparatus. This jumping behaviour seemed to parallel the apparently ***escape-directed jumping*** reported by Huck and Price (1975). As Russell (1983) points out, escape from a novel and well-lit environment to one that is familiar, sheltered and darker is highly adaptive in "predation-susceptible" rats. However, in this experiment, the experimental box was lit from above, so ***jumping towards the lid*** would not have taken the rat towards a darker area. Dinsmoor et al (1986) would suggest that such ***escape-directed exploration*** would occur as a result of the aversive stimuli present during the PRPs. ***Digging/burying*** could also be ***escape-directed***, in those instances where ***digging*** took place along the peripheral edges of the box. ***Pica*** involved the rats eating the sawdust, and in particular the larger pieces of bark.

Falk's (1971) assertion that ***schedule-induced behaviours*** are ***excessive*** forms of ***displacement*** activities must be called into question. ***Displacement behaviours*** were present in this study, as well as in Litchfield's (1987) study, but they were just one of a number of behaviours engaged in. The ***adjunctive behaviours*** that Falk (1971) describes may occur as a result of the animal's search for novel stimulation during the aversive PRPs. If the chance to explore a number of objects or other novel stimuli is provided, then there is every possibility that ***excessive adjunctive behaviours*** (such as ***polydipsia***) would not occur, or would be indulged in to a lesser extent. This will be investigated in Experiment 3. On the whole, the rats behaved in an adaptive manner during the PRPs, which could in no way be considered as a conglomeration of ***displacement behaviours***.

The findings suggest that if rats are given the chance to explore during a ***fixed-interval*** schedule (FIOS group), they will do so during periods of zero instrumental responding. The rats are free to engage in other behaviours during these periods. PRPs give the opportunity to engage in other more "stimulating" behaviours, but not all behaviour takes place during the PRPs. When ***bar pressing*** did not occur, heightened activity was observed in the rats. The behaviours engaged in are significant for adaptation, and under natural conditions would lead the rat to alternate sources of food and safe, sheltered hideouts. Forster (1986) suggested that ***extinction*** produced ***exploratory behaviour***. These findings are compatible with Forster's, since the FI60-s schedule used was composed of periods of "intermittent extinction". Thus, the ***extinction*** inherent in the ***fixed-interval*** schedule similarly produced ***exploratory behaviour*** and a number of other behaviours.

For the ***variable-interval*** groups, most of the behaviours scored took place outside the PRPs. As was seen in the other sections (see Hypothesis 3), a variety of behaviours also occurred during periods of non-instrumental responding, or at other times during the interval (not PRP) for the ***variable-interval*** schedule.

6.4.1.2 HYPOTHESIS TWO: EFFECT OF NOVEL STIMULUS OBJECTS ON PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s AND VI60-s SCHEDULES

Some support was found for the prediction that the presence or absence of objects during ***schedule*** sessions would have an effect on the proportion of non object-related behaviours that occurred during PRPs.

When objects were absent during ***fixed-interval*** sessions (FIOE group), the proportions were lower than for the FIOS group (by up to 13%) for the frequency of ***pica***, ***digging/burying***, ***propping*** and ***bar-related behaviour*** and the duration of ***digging/burying*** and ***propping***. For this same group, the proportion was higher for one behavioural measure (by about 7%), namely the duration of ***rearing***. The duration measures are perhaps the most interesting. In the absence of objects, rats on the ***fixed-interval*** schedule spent less proportion of time ***digging/burying*** and ***propping*** (both potentially ***escape-directed behaviours***) during the PRPs, but more time ***rearing*** (possibly ***inspection*** of surroundings for predators, conspecifics etc). ***Jump at lid*** only occurred if objects were absent. The proportions were very similar (<5% difference) irrespective of presence or absence of objects for the frequency of ***rearing*** and ***displacement*** and the duration of ***pica***, ***displacement*** and ***bar-related behaviour***. Thus, the presence of objects during ***fixed-interval*** sessions did not affect the proportion of every category of behaviour that occurred during PRPs.

When objects were absent (VIOE group) during ***variable-interval*** sessions, the proportions were lower than for the VIOS group (by more than 10% in a number of cases) for every category of "non-object directed" behaviour. This finding suggests that PRP development was more likely to occur when objects were present. The presence of objects to explore immediately after consumption of a food pellet elicited a range of behaviours apart from the operant response. A particularly high proportion of frequency of ***chew/bite object*** took place during the PRPs (VIOS group). Whether objects were present or not clearly did have an effect upon the proportion of behavioural measures that took place during PRPs of ***variable-interval*** sessions.

6.4.2 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE DURING THE PRPs, OVER SESSIONS, AND BETWEEN GROUPS

The graphs were examined purely for descriptive purposes, and only tendencies to change in the behavioural measures over sessions and between groups were indicated. A number of differences over sessions were not statistically significant (as will be discussed in the next section). Nevertheless, a descriptive examination of the graphs may indicate some tendencies to change in the behavioural measures, which would perhaps become statistically significant if larger sample sizes (>4 rats per group) were employed.

Visual inspection of Figures 6.11-6.14 (II) indicates that the frequency and duration measures during the PRPs for ***digging/burying***, ***rearing***, ***propping***, ***displacement***, and ***bar-related behaviour*** were highest for the ***fixed-interval*** groups, throughout the three ***schedule*** sessions. ***Pica*** scores were generally also higher for these groups.

The ***object-directed behaviours*** (***sniff object***, ***sniff & touch object***, & ***chew/bite object***) were markedly higher for the ***fixed-interval*** (FIOS) group, in all three sessions. No ***pica*** was observed for the VIOE group, and no instances of ***jump at lid*** were observed for the FIOS group. The ***jump at lid*** score was higher for the two groups with objects absent in these sessions.

The patterns of change over sessions varied depending on the behavioural measure. The frequency and duration of ***object-directed behaviours*** during the PRPs decreased over the three schedule sessions. However, ***chew/bite object*** was not observed in all rats during the PRPs.

6.4.3 CHANGES IN BEHAVIOURS DURING PRPs OVER SCHEDULE SESSIONS, BETWEEN SCHEDULES AND BETWEEN OBJECT CONDITIONS

Three behavioural categories (***pica***, ***jump at lid*** & ***chew/bite object***) were not included in the statistical analysis, since these behaviours occurred too infrequently in the four groups. The remaining behaviours included in the statistical analysis were: ***bar-related behaviour***, ***sniff object***, ***sniff and touch object***, ***propping***, ***displacement***, ***digging/burying*** and ***rearing***.

(a) Changes over schedule sessions

Over the three ***schedule*** sessions only the frequency of ***sniff object*** and duration of ***sniff and touch object*** showed statistically significant differences. The number of times objects were ***sniffed*** during PRPs, as well as the time spent ***sniffing and touching*** objects during the PRPs tended to decrease over sessions (perhaps as a result of habituation- i.e. the less "novel" objects were less likely to attract the rats' attention immediately after pellet consumption). Over time, a greater proportion of these behaviours took place outside the PRPs, and during other times of non-operant responding. Therefore, overall, the PRPs remained fairly constant or stable over sessions, except for these two ***object-directed behaviours***.

(b) Differences between schedules

The differences between the ***fixed-interval*** and ***variable-interval*** schedules were statistically significant for the frequency and duration measures of all behavioural categories. The schedule that rats were run on affected the frequency and duration of behaviours during the PRPs. Rats run on the ***variable-interval*** schedule engaged in less ***object exploration***, ***propping***, ***displacement***, ***digging/burying***, ***rearing*** and ***bar-related behaviour*** during the PRPs. These findings show that all the behaviours were less likely to take place during PRPs on ***variable-interval*** schedules. This is not surprising, since ***variable-interval*** schedules are "unpredictable", and typically lack PRPs. Behaviours were engaged in throughout the interval, at other times when operant responding did not take place.

(c) Differences between object conditions

No measure of behaviour showed statistically significant differences between the object conditions. That is, the presence or absence of objects during these sessions had no apparent effect upon the frequency or duration of non object-directed behaviours occurring during the PRPs. Thus a certain amount of each non object-directed behavioural category took place during the PRPs even if there were objects to explore and manipulate.

6.4.4 THE MOST FREQUENTLY OCCURRING BEHAVIOURS, AND ONES OF LONGEST DURATION IN SCHEDULE AND EXTINCTION SESSIONS

6.4.4.1 HYPOTHESIS THREE: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING FI60-s AND VI60-s SCHEDULES

Hypothesis three predicted that higher frequency and duration measures of non-object behaviours would be observed in the FIOE and VIOE groups (when compared to the FIOS & VIOS groups, respectively). The absence of objects to explore and manipulate during these sessions allowed more time and effort to be devoted to other behaviours.

As expected, the frequency and duration of non object-directed behaviours were markedly higher in the FIOE group than for the FIOS group during ***fixed-interval*** sessions, especially frequency of ***bar-pressing*** and ***bar-related behaviour***. The only exception was frequency of ***displacement***, which was higher if objects were present (FIOS group). The frequency and duration of non object-directed behaviours were also markedly higher in the VIOE group during ***variable-interval*** sessions, with two exceptions. There were no instances of ***pica***, and ***digging/burying*** was higher if objects were present (VIOS group).

Hypothesis three also predicted that the frequency and duration of ***bar pressing*** would be higher in the FIOE and VIOE groups (compared to the FIOS & VIOS groups, respectively). As expected, without objects to "distract" them during ***fixed-interval*** sessions, the frequency and duration of ***bar-pressing*** scores were higher in the FIOE and VIOE groups (markedly higher for the former).

6.4.4.2 HYPOTHESIS FOUR: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

Hypothesis four predicted that the FIOE group would engage in more ***object-directed behaviours*** during ***extinction***, since this was the first time that objects were encountered. Some support for this was found. Frequency and duration of ***sniff and touch object*** were higher in this group, as was frequency of ***sniff object***. The frequency and duration of ***chew/bite object*** and duration of ***sniff object***, however, were noticeably less. Thus the topography of the response was important. If objects had not been encountered prior to ***extinction***, then ***extinction*** elicited more ***sniffing and touching*** of objects, or manipulation with the forepaws. Rats with prior experience of objects were more likely to ***bite or chew*** the objects during ***extinction***. With respect to the other behaviours, for the FIOE group the frequency and duration of ***pica*** and ***bar-related behaviour***, as well as the frequency of ***rearing*** and ***displacement***, and the duration of ***digging/burying*** and ***propping*** were lower.

Hypothesis four also predicted that the VIOE group would direct less ***behaviour towards novel stimulus objects*** during ***extinction***, despite the fact that this was the first time that objects were encountered. The VIOE rats were most likely to be under the "control" of the previous ***variable-interval*** schedule, and would have difficulty in discriminating between the previous ***schedule*** and the new ***extinction*** conditions. Indeed, the VIOE group engaged in less ***object-directed behaviour*** during ***extinction*** sessions, with one exception. Only the duration of ***sniff and touch object*** was higher in this group. Again, irrespective of previous schedule, if rats had no prior experience with objects, then ***extinction*** elicited longer bouts of ***sniffing and touching*** with the forepaws. That is, the topography of the exploratory response was affected. During ***extinction*** sessions, the frequency and duration of ***pica***, ***digging/burying***, ***bar-related behaviour*** and ***bar pressing*** was lower for the VIOE group.

6.4.4.3 HYPOTHESIS FIVE: FREQUENCY AND DURATION OF BEHAVIOURS DURING FI60-s AND VI60-s SCHEDULES

Hypothesis five predicted, that rats run on the more predictable ***fixed-interval*** schedule would demonstrate lower frequency and duration of ***bar pressing*** than their ***variable-interval*** schedule counterparts (since ***variable-interval*** schedules evoke high rates of operant responding). When objects were present, the frequency of ***bar pressing*** was indeed lower for the ***fixed-interval*** rats. However, when objects were absent the frequency of ***bar pressing*** was higher for rats run on the ***fixed-interval*** schedule. Surprisingly, the presence of objects led to more typical patterns of operant responding in the "open-field" Skinner box. Thus the patterns of operant responding in a more naturalistic experimental chamber appear to be less predictable, particularly if size of the box rather than complexity of the environment (objects to serve as potential alternative sources of food or stimulation) is increased.

Hypothesis five also predicted that frequency and duration of behaviours other than ***bar pressing*** would be higher for rats run on the more predictable ***fixed-interval*** schedule. These rats would be less "under control" of the schedule (i.e. less time spent ***bar pressing***), which would allow more time to be spent on other behaviours. The frequency and duration of ***bar-related behaviour*** was higher for the ***fixed-interval*** rats (duration was markedly higher). Therefore, although the ***fixed-interval*** schedule was more predictable, it still elicited higher amounts of ***bar-related behaviours*** (which are clearly related to ***bar pressing***).

Frequency of ***jump at lid*** was either non-existent (FIOS) or much lower for the ***fixed-interval*** groups. Thus, the more predictable schedule elicited fewer bouts of this unusual and potentially ***escape-directed behaviour***. As expected, the three ***object-directed behaviours*** were higher in the FIOS group (although ***sniff object*** was almost the same). For rats run on the ***fixed-interval*** schedule, the duration of ***rearing***, ***displacement*** and the three ***object-directed behaviours*** were higher. Therefore, the more predictable schedule did appear to allow more time and effort to be devoted to ***exploration of the stimulus objects*** and ***rearing*** (possibly to inspect the surroundings for predators or conspecifics). In natural environments, if food availability is more predictable (like the ***fixed-interval*** schedule), the survival of rats may be enhanced. Without the pressure of having to rely on an unpredictable food source, rats would be able to engage in more ***exploration*** of their surroundings and pay more attention to whether predators or conspecifics (in competition for resources) are in the immediate area. However, the more predictable schedule also led to longer bouts of ***displacement***, which suggests that the stimuli present during the ***fixed-interval*** schedule were more aversive, or aroused more conflict (somewhat counter-intuitive).

If objects were present (FIOS group), the frequency scores of ***rearing*** and ***displacement*** and frequency and duration of ***propping*** were higher for the ***fixed-interval*** rats, whereas the frequency and duration of ***pica*** and ***digging/burying*** were lower. However, if objects were absent (FIOE group), this trend was reversed. Clearly, the presence or absence of objects (and not just predictability of the schedule) had an effect on some categories of behaviour. If the schedule was predictable and objects could be explored, then more time was spent engaged in the ***propping*** (***escape-directed behaviour***). The presence of objects may have elicited higher amounts of ***general exploratory responses***, which may have included exploration of areas beyond the confines of the box. If the schedule was predictable and objects could be explored, then less time was spent engaged in ***pica*** and ***digging/burying***. Both of these behaviours may be related to ***foraging*** or finding and eating alternative sources of food. With objects to explore as alternative sources of food or stimulation, these behaviours may have been suppressed if food availability was predictable.

6.4.4.4 HYPOTHESIS SIX: FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

Hypothesis six predicted that the ***fixed-interval*** groups would demonstrate lower frequency and duration of ***bar pressing***, since these rats should more readily discriminate between the previous ***fixed-interval*** schedule and the new ***extinction*** sessions. Unexpectedly, the frequency and duration of ***bar pressing*** was higher for rats in the ***fixed-interval*** groups, especially for the group with objects first present during ***extinction*** (FIOE group). Again, as during the ***schedule*** sessions, the pattern of operant responding during ***extinction***, in a more naturalistic experimental chamber with objects to explore, appeared to be less predictable. The presence of objects following the predictable ***fixed-interval*** schedule (especially if none had previously been encountered) interfered with the ***extinction*** of the ***bar pressing*** response or increased the ***resistance to extinction***. That is, the objects appeared to affect the rats' ability to register that the food source was depleted. Despite the previous experience with an unpredictable source of food, the ***variable-ratio*** rats more readily recognised the depletion of the food source. Therefore, the ***discrimination hypothesis*** (Church, 1963) appears to be applicable only to the more traditional Skinner box.

Hypothesis six also predicted that the ***fixed-interval*** groups would demonstrate higher frequency and duration of behaviours other than ***bar pressing***, since these rats should more readily discriminate between the previous ***fixed-interval*** schedule and the new ***extinction*** sessions (thus allowing more time for other activities). The frequency and duration of ***bar-related behaviour*** was indeed higher for ***fixed-interval*** groups. However, the frequency of the three ***object-directed behaviours*** was lower for rats previously run on the ***fixed-interval*** schedule, and the frequency of ***jump at lid*** was much lower for these groups.

As predicted, the duration of ***pica***, ***digging/burying***, ***rearing***, and ***displacement*** were higher for the ***fixed-interval*** groups, however, the duration scores for ***chew/bite object*** and ***jump at lid*** were lower. With respect to the time spent engaged in behaviours (duration), the ***fixed-interval*** groups spent more time eating alternative foods (***pica***), foraging or attempting to escape by ***digging/burying***, visually inspecting the surroundings (***rearing***), ***exploring*** the objects by ***sniffing and touching*** them, and engaged in conflict-related ***displacement activities***. These groups spent less time ***chewing and biting*** the objects (again, the topography of the exploratory response is important) and attempting to escape from the box by ***jumping at the lid***. Therefore, it appears to be difficult to predict exactly which behaviours (number of bouts and length of bouts) will be engaged in to a greater extent during ***extinction*** following a more predictable schedule (lower ***resistance to extinction***).

If objects were present during ***schedule*** sessions, the frequency scores of ***pica*** and ***digging/burying*** and the duration scores of ***sniff object*** and ***sniff and touch object*** were lower for the ***fixed-interval*** group (FIOS). However, for this same group, the frequency scores of ***rearing*** and ***displacement*** and the frequency and duration of ***propping*** were higher. If objects were first present during ***extinction*** sessions, the reverse was the case for these behaviours in the ***fixed-interval*** group (FIOE). These findings illustrate that, when objects are first encountered by rats (***schedule*** or ***extinction*** sessions), makes any predictions about frequency or duration of a range of behaviours during ***extinction*** even more problematic. However, clearly the topography of the ***object-directed behaviours*** seemed to vary between groups. Specifically, the groups that ***sniff and touch objects*** more appeared to spend less time ***chewing or biting the objects***. Earlier experience with objects appeared to increase ***chewing/biting*** of objects, which may be related to a form of ***aggression***. ***Aggressive behaviours*** are dealt with in more detail in Experiment 3.

6.4.5 PERCENTAGE OF TOTAL SESSION TIME SPENT ENGAGED IN EACH BEHAVIOURAL CATEGORY, OVER SESSIONS, AND BETWEEN GROUPS

(a) The schedule sessions

Not scored **category**

All groups spent more than 40% of ***schedule*** session time (<70%) engaged in behaviours that were ***not scored***. Although eleven categories of behaviour were scored, not every possible category could be included. Much of the ***not scored*** category was ***general ambulatory behaviour***. Overall, the percentages were higher for both ***variable-interval*** groups. This finding is perhaps surprising, since one might expect the ***variable-interval*** schedule to encourage higher rates of ***bar pressing***, and allow little time for other behaviours, especially ***general ambulatory behaviour*** around the box. However, movement away from an unpredictable food source may lead to discovery of alternative food sources, so such behaviour may have adaptive significance.

Presence or absence of objects had no apparent effect upon the amount of ***not scored*** behaviour during the ***fixed-interval*** sessions. By contrast, the presence of objects resulted in higher amounts of this category during ***variable-interval*** sessions. In order to physically explore the objects the rats had to move around the box, resulting in higher amounts of ***general ambulatory behaviour***. The ***fixed-interval*** schedule with its predictable periods of non-reinforcement may have encouraged higher amounts of movement around the box, irrespective of whether there were objects to investigate or not. There was a between-session decrease in the ***not scored*** category for all groups. ***General ambulatory activity*** may have decreased over sessions as a result of habituation to the experimental chamber itself.

Behaviours directed at the bar and food-trough area

With one exception (19.63%), the ***fixed-interval*** groups spent more than 20% of session time (<29%) engaged in ***behaviour directed at the bar and food-trough area***. The ***variable-interval*** groups engaged in these behaviours for more than 9% of time (<22%). Thus, the ***fixed-interval*** schedule evoked higher amounts of behaviours centered at the food source. Therefore predictability of reinforcement, or a reliable food source enhanced activities around that site. One might have expected the ***variable-interval*** rats to focus their efforts around the unpredictable food source, since the next operant response might be rewarded.

If objects were absent (FIOE & VIOE), rats spent more time engaged in ***behaviour directed at the bar and food-trough area***. That is, there were no objects to "distract" them by providing a possible alternative source of food or stimulation. There was a between-session increase in time spent centered at the food source. This suggests that a stable operant performance had not yet been reached, and more time was needed to habituate to the larger and more complex environment of the open-field Skinner box (which was "distracting" the rats).

Behaviours directed at the stimulus objects

During ***schedule*** sessions, the FIOS group spent less than 17% (>9.5%) of total session time engaged in ***object-directed behaviours***. By contrast, less than 10% of the VIOS group's time was spent engaged in these behaviours. (The ***chew/bite object*** category took up <1.5% of total session time in all cases). If the supply of food (reinforcement) was predictable, rats devoted more time to ***exploration of the stimulus objects***, which represented potential alternative sources of food. Irrespective of schedule type, a between-session decrease in time spent ***exploring objects*** was observed, reflecting a habituation effect. Little time was spent in ***aggressive behaviour*** directed at the objects (***chew/bite object***).

Behaviours directed at the peripheral areas of the box

Less than 12% of total session time was spent engaged in ***behaviour directed at the peripheral areas of the box*** if objects were present during ***schedule*** sessions, and a between-session increase was observed. Furthermore, more time was spent in these activities during the ***fixed-interval*** sessions. If objects were absent, more than 12% of time (<21%) was spent engaged in these behaviours, and a between-session decrease was observed. In addition, more time was devoted to ***behaviour directed at the peripheral areas of the box*** during the ***variable-interval*** sessions. Since the ***jump at lid*** category took up <1% of total session time in all cases, most of the ***behaviour directed at the peripheral areas*** was in the form of ***propping***.

Clearly, the presence or absence of objects affected this category of behaviour. Rats spent more time trying to ***escape*** the box if there were no objects to ***explore***. That is, they were attempting to explore beyond the confines of the box, since there were no objects or sites to explore within the box. If the availability of food was unpredictable, they spent even more time trying to escape from the box. Over sessions, however, slightly less time was spent trying to escape the box. Perhaps they were habituating to the experimental environment and beginning to show a more stable operant performance.

If objects were present, rats devoted less time to trying to explore outside the box. As they habituated towards the objects, they increased their efforts to escape from the box. If food availability was predictable, rats spent more time engaged in ***behaviour directed at the peripheral areas of the box***. Perhaps the presence of objects and predictability of reinforcement resulted in more exploration in general (inside and outside the immediate surroundings). However, an alternative explanation may exist. Food was available at predictable times in a well-lit environment. During periods of non-reinforcement, rats may have been attempting to seek shelter from potential predators (Russell, 1983).

Other behavioural categories

If objects were absent, less than 13% of total session time was spent ***rearing***, whereas for groups with objects present, less than 10% of time was spent engaged in this behaviour (<5% for the VIOS group). The presence of objects clearly reduced the amount of time spent ***rearing***. This behaviour increased the height of the rats, thereby increasing the area that could be inspected visually (for predators, conspecifics or alternative sources of food). The presence of objects suppressed this activity. There was a between-session decrease in ***rearing*** for all groups. If this behaviour was related to ***inspection*** of the surroundings, then as the rats habituated to the experimental box and the experimental conditions (no apparent risk of competition with conspecifics), they spent less time inspecting their immediate environment.

All groups spent less than 5% of time engaged in ***displacement*** (a slight between-session increase for all groups), less than 3% engaged in ***pica***, and less than 1.5% engaged in ***digging/burying***. None of these behaviours appeared to be ***schedule-induced***. The conflict aroused by the periods of non-reinforcement, were clearly not excessive for either schedule (low levels of ***displacement***). The potentially inappropriate alternative feeding (***pica***) elicited by these schedules was also not excessive. Similarly, ***digging/burying*** (which may represent ***escape-directed behaviour***, ***foraging*** or flurries of ***burying behaviour*** elicited by aversive stimuli) did not take up much of the rats' time.

(b) The extinction sessions

Not scored category

More than a quarter (<47%) of ***extinction*** session time was spent engaged in behaviours that were ***not scored***. All groups spent slightly less time devoted to these behaviours during ***extinction*** than before. Thus ***extinction*** apparently resulted in less ***general ambulatory behaviour***. The percentages were noticeably higher in every session for the VIOS group. Thus prior experience with objects during an "unpredictable" schedule (higher ***resistance to extinction***) resulted in higher levels of this category of behaviour. A between-session decrease in the ***not scored*** behaviours was observed. Thus, as the ***bar pressing*** response extinguished, and the rats habituated to the objects, less time was devoted to ***general ambulatory behaviour***.

Behaviours directed at the bar and food-trough area

Less than 23% of total session time (>8%) was spent engaged in ***behaviour directed at the bar and food-trough area***. A between-session decrease in this category showed that ***extinction*** of the operant response was taking place. However, since more than 8% of session time was still devoted to behaviours centered at the food source by all groups, the ***bar pressing*** response had not completely extinguished and rats were still returning to the only known food source, even though it was now depleted. Prior experience with objects ("OS" groups) resulted in higher levels of ***behaviour directed at the bar and food-trough area*** during the first two ***extinction*** sessions. These rats had already discovered that stimulus objects were an unlikely alternative source of food. Therefore, they still focussed more attention towards the only known source of food.

Behaviours directed at the stimulus objects

During ***extinction*** sessions, between 9% and 20% of total session time was spent engaged in ***object-directed behaviours*** in all cases. (The ***chew/bite object*** category took up <1.5% of total session time in all cases). There was either little change in ***object-directed exploration*** over sessions (***fixed-interval*** groups) or an increase over sessions (***variable-interval*** groups), suggesting that habituation towards the objects was not yet taking place. Depletion of the previously unpredictable food source (***variable-interval*** schedule) and extinction of ***bar pressing*** clearly increased the time devoted to exploration of the objects. Further encounters with the objects were needed, if exploration of the objects was to diminish. Again, as during ***schedule*** sessions, little time was spent in ***aggressive behaviour*** directed at the objects (***chew/bite object***).

Behaviours directed at the peripheral areas of the box

The ***fixed-interval*** and VIOS groups spent less than 15% of time (>9.5%) engaged in ***behaviour directed at the peripheral areas of the box***, whilst the VIOE group engaged in these behaviours for more than 20% of time (<28%). (The ***jump at lid*** category took up <1% of total session time in all cases). Furthermore, rats tended to devote more time to these ***escape-directed behaviours*** over sessions during ***extinction***. With the exception of the FIOE group, more time was also spent engaged in ***behaviour directed at the peripheral areas of the box*** during ***extinction*** than the previous schedule sessions. Depletion of the food source, which no longer "justified the cost" of exposure to potential predators by remaining in this well-lit environment (Russell, 1983), may have resulted in an increased attempt to leave the box and seek shelter and/or alternative sources of food. For the VIOE group, the amount of time spent trying to leave the box seemed particularly ***excessive*** (almost 30% of session 5 was spent engaged in this category).

Other behavioural categories

Less than 20% of total session time (>5%) was spent ***rearing*** by all groups. The amount of time spent ***rearing*** increased over ***extinction*** sessions, and was higher than during the previous ***schedule*** sessions (except in the first ***extinction*** session for the "OE" groups, when objects were encountered for the first time). Thus, once the food source was depleted, rats spent more time inspecting the immediate surroundings (for predators, conspecifics and other sources of food). The lack of food would alter the cost-benefit structure of the situation. Rats would be at risk in the open and well-lit environment, without the benefit of finding food, which might result in heightened vigilance (***rearing***). The levels of ***rearing*** appear to be excessive in three of the four groups (between 10% & 20%).

All groups spent less than 9% of time engaged in ***pica*** (between-session increase), less than 8% of time engaged in ***displacement*** (between-session increase), and less than 1.2% of time was spent ***digging/burying***. None of these behaviours appeared excessive. However, given more sessions, rats may have continued to spend more time eating inappropriate food (***pica***) in an attempt to assuage their hunger, thus developing an "eating disorder". Similarly, the conflict inherent in the situation (depleted food source in an unsheltered environment, with no way to escape the box) increased over ***extinction*** sessions (higher levels of ***displacement***). This may have resulted in excessive levels of ***displacement*** (akin to ***excessive grooming*** observed in some other captive environments).

6.4.6 PATTERNS OF CHANGE IN BEHAVIOURAL MEASURES OVER SESSIONS, AND BETWEEN GROUPS

In summary, Figures 6.17 - 6.19:II (inclusive) show that there was an overall decrease across the six sessions in all groups, for the frequency and duration of ***bar pressing*** and ***bar-related behaviour*** (except for the VIOS group), and duration of ***jump at lid*** (except for the FIOS group). There was an overall increase across the six sessions in all groups for the frequency and duration of ***displacement*** (except frequency for the FIOS group), ***rearing*** and ***pica***, as well as the frequency of ***digging/burying*** (except for the FIOE group), and duration of ***propping*** (except for the FIOE group).

Across the six sessions, there was an overall decrease in frequency of ***propping*** for the VIOE and FIOE groups. There was also an overall decrease in frequency of ***jump at lid*** for the VIOE and FIOE groups, and duration of ***digging/burying*** for the FIOE and VIOS groups. Thus, for some measures, the object (objects first present during ***schedule*** or ***extinction*** sessions) condition had an effect on the pattern observed.

For groups with objects first present during ***schedule*** sessions, there was an overall decrease across the six sessions in the frequency and duration of ***sniff object***, whereas there was an overall increase in the duration of ***chew/bite object***. The frequency and duration of ***sniff and touch object*** and frequency of ***chew/bite object*** increased across the six sessions for the VIOS group, but decreased for the FIOS group. When objects were first encountered during ***extinction***, there was an overall decrease across sessions for the frequency and duration of ***sniff object*** and ***sniff and touch object*** (almost negligible increase for duration in the VIOE group). There was a slight overall increase in frequency and duration of ***chew/bite object*** in the FIOE group, whereas these scores decreased slightly across ***extinction*** for the VIOE group.

It should be noted that these Figures were presented as an adjunct to statistical analysis. General trends observed in these graphs (even if the differences between groups were not statistically significant as discussed in the next section) could indicate that patterns exist and could become more apparent if larger sample sizes are used.

6.4.7 CHANGES IN BEHAVIOURS OVER SESSIONS, BETWEEN SCHEDULES, AND BETWEEN OBJECT CONDITIONS

Visual inspection of the Figures mentioned in the previous section highlighted general patterns or trends. This section discusses the statistically significant differences that were found.

6.4.7.1 SCHEDULE SESSIONS

(a) Changes over schedule sessions

Over the three ***schedule*** sessions, most of the behavioural measurements showed statistically significant differences. The exceptions were frequency of ***bar-related behaviour*** and frequency and duration of ***digging/burying*** and ***propping***. Thus, the number of bouts of ***bar-related behaviour*** remained stable over sessions, although the length of bouts increased. The number of bouts and length of bouts of ***digging/burying*** and ***propping*** remained stable over sessions.

The frequency and duration of ***bar pressing*** increased over ***schedule*** sessions, as did the duration of ***bar-related behaviour***. This suggests that the ***schedule*** performance was not quite stable yet, although it had appeared as though the operant performance was stable after 14 days of schedule sessions (***fixed-interval*** or ***variable-interval***). Other factors, such as the presence of objects may have affected the schedule performance over these three sessions.

The frequency and duration of the two ***object-directed behaviours*** declined over the three sessions. This decrease in ***exploratory behaviour directed at the stimulus objects*** depicts a habituation effect, as the ***exploratory responses*** to the stimuli habituate (Berlyne, 1950). Repeated exposure to the stimulus objects present during ***schedule*** sessions would have resulted in lower arousal, and consequently, less ***exploration*** in the form of ***sniffing and touching***.

Both measures of ***displacement*** tended to increase over ***schedule*** sessions. Animals tend to engage in ***displacement behaviour*** if competing or conflicting stimuli are present (Fantino & Logan, 1979). Berlyne (1960) suggests that food-deprived animals are put into a conflict situation if unfamiliar or novel stimuli are present. That is, an "antagonistic relationship between exploratory and eating responses" appears to exist (Berlyne, 1960, p.119). However, only two of the four groups had objects present, and ***displacement*** actually increased as the objects became more familiar. The unpredictability of the ***variable-interval*** schedule could have increased the conflict, since leaving the bar area could delay the next reinforcement, but not leaving the bar area left possible alternate sources of food undiscovered. In addition, spending large amounts of time in an area that offered no shelter or escape from predators would increase a rats' risk of predation in natural environments.

The frequency and duration of ***rearing*** increased over the three sessions. That is, inspection of the environment (for possible predators, conspecifics in competition for resources & alternative food sources) appeared to take up more of the rats' time, the longer they spent in the box under conditions of intermittent food reinforcement (with or without objects present). The test environment represented a less than ideal foraging environment for the rats. The area around the food source was brightly lit and provided no shelter for the rats during times of non-reinforcement. In natural environments, the rats could be putting themselves at greater risk over time by remaining around this only source of food, out in the open. Their hunger might be assuaged, but their risk of possible predation might also be increased. This could be reflected in the increase in both measures of ***rearing*** and ***displacement***.

(b) Differences between schedules

The differences between the ***fixed-interval*** and ***variable-interval*** schedules were statistically significant for only one measure of behaviour. Thus, the frequency of the various behavioural events as well as the time spent performing most of these behaviours was similar in both ***fixed-interval*** and ***variable-interval*** groups. However, the schedule that rats were run on affected the duration of ***bar-related behaviour*** during ***schedule*** sessions. The ***fixed-interval*** group rats engaged in a similar number of bouts, but the duration of these bouts was much longer in every session. Thus, the more predictable schedule resulted in more time being spent around the food source. In natural environments, one would certainly expect a hungry rat to spend time around a reliable source of food.

(c) Differences between object conditions

Three measures of behaviour showed statistically significant differences between the object conditions. That is, the presence or absence of objects during the ***schedule*** sessions had an effect upon the frequency and duration of ***rearing***, and the duration of ***propping***. If objects were absent (FIOE & VIOE groups), these measures were higher during every ***schedule*** session. These rats engaged in more bouts of ***rearing***, and spent more time engaged in this behaviour. Without objects to explore as potential sources of food or shelter, rats spent more time inspecting the immediate surroundings. In natural environments such vigilance could lead to early detection of predators or competition for limited resources.

Both measures of ***rearing*** increased over sessions, irrespective of presence or absence of objects. The number of bouts of ***propping*** was similar irrespective of presence or absence of objects. However, if objects were absent, the bouts were longer in every session. Without objects to explore, rats devoted more time to this ***escape-directed behaviour***, in an attempt to find alternative sources of food, stimulation or shelter. This measure increased over sessions if objects were present (as a result of habituation), and decreased over sessions if objects were absent.

(d) Interaction effects

Schedule by session interaction effect

A ***schedule by session*** interaction was found for the duration of ***digging/burying***, indicating that both the schedule (***fixed-interval*** & ***variable-interval***) and the session affected this behavioural measure. Less time was spent ***digging/burying*** over time, but this decrease was only observed in the rats run on the ***fixed-interval*** schedule. Time spent ***digging/burying*** remained stable over sessions for the ***variable-interval*** rats. Thus, an unpredictable source of food appears to elicit low levels of ***digging/burying***, which may represent a ***foraging behaviour***, ***escape-directed behaviour*** or behaviour linked to the presence of ***aversive stimuli***.

Object x schedule x session interaction effect

The frequency of ***bar-related behaviour*** was affected by all three grouping variables (***object x schedule x session*** interaction effect). More bouts of ***bar-related behaviour*** occurred over sessions, but the number of bouts were higher in every session for rats run on the ***fixed-interval*** schedule and for rats with objects absent. The more reliable food source may have resulted in rats making quick regular checks of the food source more often. In the absence of objects to explore, rats may have engaged in checks of the food source more often as well.

6.4.7.2 EXTINCTION SESSIONS

(a) Changes over extinction sessions

Over the three ***extinction*** sessions, a number of the behavioural measurements showed statistically significant differences. The exceptions were frequency of ***displacement*** and ***sniff and touch object***, duration of ***bar-related behaviour***, and frequency and duration of ***digging/burying*** (***object x schedule*** interaction effect) and ***propping***. It is somewhat surprising that a number of behaviours do not show statistically significant differences over the three sessions, in the form of either declines or increases.

The frequency and duration of ***bar pressing*** decreased over ***extinction*** (the instrumental response extinguished). The frequency of ***bar-related behaviour*** also declined over ***extinction***. Thus the number of bouts of behaviour centered at the food source decreased once this source was depleted. However, the time spent in ***bar-related behaviour*** remained stable over sessions. That is, there were fewer bouts, but each bout was longer as the rats thoroughly investigated the only known food source.

Over ***extinction***, the frequency and duration of ***sniff object*** decreased, as a result of habituation towards the stimulus objects. That is, the number of ***orienting responses*** declined and less time was spent visually ***inspecting*** the now familiar objects. By contrast, duration of ***sniff and touch object*** tended to increase over the three ***extinction*** sessions. Thus, for this measure, a habituation effect was not apparent. The objects did not appear to decrease in novelty or their ability to arouse the rats. The bouts of ***sniff and touch object*** remained constant during ***extinction***, but these bouts became longer. That is, the rats spent more time engaged in ***manipulation and exploration*** of the objects with the forepaws and snout. This finding is in accordance with Forster's (1986) hypothesis that ***extinction*** produces ***exploration***. Clearly, the topography of the ***exploratory responses*** is relevant. Less time is devoted to ***visual inspection*** over time, but more time is taken up with ***sniffing and touching***.

Although the number of bouts of ***displacement*** showed little change over ***extinction***, the duration of this behaviour increased over the three sessions. That is, the bouts became much longer over ***extinction***. Thus the conflict inherent in the experimental session appeared to increase over time. The food source was depleted, but the rats could not leave the box. Objects could be explored, but they provided no alternative source of food or shelter.

The frequency and duration of ***rearing*** increased over sessions. Once the food source was depleted, the rats were still stuck in an exposed position but without any food to compensate for this potential risk. That is, the cost-benefit tradeoff was different. They were out in the open (high risk) without any food to satisfy their hunger (low benefit). This may have resulted in increased ***vigilance*** in the form of ***rearing*** or ***visual inspection*** of the immediate surroundings.

(b) Differences between schedules

The differences between the ***fixed-interval*** and ***variable-interval*** rats were not statistically significant for any measure of behaviour (although a statistically significant ***object by schedule*** interaction was found for the frequency of ***digging/burying***). Thus, the frequency of the various behavioural events as well as the time spent performing these behaviours during ***extinction*** was similar whether rats had previously been run on ***fixed-interval*** or ***variable-interval*** schedules.

It was expected that ***fixed-interval*** rats would engage in ***exploration*** and behaviours other than ***bar pressing*** to a greater extent, based on the ***discrimination hypothesis*** (Church, 1963). Extinction of ***bar pressing*** should have occurred more rapidly in the ***fixed-interval*** groups, since these rats should have discriminated more readily between the ***fixed-interval*** and ***extinction*** conditions. However, this was not found to be the case. In fact, higher ***bar pressing*** frequency scores were observed for the FIOE group in every session. A greater ***resistance to extinction*** in the ***variable-interval*** groups was not apparent, as there were no statistically significant differences between ***variable-interval*** and ***fixed-interval*** groups during ***extinction***, with respect to ***bar pressing*** or other behaviours. Therefore, the ***discrimination hypothesis*** may only be relevant for rats run in the typical Skinner box. If the box provides a larger and more naturalistic environment, and extends the repertoire of possible responses, then ***resistance to extinction*** may be altered and less predictable.

(c) Differences between object conditions

No measures of behaviour showed statistically significant differences between the object conditions (although frequency of ***digging/burying*** yielded a statistically significant ***object by schedule*** interaction). That is, whether objects were first present during ***schedule*** or ***extinction*** sessions had no effect upon the frequency and duration of the various behavioural categories during ***extinction***. It is somewhat surprising that prior exposure to novel stimulus objects did not have any effect on the majority of behaviours. Again, the size and style of the open-field apparatus may complicate the issue and make behavioural predictions more problematic.

(d) Interaction effects

Object by schedule **interaction effect**

An ***object by schedule*** interaction was found for the frequency of ***digging/burying***, indicating that both the object (objects first present during ***schedule*** or ***extinction*** sessions) and the ***schedule*** used prior to ***extinction*** (***fixed-interval*** or ***variable-interval***) conditions affected this behavioural measure. The number of bouts of this behaviour showed relatively little change over sessions if rats were previously run on the ***variable-interval*** schedule or if rats first encountered objects during ***extinction***. The number of bouts increased over sessions for rats previously run on the ***fixed-interval*** schedule or for groups with prior exposure to objects. Thus depletion of a previously predictable food sources and prior exposure to objects resulted in more bouts of ***digging/burying*** over time. However, it is not possible to determine whether there were more flurries of ***sawdust pushing*** (linked to aversive stimuli) or more cases of ***digging*** related to ***foraging*** or ***escape***.

6.4.7.3 ALL SIX SESSIONS

(a) Changes over all six sessions

Four behavioural measures showed statistically significant differences over the six sessions. ***Object by session***, and ***schedule by session*** interactions were found for a number of behavioural measures, which will be discussed subsequently.

The frequency of ***bar pressing*** increased substantially over ***schedule*** sessions, and then decreased markedly over ***extinction*** sessions for all groups. The increase over ***schedule*** sessions suggests that the 14 days spent running on either the ***fixed-interval*** or ***variable-interval*** schedule (one half-hour session per day) may not have been enough to yield a stable baseline (although it had been considered stable prior to commencement of the observation sessions). Nevertheless, it is somewhat unexpected to find such a noticeable increase across all groups. The decrease over ***extinction*** sessions was expected, as the ***bar pressing*** response extinguished.

The duration of ***displacement*** increased over ***schedule*** sessions, tended to decrease in the first ***extinction*** session, and then increased steadily over ***extinction*** sessions. A number of factors may have contributed to the increase over ***schedule*** sessions. The presence of novel stimuli (FIOS & VIOS groups) and the unpredictability of the ***variable-interval*** schedule (VIOS & VIOE groups) may have increased the ***conflict*** in the situation over time. During ***extinction***, there were stimulus objects present in every group. Again, there was an increase in the length of bouts over ***extinction*** sessions. As the ***bar pressing*** response extinguished, and rats became habituated to the stimulus objects, the ***conflict*** may have increased. That is, the food source was depleted, the objects did not provide an alternative source of food, and it was not possible to leave the box in search of other resources.

A statistically significant difference in the duration of ***digging/burying*** over the six sessions was found. The bouts of ***digging/burying*** tended to become shorter over ***schedule*** sessions and then longer over ***extinction*** sessions. Therefore, depletion of the food source appeared to elicit higher levels of ***digging/burying***. Again, it is not possible to differentiate between flurries of ***sawdust pushing*** (linked to aversive stimuli) and ***digging*** related to ***foraging*** or ***escape***.

The duration of ***rearing*** increased over ***schedule*** sessions and then continued to increase over ***extinction*** sessions (Figure 6.23:I). The longer the rats spent in the apparatus (out in the open, without shelter), the more time they spent inspecting their surroundings (for predators, competitors, other food sources). Depletion of the food source resulted in higher levels of

rearing. Their "out-of-nest-time" was high, without any benefit in the form of food (Lucas, Timberlake & Gawley, 1988). The rats spent more time visually scanning the area for early detection of predators, or attempted to look outside the box (escape) during ***extinction***.

(b) Differences between schedules

The differences between the ***fixed-interval*** and ***variable-interval*** rats were not statistically significant for any measure of behaviour. However, statistically significant ***object by schedule*** interactions and ***schedule by session*** interactions were found a number of measures (to be discussed subsequently). Therefore, the frequency of the various behavioural events as well as the time spent performing these behaviours over all six sessions was similar irrespective of schedule group.

(c) Differences between object conditions

No measures of behaviour showed statistically significant differences between the object conditions. That is, whether objects were first present during ***schedule*** or ***extinction*** sessions had no effect upon the frequency and duration of the various behavioural categories. Statistically significant ***object by session*** interactions and ***object by schedule*** interactions were found for some behavioural measures (these will be discussed subsequently).

(d) Interaction effects

Schedule by session interaction effect

A statistically significant ***schedule by session*** interaction was found for three measures of behaviour, indicating that both the schedule (***fixed-interval*** or ***variable-interval***) and session grouping variables had an affect. These measures were frequency of ***sniff and touch object***, and duration of ***bar pressing*** and ***bar-related behaviour***.

The duration of ***bar pressing*** and ***bar-related behaviour*** increased over ***schedule*** sessions and decreased over ***extinction*** sessions for all groups. The duration of ***bar pressing*** tended to be higher for the ***variable-interval*** groups during ***schedule*** sessions, whereas duration of ***bar-related behaviour*** was lower for these groups for the same sessions.

Rats engaged in fewer bouts of ***sniff and touch object*** over ***schedule*** sessions (as they habituated to the objects), engaged in more bouts of this activity in the first ***extinction*** session (new objects), and then engaged in fewer bouts ***over extinction*** (as they habituated to the objects). However, overall, if objects were present during all six sessions, the frequency of ***sniff and***

touch object increased over the six sessions for the VIOS group (on the less predictable schedule), whereas it decreased over the six sessions for the FIOS group.

Object by schedule **interaction effect**

The frequency of ***digging/burying*** yielded a statistically significant ***object by schedule*** interaction. Irrespective of presence or absence of objects, this measure decreased over ***schedule*** sessions. If objects had first been encountered during ***schedule*** sessions, the frequency of ***digging/burying*** increased in the first ***extinction*** session, but showed little overall change across ***extinction***. By contrast, if objects were first encountered during ***extinction***, the frequency of this behaviour increased noticeably over ***extinction***. Thus, prior experience with objects resulted in less ***digging/burying*** once the food source was depleted.

As already mentioned, it is not possible to determine whether ***digging/burying*** represented an ***escape-directed behaviour***, a form of ***foraging*** or flurries of ***sawdust pushing*** as a result of aversive stimuli (e.g., depleted food source & no possibility of escape from the box). The ***fixed-interval*** groups and ***variable-interval*** groups also showed different patterns for this behaviour. The ***variable-interval*** groups gradually engaged in more bouts of ***digging/burying*** over ***variable-interval*** and ***extinction*** sessions. By contrast, the frequency of this behaviour declined noticeably over ***fixed-interval*** sessions and then increased again over ***extinction*** sessions. Thus, fewer bouts of ***digging/burying*** occurred over time if the schedule was predictable, and then increased when food was no longer available. The increase over ***extinction*** may reflect an increase in the aversiveness of the situation (food source depleted), resulting in an increase in attempts to ***escape***, ***forage*** or engage in bouts of ***sawdust pushing***.

Object by session **interaction effect**

A statistically significant ***object by session*** interaction was found for a number of measures. The frequency and duration of ***bar–related behaviour*** increased over ***schedule*** sessions and decreased over ***extinction*** sessions. If objects were absent during ***schedule*** sessions (FIOE & VIOE), then rats engaged in more bouts of ***bar-related behaviour*** and spent far more time devoted to this behaviour. Then when these groups first encountered objects during ***extinction***, lower ***bar-related behaviour*** scores (frequency & duration) were observed during ***extinction***. This suggests that these groups were not "distracted" by objects during ***schedule*** sessions. They were able to devote more time and effort to activities centered at the food source. Once the food source was depleted, the objects exerted maximum stimulus novelty and these rats spent less time checking the previous source of food.

The frequency and duration of ***sniff object*** decreased over ***schedule*** sessions if objects were present. These measures also decreased over ***extinction***. During ***extinction***, the scores were similar in all groups for sessions 4 and 6, but the was a noticeable drop in the frequency and duration of ***sniff object*** for the "OE" groups during session 5. Thus prior experience with objects led to a more gradual decline in the ***inspective*** form of ***object exploration*** (as a result of habituation to the objects).

There was a marked decline in frequency and duration of ***sniff and touch object*** over ***schedule*** sessions (as a result of habituation to the objects), if objects were present. Over ***extinction*** sessions, the number of bouts of this behaviour decreased, whereas the duration of ***sniff and touch object*** increased. However, prior experience with objects resulted in a less noticeable change in frequency of ***object manipulation*** over ***extinction***, accompanied by a marked increase in duration (FIOS & VIOS groups). If objects were first encountered during ***extinction***, more time was actually spent in this form of object manipulation in every session, and there was little overall change over sessions. Therefore depletion of the food source did result in more time spent ***exploring objects*** (***sniffing & touching***), in accordance with Forster's (1986) findings, but there was no apparent habituation effect over the three sessions (more sessions would have been required).

The frequency of ***rearing*** increased over ***schedule*** sessions and then continued to increase over ***extinction***. There were fewer bouts of this behaviour in every session for groups who first encountered objects during ***schedule*** sessions (FIOS & VIOS groups), but the increase in sessions was more pronounced. Thus the presence of objects resulted in less ***visual inspection*** of the surroundings. The objects provided potential sources of food, shelter or stimulation, but once the objects had been thoroughly investigated, the rats' attention was once more directed towards early detection of potential predators, competitors or escape (seeking shelter & food).

6.5 CONCLUSIONS BASED ON THE FINDINGS OF EXPERIMENT I

This section provides a summary of the general findings of this study. Following this, some practical implications of these findings are discussed, particularly with respect to schedules of reinforcement in other captive environments.

6.5.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

During ***schedule*** sessions, the ***fixed-interval*** groups spent at least 19% (& up to almost 30%) of total session time engaged in ***behaviour directed at the bar and food-trough area***. For the ***variable-interval*** groups these behaviours represented more than 9% (& up to 21%) of total session time. For the ***fixed-interval*** groups, the time spent engaged in ***behaviour directed at the bar and food-trough area*** may seem ***excessive***. However, these levels are unlikely to be maladaptive, since the rats had to press the bar (in order to be reinforced) and they had to spend time retrieving the pellets.

During ***extinction*** sessions, the ***fixed-interval*** groups spent more than 10% (& in some cases >20%) of total session time engaged in ***behaviour directed at the bar and food-trough area.*** The ***variable-interval*** groups spent at least 8% (& up to 20%) of ***extinction*** sessions engaged in these behaviours. Less time was spent in ***behaviour directed at the bar and food-trough area*** during ***extinction***, since the ***bar pressing*** response was extinguishing. However, in some cases at least, the levels still appear somewhat ***excessive*** (especially if >20%), but could not be considered maladaptive, since the now depleted food source is nevertheless the only known source of food.

Most bouts of ***bar-related behaviours*** (>75%) took place outside the PRPs for the ***fixed-interval*** groups, although more than 50% of the duration measure occurred during the PRPs. Therefore, the longer bouts occurred during the PRPs. That is, the food source was thoroughly investigated just after food was available at the source. At other times, the rats no doubt made brief checks for food at the only known source. The ***variable-interval*** rats, on the other hand, engaged in even fewer bouts of ***bar-related behaviour*** (<14%), and the bouts were brief (<25% of total session time). Thus, when the food source was unpredictable, more checks were made throughout the interval (a stable PRP was unlikely to develop anyway).

In summary, ***behaviour directed at the bar and food-trough area*** might be considered somewhat ***excessive*** during some sessions (especially ***fixed-interval*** sessions), but not maladaptive. Less than 25% of bouts of ***bar-related behaviour*** took place during the PRPs for all groups. For the ***fixed-interval*** rats, more than 50% of the duration measure of this behaviour occurred during PRPs, whereas this figure was less than 25% for the ***variable-interval*** rats.

6.5.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

During ***schedule*** sessions, the FIOS group spent more than 9% (<17%) of total session time engaged in *behaviour directed at the stimulus objects*. For the VIOS groups these behaviours represented at least 7% (<10%) of total session time. Stimulus objects represent a source of stimulation and potential source of food. The levels of ***exploratory behaviour*** observed were not ***excessive*** and these behaviours should be considered adaptive.

In most cases (except session 5 & 6 for the VIOE group), at least 10% (but <20%) of total session time during ***extinction*** was devoted to ***behaviour directed at the stimulus objects***. Once the food source was depleted, rats would be expected to search for alternative sources of food. The levels of ***exploratory behaviour*** observed were adaptive and could not be considered ***excessive***. Forster (1986; 1992; 1995) found that ***extinction*** resulted in higher levels of ***object exploration***.

For the FIOS group, at least 50% of bouts of ***object-directed behaviours*** occurred during PRPs, as did at least 46% (up to 63%) of the total duration. That is, rats on the predictable schedule tended to ***explore objects*** immediately after consumption of the food pellet, but they also directed ***exploratory responses*** towards the objects at other times during the interval. For the VIOS group, less than 30% of bouts of ***sniff object*** and ***sniff and touch object*** (frequency & duration) took place during PRPs, whereas most bouts of ***chew/bite object*** (>66%) occurred during the PRPs, but they were of a short duration (<22% of total duration). Thus, rats run on the unpredictable schedule tended to ***explore objects*** outside the PRPs (not surprising, since a stable PRP was unlikely to develop), although numerous short bouts of ***chew/bite object*** or ***aggressive behaviour*** took place immediately after reinforcement.

In summary, levels of ***behaviours directed at the stimulus objects*** were not found to be ***excessive*** during ***fixed-interval***, ***variable-interval*** or ***extinction*** sessions. For the FIOS group, more than 46% of ***object-exploration*** (frequency & duration) took place during the PRPs. For the VIOS group, less than a third of these behaviours (frequency & duration) occurred during the PRPs (except frequency of ***chew/bite object***).

6.5.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

During ***schedule*** sessions, the presence of objects resulted in less than 12% (>5%) of total session time being devoted to ***behaviour directed at the peripheral areas of the box***. If objects were absent, these behaviours represented more than 12% (& up to 20%) of total session time. For both schedule types (***fixed-interval*** & ***variable-interval***), in the absence of objects, the time spent engaged in these ***escape-directed behaviours*** (mainly ***propping***) appears ***excessive***. This category of behaviour may represent attempts to explore outside the box, for shelter or food or even water. The presence of objects clearly reduced the amount of activity directed towards the ***peripheral areas of the box***.

During ***extinction*** sessions, at least 10% (9% for the VIOS group during session 5 & 6) of total session time was spent engaged in ***behaviour directed at the peripheral areas of the box.*** For the VIOE group, more than 20% of total session time was devoted to these ***escape-directed behaviours***. The depletion of the food source resulted in increased attempts to leave the box, where they were potentially vulnerable (no shelter from predators) and unlikely to find food. Attempts to seek shelter during periods of non-reinforcement may reduce the rats' susceptibility to predation (Russell, 1983; Lucas, Timberlake & Gawley, 1988). The time spent in this category of behaviour could be considered ***excessive***, especially in the VIOE group. It would be difficult to determine whether such behaviour could be considered as adaptive or maladaptive. On the one hand, attempting to leave the box to seek food and shelter could be considered adaptive. On the other hand, constantly struggling to leave a captive situation unsuccessfully could be considered a waste of energy and potentially maladaptive. If ***excessive*** and ***repetitive*** enough, it could be considered to be a form of ***stereotypic behaviour***.

The ***jump at lid*** category, found to occur during a ***fixed-ratio*** schedule of reinforcement (Litchfield, 1987) was again present during the ***fixed-interval*** and ***variable-interval*** schedules investigated in this study. As mentioned in section 3.9.2.1, other researchers (Aldis, 1975; Hole & Einon, 1984; Rensch & Ducker, 1959) have observed similar behaviours in a number of rodents. Hole and Einon (1984) suggest that the explosive leaps, sudden catapults or aerial somersaults that have been observed in rodents may be ***anti-predator*** or ***escape behaviours***. Therefore, the ***jump at lid*** category may have adaptive significance, and should not be considered bizarre.

For the ***fixed-interval*** groups, more than 40% of bouts of ***propping*** and more than 50% of duration occurred during the PRPs. Thus, bouts of ***propping*** were just as likely to take place outside the PRPs, but the ones that occurred immediately after reinforcement tended to be longer. That is, slightly more time was devoted to this ***escape-directed behaviour*** during the PRPs, when stimuli associated with non-reinforcement were present. Most bouts of ***jump at lid*** (>70% frequency & duration) occurred during the PRPs for the FIOE group. This behaviour was not observed in the other ***fixed-interval*** group. Most bouts of ***propping*** and ***jump at lid*** (>75%

frequency & duration) took place outside the PRPs for the ***variable-interval*** groups (for which a stable PRP was unlikely to develop).

In summary, levels of ***behaviour directed at the peripheral areas of the box*** were ***excessive*** during ***fixed-interval*** and ***variable-interval*** sessions, if objects were absent, and during ***extinction*** for all groups (objects present in all groups). For the ***fixed-interval*** groups, more than 40% of these ***escape-directed behaviours*** (frequency & duration) occurred during PRPs, whereas very few bouts (frequency & duration) took place during PRPs for the ***variable-interval*** rats.

6.5.4 OTHER BEHAVIOURAL CATEGORIES

Less than 5% of total ***fixed-interval*** and ***variable-interval*** time was spent engaged in ***displacement***. Although rats tended to spend slightly more time engaged in ***displacement*** during ***extinction***, less than 10% of total time was devoted to this activity. Therefore, even when the food source was depleted, (and rats became habituated to the objects) the level of this ***conflict-related behaviour*** was not ***excessive***.

Approximately half of the bouts of ***displacement*** took place during the PRPs for the ***fixed-interval*** groups, although more than 60% of total duration occurred during the PRPs. Thus, immediately after reinforcement, the bouts of ***displacement*** tended to be longer. More time was devoted to this ***conflict-related behaviour*** at times when food delivery was least likely to occur. If rats were run on the unpredictable schedule (***variable-interval***), most bouts of ***displacement*** (frequency & duration) took place outside the PRPs. The levels of ***conflict*** were higher outside the PRP. The period coinciding with delivery and consumption of the food pellet was less ***conflict arousing*** than other periods throughout the interval.

All groups spent less than 1.5% of total session time (***fixed-interval***, ***variable-interval*** & ***extinction***) engaged in ***digging/burying***. This category of behaviour incorporated a variety of responses. ***Digging/burying*** may be related to ***foraging*** or it may be ***escape-related***. At times it may have included flurries of ***sawdust pushing with the forepaws***, which may occur in the presence of aversive stimuli or as an ***anti-predator response*** (Litchfield, 1987). Certainly, the levels observed were low.

For the ***fixed-interval*** groups, most instances of ***digging/burying*** (frequency & duration) took place during the PRPs (>75%). Less than a third of ***digging/burying*** (frequency & duration) occurred during the PRPs in the VIOS group, and for the VIOE group almost all instances (>85%) of this behaviour took place outside the PRPs.

If objects were present during ***fixed-interval*** or ***variable-interval*** sessions, rats spent less than 10% of total session time engaged in ***rearing***. In most cases, the absence of objects during these sessions resulted in slightly higher proportions (<13%). Therefore the presence of objects ensured that rats did not engage in ***rearing*** excessively. This behaviour allowed rats to increase their height, thereby increasing the distance that could be ***visually inspected***. Such ***visual inspection*** would represent critical survival behaviour for rats in natural surroundings, allowing early detection of predators, competitors for limited resources, or even alternative food sources.

The absence of objects in the open and well-lit surroundings resulted in slightly greater inspective behaviour (***rearing***). For the VIOS group, the time spent ***rearing*** during ***extinction*** sessions remained below 10% of total session time. For the other groups, however, more than 10% (& in some cases, almost 20%) of total ***extinction*** session time was devoted to ***rearing*** (except session 4 for the VIOS & FIOE groups). For three of the four groups, the amount of ***rearing*** observed during ***extinction*** could be considered ***excessive***, and perhaps an ***extinction-induced behaviour***. The high levels of ***rearing***, coupled with the high levels of ***propping***, may indicate just how aversive the situation had become. The food source was depleted, the objects provided no alternative food source, there was no shelter from predators, and there was no possibility of escape from the box.

More than half (<62%) of the bouts of ***rearing*** (frequency & duration) took place during the PRPs for the ***fixed-interval*** groups. Less than a quarter of the bouts (frequency & duration) of this behaviour occurred during the PRPs for the ***variable-interval*** groups (<15% for the VIOE group).

Less than 3% of total ***fixed-interval*** or ***variable-interval*** session time was spent in ***pica***. Over ***extinction*** there was an increase in the time spent in ***pica*** for all groups. If objects were first present during ***extinction***, less than 5% of time was spent engaged in this behaviour. For the other two groups, more than 5% of the last session was spent in ***pica*** (for the FIOS group it was approaching 10%). For the "OS" groups, ***pica*** may have been developing into a true ***eating disorder***. Prior exposure to objects had shown that these objects did not provide an alternative source of food. ***Pica*** provided the rats with an alternative source of food. The wood shavings may have helped satiate the rats, but as a source of nutrients they were inappropriate (not nutritious & may have been harmful in large quantities).

Most bouts of ***pica*** (frequency & duration) occurred during the PRPs for rats run on the ***fixed-interval*** schedule. About a third of bouts took place during the PRPs for the VIOS group. ***Pica*** was not observed during ***schedule*** sessions for the VIOE group.

In summary, the amounts of ***displacement***, ***digging/burying*** and ***pica*** observed during ***fixed-interval***, ***variable-interval*** and ***extinction*** sessions were not considered to be ***excessive***. The levels of ***rearing*** observed during ***extinction*** in three of the four groups, on the other hand, were considered to be ***excessive***. Clearly, more stable PRPs occurred during the predictable ***fixed-interval*** sessions (high proportions of total frequency & duration). The unpredictable ***variable-interval*** session lacked stable PRPs (low proportions of total frequency & duration).

6.5.5 PRACTICAL IMPLICATIONS OF THESE FINDINGS

One of the important findings of this study was that the ***discrimination hypothesis*** (Church, 1963) appears only to be relevant for rats run in the typical Skinner box. The larger and more naturalistic open-field environment extended the repertoire of possible responses. This appeared to alter the ***resistance to extinction*** of the schedules, making behavioural predictions (of the operant response & other behaviours) more problematic. Extinction of ***bar pressing*** did not occur more rapidly in the ***fixed-interval*** groups (these rats should have discriminated more readily between the ***fixed-interval*** and ***extinction*** conditions). A greater ***resistance to extinction*** in the ***variable-interval*** groups was not apparent.

The amount of session time (***fixed-interval***, ***variable-interval*** & ***extinction***) spent engaged in ***displacement***, ***digging/burying***, ***pica*** and the three ***object-directed behaviours***, was not excessive (<10% of total session time for each behaviour). ***Behaviour directed at the bar and food-trough area*** might be considered somewhat ***excessive*** during some sessions (especially ***fixed-interval*** sessions). Levels of ***behaviour directed at the peripheral areas of the box*** were ***excessive*** during ***fixed-interval*** and ***variable-interval*** sessions, if objects were absent, and during ***extinction*** for all groups. The levels of ***rearing*** observed during ***extinction*** (in three of the four groups) were considered to be ***excessive***. Thus, the behaviours that occurred to excess were those that ***centered at the food source*** (not maladaptive), ***escape-directed behaviour*** or ***visual inspection of the surroundings*** (potentially also linked to seeking an escape). Although the 10% of total session time as the criterion for ***excessive*** may appear somewhat arbitrary, Shepherdson (1989) suggests that if a captive animal spends more than 10% of its day engaged in a particular behaviour, then it can be considered ***excessive*** or ***stereotypic***.

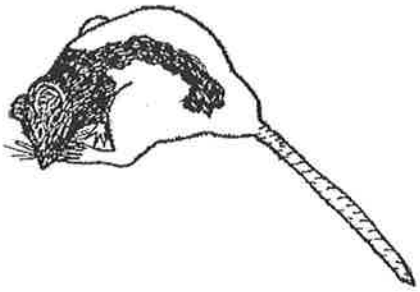
Overall, more stable PRPs occurred during the predictable ***fixed-interval*** sessions (high proportions of total frequency & duration measures occurred during PRPs). The unpredictable ***variable-interval*** sessions lacked stable PRPs (low proportions of total frequency & duration measures occurred during PRPs). Therefore, even in the larger and more naturalistic open-field environment, the predictions concerning PRP development (or lack of development) on these two types of schedules were supported. Thus, some features of operant responding (or the stimuli present immediately after reinforcement) appear to be less affected by the size or complexity of the experimental environment. The findings of this study suggest that the development of PRPs on the predictable FI60-s schedule appears to be a robust phenomenon (unlike ***resistance to extinction***). However, it should be pointed out, that a proportion of every behavioural measure did take place outside the PRPs, at other times of non-operant responding throughout the interval.

CHAPTER 7

EXPLORATORY BEHAVIOUR IN THE LABORATORY RAT:

EXPERIMENT 2:

VR30 AND DRL15-s SCHEDULES OF INTERMITTENT FOOD REINFORCEMENT



7.1 INTRODUCTION TO EXPERIMENT 2

Laboratory rats have been found to engage in exploratory behaviour (& other non-instrumental behaviours) under conditions of FR30 intermittent food-reinforcement, continuous reinforcement and extinction (Litchfield, 1987). Experiment 1 investigated exploratory and other behaviours during FI60-s, VI60-s, and subsequent extinction schedules. Experiment 2 expands the series to include a Variable-Ratio 30 schedule (VR30) and a Differential Reinforcement of Low Rates 15-second (DRL15-s) schedule, followed by extinction.

Variable schedules make it impossible for the subject to predict when the next reinforcement is due. Such "unpredictable" schedules of intermittent food-reinforcement most closely emulate conditions in natural environments (with their unpredictability of reinforcement). ***Variable-ratio*** schedules are characterised by high steady rates of instrumental responding, with few (if any) PRPs (Weiten, 1998). There is also a higher ***resistance to extinction***, since the unpredictable nature of reinforcement on ***variable-ratio*** schedules makes them less distinct initially from the new ***extinction*** schedule. Do exploration or other behaviours occur during a ***variable-ratio*** schedule, and if so, when do they occur? Are PRPs created, lengthened, or do these other behaviours interrupt runs of ***bar presses***? During DRL15-s schedule sessions (where low rates of instrumental responding are rewarded), is the incidence of exploratory behaviour and other non-instrumental responding particularly high? Experiment 2 addresses these questions.

Different subjects were used in Experiment 1, Experiment 2, and the initial 1987 study, and the studies were run at different times. However, the experimental apparatus and procedures used were the same (except for the actual schedules run), the number of subjects in each group was the same, and the behavioural categories were defined and scored in the same way, in an attempt to provide as much comparability as possible. The range of behaviours scored in Experiment 2 is identical to those scored in Experiment 1.

Experiment 2 aims to demonstrate that exploration and a number of other behaviours occur during ***variable-ratio*** (VR30) and ***differential reinforcement of low rates*** (DRL15-s) schedules of food-reinforcement. Experiment 2 also investigates whether such behaviours are present during post-reinforcement pauses. The ***variable-ratio*** schedule is quite unpredictable with respect to delivery of reinforcements. Thus, a regular post-reinforcement pause is unlikely to develop. As a result, it is expected that low proportions (or none) of behaviours will be present during post-reinforcement pauses for the VR30 schedule. ***DRL*** schedules are designed to evoke low rates of instrumental responding. Thus, the opportunity to engage in other behaviours exists.

The experimental design used two different groups, *differential reinforcement of low rates* or *variable-ratio*, further subdivided into two groups depending on whether stimulus objects were first present during schedule running (*differential reinforcement of low rates* or *variable-ratio*), or during extinction. The four groups are referred to as:

- DRLOS (*differential reinforcement of low rates*, objects first present during *differential reinforcement of low rates* sessions);
- DRLOE (*differential reinforcement of low rates*, objects first present during extinction sessions);
- VROS (*variable-ratio*, objects first present during *variable-ratio* sessions);
- VROE (*variable-ratio*, objects first present during extinction sessions).

Table 7.1 presents the experimental design in more detail.

7.1.1 HYPOTHESES PERTAINING TO THE PRPs

Hypothesis Seven: Proportion of behaviours occurring during PRPs of DRL15-s and VR30 schedules

*Whilst **DRL** schedules are not characterised by PRPs, they are typified by low rates of instrumental responding. **Variable-ratio** schedules are characterised by the absence of PRPs, and instead produce high rates of instrumental responding. Thus, it is expected that a larger proportion of each of the scored behaviours will occur during the PRPs for rats run on the **DRL** schedule, when compared with the **variable-ratio** counterpart (**DRLOS** compared to **VROS** & **DRLOE** compared to **VROE**).*

Hypothesis Eight: Effect of novel stimulus objects on proportion of behaviours occurring during PRPs of DRL15-s and VR30 schedules

*It is predicted that the presence or absence of novel stimulus objects during **DRL** and **variable-ratio** running may have some effect on the proportions of behaviours occurring during the PRPs. Thus, it is expected that there will be a difference between the "OS" groups with objects present, and the "OE" groups with objects absent during **DRL** and **variable-ratio** sessions (**DRLOS** compared to **DRLOE** & **VROS** compared to **VROE**).*

7.1.2 HYPOTHESES PERTAINING TO CHANGES IN BEHAVIOUR OVER SCHEDULE AND EXTINCTION SESSIONS

Hypothesis Nine: Effect of novel stimulus objects on frequency and duration of behaviours during DRL15-s and VR30 schedules

*If objects are absent during **differential reinforcement of low rates** and **variable-ratio** sessions, more time and effort can be devoted to behaviours that are not object-directed. Thus, it is expected that higher frequencies and durations of non-object behaviours will be observed in the **DRLOE** and **VROE** groups during schedule sessions, when compared to their same schedule counterparts. In addition, without objects present to "distract" them during schedule sessions, the frequency and duration of **bar pressing** scores is expected to be higher in the **DRLOE** and **VROE** groups (**DRLOE** compared to **DRLOS** & **VROE** compared to **VROS**), with the schedule able to exert maximal control.*

Hypothesis Ten: Effect of novel stimulus objects on frequency and duration of behaviours during extinction

*For rats previously run on the **DRL** schedule, when objects are first encountered during extinction, it is expected that higher frequencies and durations of object-directed behaviours will be observed. That is, the DRLOE group will direct more behaviour towards novel stimulus objects during extinction sessions than the DRLOS group. No firm expectations are held for the other behavioural categories.*

*Since extinction is less readily discriminated after a **variable-ratio** schedule, and the **VROE** group are more likely to be under the "control of the schedule", less behaviour will be directed towards novel stimulus objects (lower frequencies & durations) during extinction sessions (than for the **VROS** group). No firm expectations are held for the other behavioural categories.*

Hypothesis Eleven: Frequency and duration of behaviours during DRL15-s and VR30 schedules

*Rats run on the more predictable **DRL** schedule (which evokes low rates of instrumental responding) should demonstrate lower frequency and duration of **bar pressing** and higher frequency and duration of other behaviours than their counterpart rats run on the less predictable **variable-ratio** schedule (**DRLOS** compared to **VROS** & **DRLOE** compared to **VROE**).*

Hypothesis Twelve: Frequency and duration of behaviours during extinction

*During extinction, the **DRL** rats should more readily discriminate between the previous **DRL** schedule and new **extinction** sessions, than their counterpart rats previously run on the **variable-ratio** schedule (**DRLOS** compared to **VROS** & **DRLOE** compared to **VROE**). Thus, **DRL** groups should demonstrate lower frequency and duration of **bar pressing** and higher frequency and duration of other behaviours (since there is even more time available to engage in other activities).*

7.2 METHOD FOR EXPERIMENT 2

7.2.1 SUBJECTS

Twenty experimentally naive male Hooded Wistar rats, bred at the Waite Institute Central Animal House, served as subjects. They were obtained at approximately 73 days of age, and subsequently, housed in separate cages (28cm x 19cm x 18cm) in the Psychology Department's animal holding room, at the University of Adelaide.

Four of these rats were used in a pilot study, to test the apparatus. The remaining sixteen rats were randomly divided into four groups of four animals. The two experimental groups were designated as (1) Differential Reinforcement of Low Rates/ Objects during Schedule running group (DRLOS) and (2) Differential Reinforcement of Low Rates/ Objects during Extinction group (DRLOE). Similarly, the two control groups were designated as (3) Variable-Ratio/ Objects during Schedule running group (VROS) and (4) Variable-Ratio/ Objects during Extinction group (VROE). The VROS group was matched with the DRLOS group, with respect to, the experimental conditions being followed. The VROE and DRLOE groups were similarly matched. Thus, each *DRL* group was matched with a separate ***variable-ratio*** group.

The rats were housed under controlled temperature and illumination conditions (12/12 -hour light-dark cycle). All animals received *ad libitum* water, with *ad libitum* food received during the handling sessions. Prior to the start of testing, each rat was individually handled once daily for seven days. Testing commenced at approximately 80 days of age.

7.2.2 APPARATUS

The experimental apparatus (*e.g.*, exploration box, computer-operated system & objects) and observational equipment (*e.g.*, video camera & tapes) used were the same as those described previously for Experiment 1 (see section 6.2.2).

7.2.3 PROCEDURE

7.2.3.1 EXPERIMENTAL DESIGN

The experimental design used two different groups, ***differential reinforcement of low rates*** (DRL) or ***variable-ratio*** (VR), further subdivided into two groups, depending on whether stimulus objects were present during schedule running (OS), or during extinction (OE). The rats were allocated to a group at random. Table 7.1 illustrates the experimental design in more detail.

Table 7.1

The experimental design, showing which stimulus objects were present in each session (*i.e.*, objects from group A or B or none at all).

PHASE OF EXPERIMENT	SESSION	GROUP 1: DRLOS	GROUP 2: DRLOE	GROUP 3: VROS	GROUP 4: VROE
SCHEDULE	**1**	Group A Objects	No Objects	Group A Objects	No Objects
SCHEDULE	**2**	Group A Objects	No Objects	Group A Objects	No Objects
SCHEDULE	**3**	Group A Objects	No Objects	Group A Objects	No Objects
EXTINCTION	**4**	Group B Objects	Group A Objects	Group B Objects	Group A Objects
EXTINCTION	**5**	Group B Objects	Group A Objects	Group B Objects	Group A Objects
EXTINCTION	**6**	Group B Objects	Group A Objects	Group B Objects	Group A Objects

7.2.3.2 HANDLING, CONDITIONING AND OBSERVATION SESSIONS

The experimental procedure consisted of three phases: handling, conditioning and observation, and was adhered to for all four groups of rats.

HANDLING

Each rat was individually handled for the same amount of time before the experiment commenced. All rats were handled on a daily basis for seven days. Consequently, each rat received handling on seven separate occasions at the same time every day. Each handling session lasted for ten minutes, during which time the rat was removed from its home-cage and gently stroked.

CONDITIONING

The initial procedures of conditioning (***familiarisation***, ***magazine training***, ***shaping of bar pressing response***, & ***CRF*** until criterion of 200 ***bar presses*** in 50 minutes was reached) were as described for Experiment 1 (see section 6.2.3.2). Following ***CRF*** training, the VROS and VROE rats were placed on a Variable-Ratio 30 (VR30) schedule of reinforcement. Similarly, the DRLOS and DRLOE rats were placed on a Differential Reinforcement of Low Rates 15-seconds (DRL15-s) schedule of reinforcement. The rats in the VROS and VROE groups were each run for one half-hour session per day, for 14 days, by which time their VR30 baseline running was considered to be stable. The rats in the DRLOS and DRLOE groups were also run for one half-hour session per day, for 14 days, by which time their DRL15-s baseline running was considered to be stable.

OBSERVATION

The rats were observed on six different occasions: three ***variable-ratio*** or ***DRL*** schedule sessions, and three ***extinction*** sessions. Each observation session was of 30-minutes duration. During the observation sessions, the stimulus objects were present or absent according to the experimental conditions presented in Table 7.1.

As in Experiment 1, a number of behaviours other than ***bar pressing*** (outlined in section 6.2.3.3) were recorded under all the conditions specified. Details concerning all aspects of these observation sessions were as described for Experiment 1.

7.2.3.3 EVENT RECORDING

The observation sessions were all viewed upon completion of the experimental running. Scoring of the behavioural events was accomplished by means of an event-recording program, which was activated at the start of each session to be viewed. The event recorder consisted of a custom built board (fixed to the top of a table) with 15 buttons, each representing a different behavioural event.

The behavioural categories included are the same as those used in Experiment 1 (see section 6.2.3.3). Thus, the following categories were included: ***bar pressing***, ***bar-related behaviour***, ***sniff object***, ***sniff and touch object***, ***chew/bite object***, ***propping***, ***jump at lid***, ***displacement***, ***digging/burying***, ***rearing*** and ***pica***. Frequency and duration measures were recorded for all behavioural events. The appropriate button was depressed for the full duration of each event, and released upon the completion of the behaviour.

7.2.3.4 INDEPENDENT JUDGING

The three independent judges for this study (used to ensure observer reliability & replicability of behavioural findings) were the same people used for Experiment 1. Again, judges were required to score the behaviours from the 30-minute session, of one animal chosen at random (see section 6.2.3.4 for further details).

7.3 RESULTS FOR EXPERIMENT 2

7.3.1 THE PRESENCE OF EXPLORATORY AND OTHER BEHAVIOURS DURING THE POST-REINFORCEMENT PAUSES

In order to test Hypotheses 7 and 8, a separate table of means for each frequency and duration measure was set up for subjects classified by the two grouping (or independent) variables, group and session. (The tables of raw data can be found in Appendix B). Each mean was based on the behavioural responses of four subjects (four rats per group). The mean for each session was summed to give the sum of means for individual rats in the VROS, DRLOS, VROE and DRLOE groups for the three ***schedule*** sessions combined. The same procedure was followed for the behavioural measures during the PRPs. This PRP sum of means value was then calculated as a percentage of the sum of means of that particular behavioural measure for the three sessions combined (*i.e.*, as a % of the total occurrence). Table 7.2 presents the sum of means and percentages of each frequency and duration measure for the DRLOS and DRLOE groups. Table 7.3 presents the sum of means and percentages of each frequency and duration measure for the VROS and VROE groups.

7.3.1.1 HYPOTHESIS SEVEN: PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF DRL15-s AND VR30 SCHEDULES

Whilst ***DRL*** *schedules are not characterised by PRPs, they are typified by low rates of instrumental responding.* ***Variable-ratio*** *schedules are characterised by the absence of PRPs, and instead produce high rates of instrumental responding. Thus, it is expected that a larger proportion of each of the scored behaviours will occur during the PRPs for rats run on the* ***DRL*** *schedule, when compared with the* ***variable-ratio*** *counterpart (****DRLOS*** *compared to* ***VROS*** *&* ***DRLOE*** *compared to* ***VROE****).*

The frequency measures for the *DRL* groups

In order of increasing percentage of total frequency, the behavioural measures for the DRLOS group were: ***pica***; ***displacement***; ***digging/burying***; ***sniff object***; ***bar-related behaviour***; ***chew/bite object***; ***sniff and touch object***; ***propping***; and ***rearing***. The value for the percentage of total occurring during the PRPs ranged from 27.78% to 42.58%. For this group, more than a quarter (<50%) of each behavioural measure occurred during the PRPs (Table 7.2). No instances of ***jump at lid*** were recorded for the DRLOS group.

In order of increasing percentage of total frequency, the behavioural measures for the DRLOE group were: ***jump at lid***; ***propping***; ***bar-related behaviour***; ***rearing***; ***digging/burying***; ***pica***; and

displacement. The value for percentage of total occurring during the PRPs ranged from 17.65% to 33.33%. Thus, less than a third of each behavioural category occurred during the PRPs (Table 7.2).

Table 7.2
The mean frequency and duration of behaviours occurring during the PRPs (for the DRLOS & DRLOE groups) summed over the three ***DRL*** sessions as a percentage of the (total) mean frequency and duration of each behaviour summed over the three ***DRL*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS * DRLOS GROUP**	**SUM OF MEANS * DRLOE GROUP**	**SUM OF MEANS IN PRPs * DRLOS GROUP**	**SUM OF MEANS IN PRPs * DRLOE GROUP**	**% OF TOTAL * DRLOS GROUP**	**% OF TOTAL * DRLOE GROUP**
FREQUENCIES						
Pica	54	94.75	15	30.25	27.78	31.93
Digging/Burying	65.25	114	20.5	32.75	31.42	28.73
Rearing	259.5	461.75	110.5	120.75	42.58	26.15
Propping	270.5	460.25	103.75	105.75	38.35	22.98
Displacement	124.5	90	35.5	30	28.51	33.33
Bar-related behaviour	708.5	832.5	232.5	199	32.82	23.90
Sniff object	591.5	no	187.75	no	31.74	no
Sniff & Touch object	467.25	objects	154.5	objects	33.07	objects
Chew/Bite object	22	present	7.25	present	32.96	present
Jump at lid	0	4.25	0	0.75	-	17.65
DURATIONS (in seconds)						
Pica	235.46	443.56	77.73	174.76	33.01	39.40
Digging/Burying	23.1	34.31	8.28	9.83	35.84	28.65
Rearing	353.81	574.89	141.46	162.33	39.98	28.24
Propping	665.21	919.86	259.9	225.89	39.07	24.56
Displacement	368.71	282.03	86.46	67.75	23.45	24.02
Bar-related behaviour	362.01	477.61	116.66	109.36	32.23	22.90
Sniff object	234.93	no	70.31	no	29.93	no
Sniff & Touch object	1254.58	objects	423.26	objects	33.74	objects
Chew/Bite object	51.46	present	23.45	present	45.57	present
Jump at lid	0	1.14	0	0.18	-	15.79

The duration measures for the *DRL* groups

In order of increasing percentage of total duration (in seconds), the behavioural measures for the DRLOS group were as follows: ***displacement***; ***sniff object***; ***bar-related behaviour***; ***pica***; ***sniff and touch object***; ***digging/burying***; ***propping***; ***rearing***; and ***chew/bite object***. The value for the percentage of total occurring during the PRPs ranged from 29.93% to 45.57%. Thus, more than a quarter (<50%) of each duration measure occurred during the PRPs (Table 7.2).

In order of increasing percentage of total duration (in seconds), the behavioural measures for the DRLOE group were: ***jump at lid***; ***bar-related behaviour***; ***displacement***; ***propping***; ***rearing***; ***digging/burying***; and ***pica***. The value for the percentage of total occurring during the PRPs ranged from 15.79% to 39.40%. With ***pica*** (39.40%) as the exception, less than a third of each duration measure occurred during the PRPs (Table 7.2).

The frequency measures for the *variable-ratio* groups

In order of increasing percentage of total frequency, the behavioural measures for the VROS group were: ***pica***; ***rearing***; ***propping***; ***displacement***; ***sniff object***; ***sniff and touch object***; ***bar-related behaviour***; and ***chew/bite object***. The value for the percentage of total occurring during the PRPs ranged from 0.87% to 8.93%. No ***digging/burying*** took place during the PRPs. Thus, only a small percentage (<10%) of each frequency measure took place during the PRPs (Table 7.3).

In order of increasing percentage of total frequency, the behavioural measures for the VROE group were: ***propping***; ***rearing***; ***displacement***; and ***bar-related behaviour***. The value for percentage of total occurring during the PRPs ranged from 0.71% to 2.50%. Thus, only very few bouts (< 3%) of these four behaviours occurred during the PRPs. No instances of ***pica***, ***digging/burying*** or ***jump at lid*** took place during the PRPs (Table 7.3).

The duration measures for the *variable-ratio* groups

The behavioural measures in order of increasing percentage of total duration (in seconds) for the VROS group were: ***pica***; ***rearing***; ***propping***; ***displacement***; ***sniff and touch object***; ***sniff object***; ***bar-related behaviour***; and ***chew/bite object***. The value for the percentage of total occurring during the PRPs ranged from 0.46% to 10.29%. With the exception of ***chew/bite object*** (10.29%), less than 10% of each duration measure occurred during the PRPs (Table 7.3). All instances of ***digging/burying*** occurred outside the PRPs.

The behavioural measures in order of increasing percentage of total duration for the VROE group (in seconds) were: ***rearing***; ***displacement***; ***propping***; and ***bar-related behaviour***. The value for the percentage of total occurring during the PRPs ranged from 0.24% to 1.74%. Thus, less than 2% of the time spent engaged in ***rearing***, ***displacement***, ***propping*** or ***bar-related behaviour*** took place during the PRPs (Table 7.3).

Table 7.3
The mean frequency and duration of behaviours occurring during the PRPs (for the VROS & VROE groups) summed over the three ***variable-ratio*** sessions as a percentage of the (total) mean frequency and duration of each behaviour summed over the three ***variable-ratio*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS * VROS GROUP**	**SUM OF MEANS * VROE GROUP**	**SUM OF MEANS IN PRPs * VROS GROUP**	**SUM OF MEANS IN PRPs * VROE GROUP**	**% OF TOTAL * VROS GROUP**	**% OF TOTAL * VROE GROUP**
FREQUENCIES						
Pica	28.75	45	0.25	0	0.87	0
Digging/Burying	21.5	30.75	0	0	0	0
Rearing	141	333.5	1.25	2.5	0.89	0.75
Propping	223.75	385	4	2.75	1.79	0.71
Displacement	73.25	121.5	3	1	4.10	0.82
Bar-related behaviour	646.75	992	49.5	24.75	7.65	2.50
Sniff object	329	no	15.75	no	4.79	no
Sniff & Touch object	284.5	objects	16	objects	5.62	objects
Chew/Bite object	14	present	1.25	present	8.93	present
Jump at lid	0	3	0	0	-	0
DURATIONS (in seconds)						
Pica	281.7	400.61	1.3	0	0.46	0
Digging/Burying	6.79	8.83	0	0	0	0
Rearing	217.76	528.48	1.11	1.26	0.51	0.24
Propping	472.73	992.23	7.21	3.81	1.53	0.38
Displacement	327.36	341.03	17.33	0.89	5.29	0.26
Bar-related behaviour	519.76	875.13	43.99	15.25	8.46	1.74
Sniff object	159.21	no	10.03	no	6.30	no
Sniff & Touch object	1132.34	objects	67.93	objects	6.0	objects
Chew/Bite object	20.51	present	2.11	present	10.29	present
Jump at lid	0	0.81	-	0	-	0

Summary

Table 7.4 provides a summary of the percentage of total mean frequency and duration of behaviours occurring during the PRPs (summed over the three schedule sessions) for all four groups in Experiment 2 (taken from the last two columns of Table 7.2 & Table 7.3).

Hypothesis 7 was supported. As expected, without exception, the percentage of total mean frequency and duration of all the behavioural categories occurring during the PRPs was markedly higher for the ***DRL*** groups. The percentages ranged between 15.79% and 45.57% for the ***DRL*** groups. By contrast, the percentages ranged between 0% and 10.29% for the ***variable-ratio*** groups.

Table 7.4

The percentage of the (total) mean frequency and duration of each behaviour occurring during the PRPs (summed over the three schedule sessions) for all four groups.

BEHAVIOURAL MEASURE	% OF TOTAL * DRLOS GROUP	% OF TOTAL * VROS GROUP	% OF TOTAL * DRLOE GROUP	% OF TOTAL * VROE GROUP
FREQUENCIES				
Pica	27.78	0.87	31.93	0
Digging/Burying	31.42	0	28.73	0
Rearing	42.58	0.89	26.15	0.75
Propping	38.35	1.79	22.98	0.71
Displacement	28.51	4.10	33.33	0.82
Bar-related behaviour	32.82	7.65	23.90	2.50
Sniff object	31.74	4.79	no	no
Sniff & Touch object	33.07	5.62	objects	objects
Chew/Bite object	32.96	8.93	present	present
Jump at lid	-	-	17.65	0
DURATIONS (in seconds)				
Pica	33.01	0.46	39.40	0
Digging/Burying	35.84	0	28.65	0
Rearing	39.98	0.51	28.24	0.24
Propping	39.07	1.53	24.56	0.38
Displacement	23.45	5.29	24.02	0.26
Bar-related behaviour	32.23	8.46	22.90	1.74
Sniff object	29.93	6.30	no	no
Sniff & Touch object	33.74	6.0	objects	objects
Chew/Bite object	45.57	10.29	present	present
Jump at lid	-	-	15.79	0

Note. There were no objects present during the schedule sessions for the DRLOE or VROE groups. A dash (-) indicates that no instances of the behaviour were observed. A zero (0) indicates that all cases took place outside the PRPs.

7.3.1.2 HYPOTHESIS EIGHT: EFFECT OF NOVEL STIMULUS OBJECTS ON PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF DRL15-s AND VR30 SCHEDULES

It is predicted that the presence or absence of novel stimulus objects during ***DRL*** *and* ***variable-ratio*** *running may have some effect on the proportions of behaviours occurring during the PRPs. Thus, it is expected that there will be a difference between the "OS" groups with objects present, and the "OE" groups with objects absent during* ***DRL*** *and* ***variable-ratio*** *sessions (****DRLOS*** *compared to* ***DRLOE*** *&* ***VROS*** *compared to* ***VROE****).*

The *DRL* groups

There was ***partial support for Hypothesis 8***, with respect to the frequency and duration measures. The presence or absence of novel stimulus objects during ***DRL*** sessions had an effect on the proportion of frequency and duration of some of the behaviours that occurred during PRPs (see Table 7.4).

When objects were absent (DRLOE group), the proportions were lower for the frequency of ***rearing***, ***propping*** and ***bar-related behaviour***. ***Jump at lid*** only took place if objects were absent. The proportions were very similar (<5% difference) irrespective of presence or absence of objects for the frequency of ***pica***, ***digging/burying***, and ***displacement*** (Table 7.4).

When objects were absent (DRLOE group), the proportions were lower for the duration of ***rearing***, ***propping***, ***bar-related behaviour*** and ***digging/burying***. For this same group, the proportion was higher (by about 6.5%) for the duration of ***pica***. ***Jump at lid*** only took place if objects were absent. The proportions were very similar (<5% difference) irrespective of presence or absence of objects for the duration of ***displacement*** (Table 7.4).

The *variable-ratio* groups

Again, some support was found for the prediction that the presence or absence of novel stimulus objects during ***variable-ratio*** sessions would have an effect on the proportions of frequency of non-object related behaviours that occurred during the PRPs. That is, there was ***partial support for Hypothesis 8*** (see Table 7.4).

When objects were absent (VROE group), the proportions were slightly lower (a miniscule difference in most cases) for the frequency of ***displacement***, ***bar-related behaviour***, ***pica***, ***rearing*** and ***propping***. No instances of ***digging/burying*** took place during the PRPs for either group. ***Jump at lid*** was only observed if objects were absent, and all instances occurred outside the PRPs (Table 7.4).

When objects were absent (VROE group), the proportions were slightly lower (<1.5% in most cases) for the duration of ***displacement***, ***bar-related behaviour***, ***pica***, ***rearing*** and ***propping***. With respect to ***digging/burying***, no instances occurred during the PRPs for either group (Table 7.4).

7.3.2 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE DURING THE PRPs, OVER SESSIONS, AND BETWEEN GROUPS

The changes in each behavioural measure (frequency & duration) occurring during the PRPs over the three schedule sessions are presented graphically in Figures 7.1 – 7.4 (II) inclusive. The scores for all four groups are plotted on each graph (except for ***object-directed behaviours***, since only two groups had objects present), allowing some comparison in trends across the sessions. This section only covers the patterns of change during the PRPs. The patterns of change for each session in full (not just during the PRPs) are provided in section 7.3.6.

No firm expectations were held concerning the patterns of change within PRPs over the three schedule sessions. However, it was predicted that the frequency and duration scores of ***object-directed behaviours*** during PRPs might reflect a decrease in these behaviours overall as a result of habituation.

7.3.2.1 BEHAVIOUR DIRECTED AT THE FOOD-TROUGH AREA

The mean frequency and duration scores of ***bar-related behaviour*** during the PRPs were noticeably higher for the ***DRL*** groups across all sessions (Figure 7.1). For the DRLOE group, a steady increase in the both measures was observed over sessions. For the DRLOS group, there was a slight overall increase in frequency, but an overall decrease in duration over these sessions (with a marked decrease in both measures in the second session). The VROS group also showed a slight overall increase in frequency and small overall decrease in duration. Few instances of short duration occurred in the VROE group during PRPs (with minimal change over sessions).

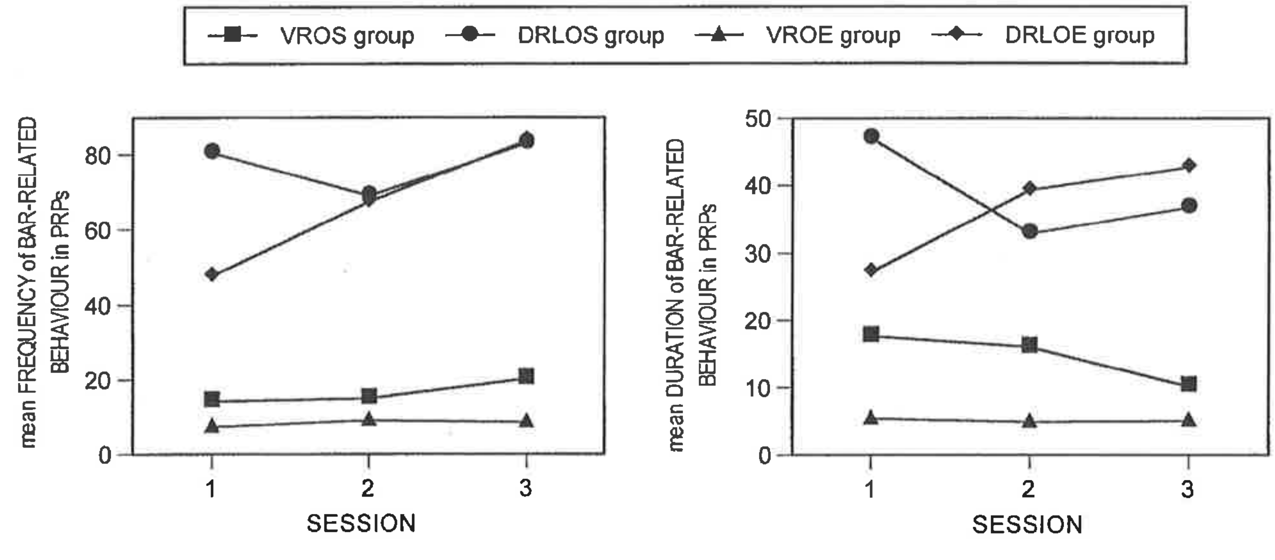


Figure 7.1. Mean frequency (left) and duration (right) scores of ***bar-related behaviour*** during the PRPs for all four groups in Experiment 2

7.3.2.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

All three ***object-directed behaviours*** showed markedly higher frequency and duration scores for the ***DRL*** group (DRLOS) during the PRPs (Figure 7.2), except ***chew/bite object*** measures in session 1 (similar in both groups). Some support was found for the prediction that both measures of ***object-directed behaviours*** would decrease over sessions. The frequency and duration scores of all three behaviours indicate a slight overall decrease across sessions in the VROS group. Typically, few instances of these behaviours of short duration occurred during the PRPs for this group. For the DRLOS group, the frequency and duration of ***sniff object*** scores during the PRPs showed a decrease over the three sessions. However, both measures of ***sniff and touch object*** and ***chew/bite object*** increased across the same sessions.

7.3.2.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

The mean frequency and duration scores of ***propping*** during the PRPs were markedly higher for the ***DRL*** groups across all sessions (Figure 7.3). For these groups, there was an overall decrease in these measures over the three sessions (slight for the DRLOE group, steady & almost linear for the DRLOS group). Virtually no ***propping*** occurred during the PRPs, in any session, for the ***variable-ratio*** groups (or in some cases none at all).

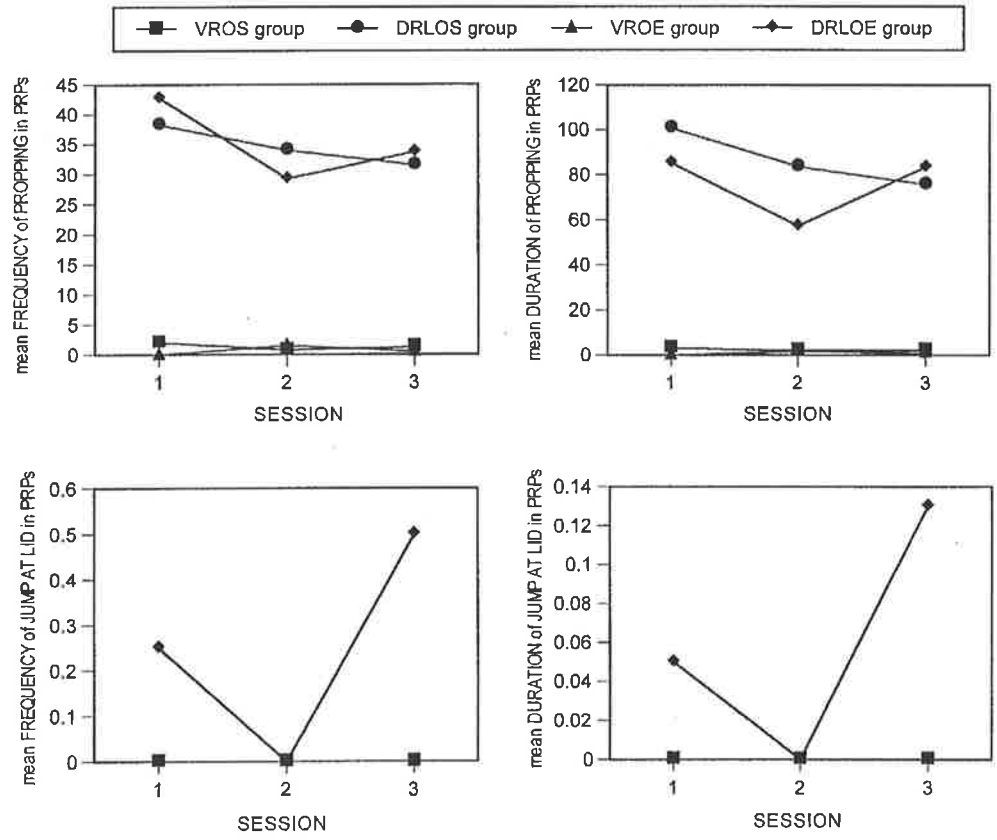


Figure 7.3. Mean frequency (left) and duration (right) scores of ***behaviour directed at the peripheral areas of the box*** during the PRPs for all four groups in Experiment 2 (top- ***propping*** & bottom- ***jump at lid***)

Jump at lid was only observed during the PRPs in the DRLOE group (Figure 7.3) in two of the three sessions. A slight overall increase in frequency and duration scores was seen across sessions, but these scores were almost negligible.

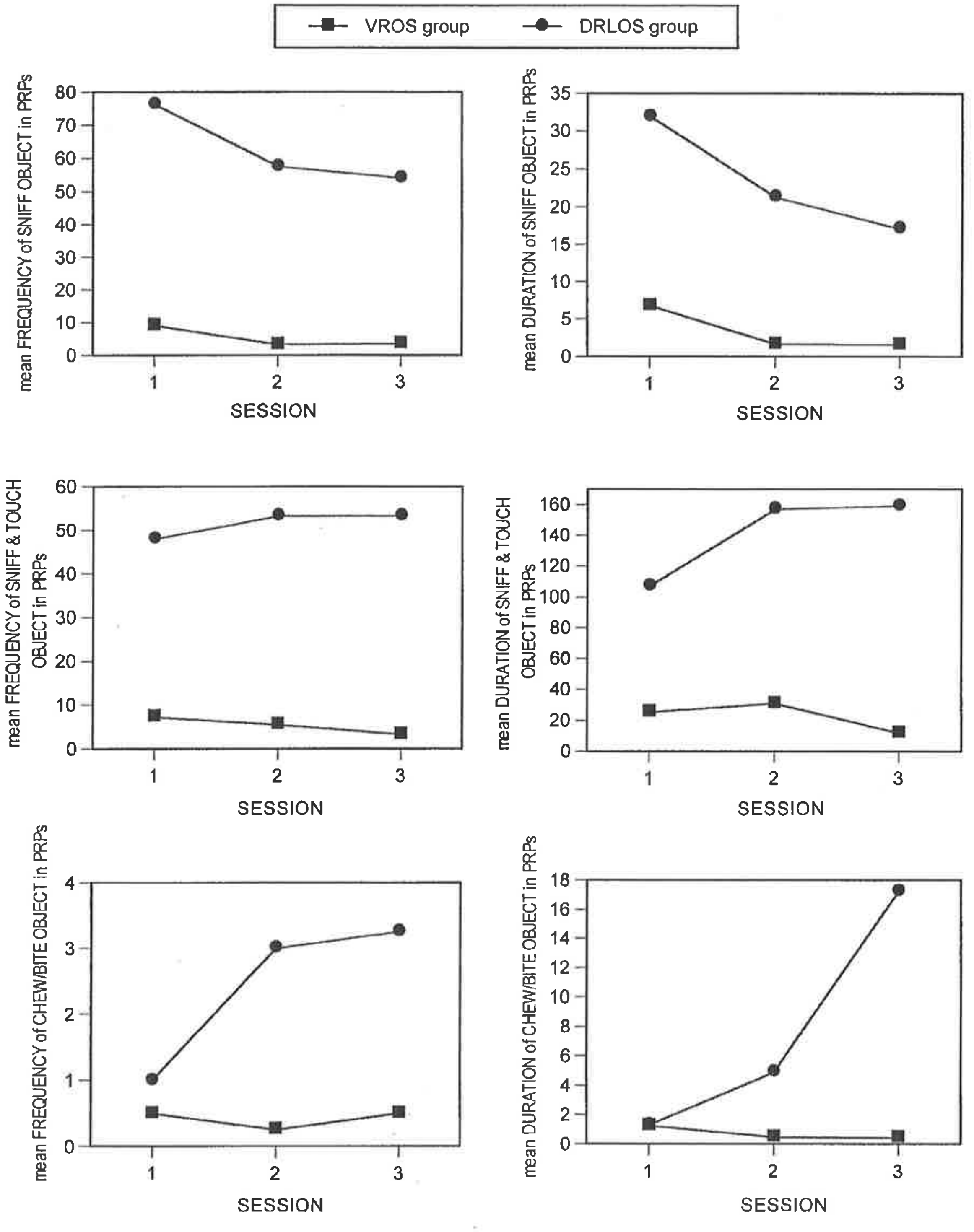


Figure 7.2. Mean frequency (left) and duration (right) scores of ***behaviour directed at the stimulus objects*** during the PRPs for the DRLOS and VROS groups in Experiment 2 (top- ***sniff object***, middle- ***sniff & touch object*** & bottom- ***chew/bite object***)

7.3.2.4 OTHER BEHAVIOURAL CATEGORIES

Figure 7.4 (I) indicates that the mean frequency and duration scores of ***displacement*** during the PRPs were higher for the ***DRL*** groups across all sessions. A slight increase in the frequency and decrease in the duration scores over the three sessions was observed for the DRLOS group, whilst for the DRLOE group this pattern was reversed (*i.e.*, decrease in frequency & increase in duration). Virtually no ***displacement*** occurred during the PRPs for the ***variable-ratio*** groups (or in some cases none at all).

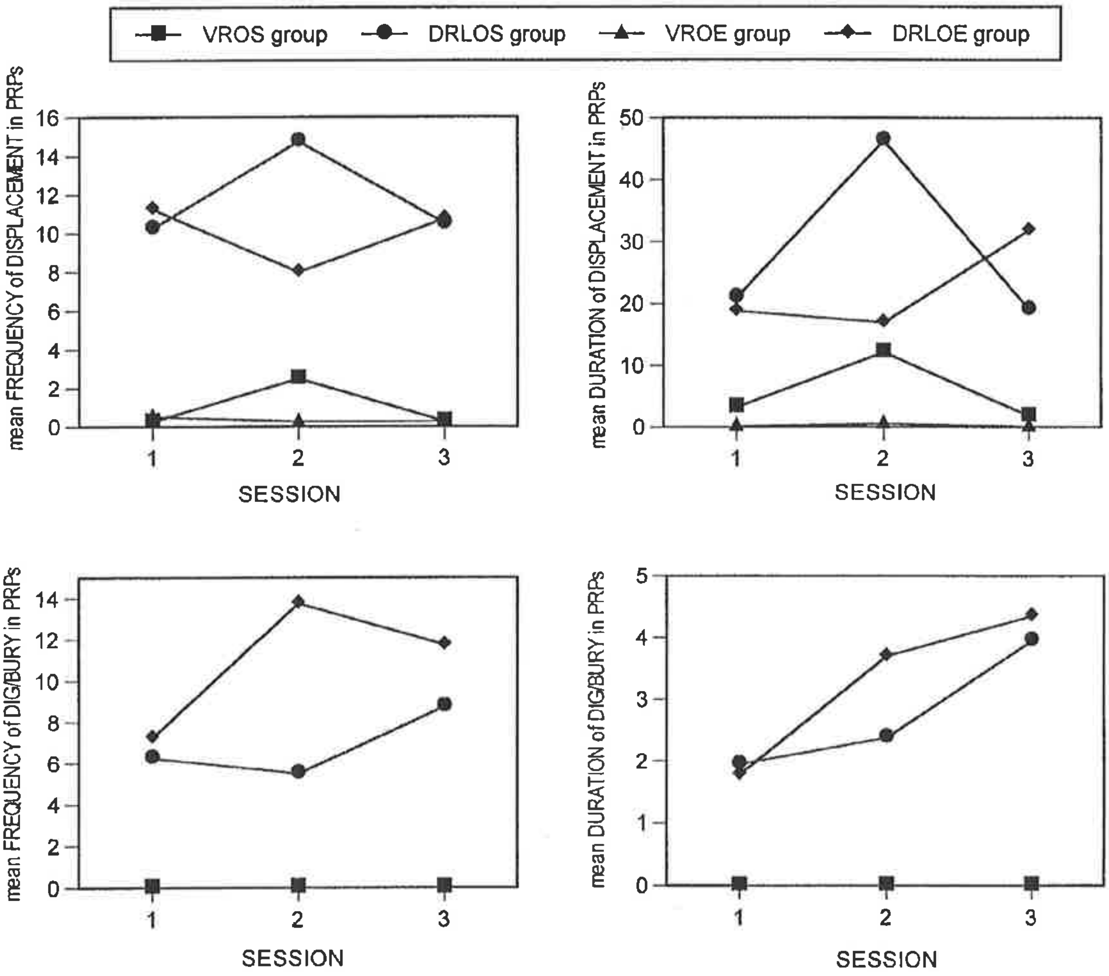


Figure 7.4 (I). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** during the PRPs for all four groups in Experiment 2 (top- ***displacement*** & bottom- ***digging/burying***)

No instances of ***digging/burying*** occurred during the PRPs for the ***variable-ratio*** groups (Figure 7.4: I). An overall increase in frequency and duration of ***digging/burying*** scores over sessions was seen for the ***DRL*** groups, with scores higher for the DRLOE group (except duration in the first session).

Figure 7.4 (II) shows that the mean frequency and duration scores of ***rearing*** during the PRPs were higher for the ***DRL*** groups across all sessions. An overall decrease in both measures over the three sessions was seen in the VROS and DRLOE groups. For the DRLOS group, a decrease in frequency but increase in duration scores was observed, whilst for the VROE group this pattern was reversed (*i.e.*, increase in frequency & overall decrease in duration).

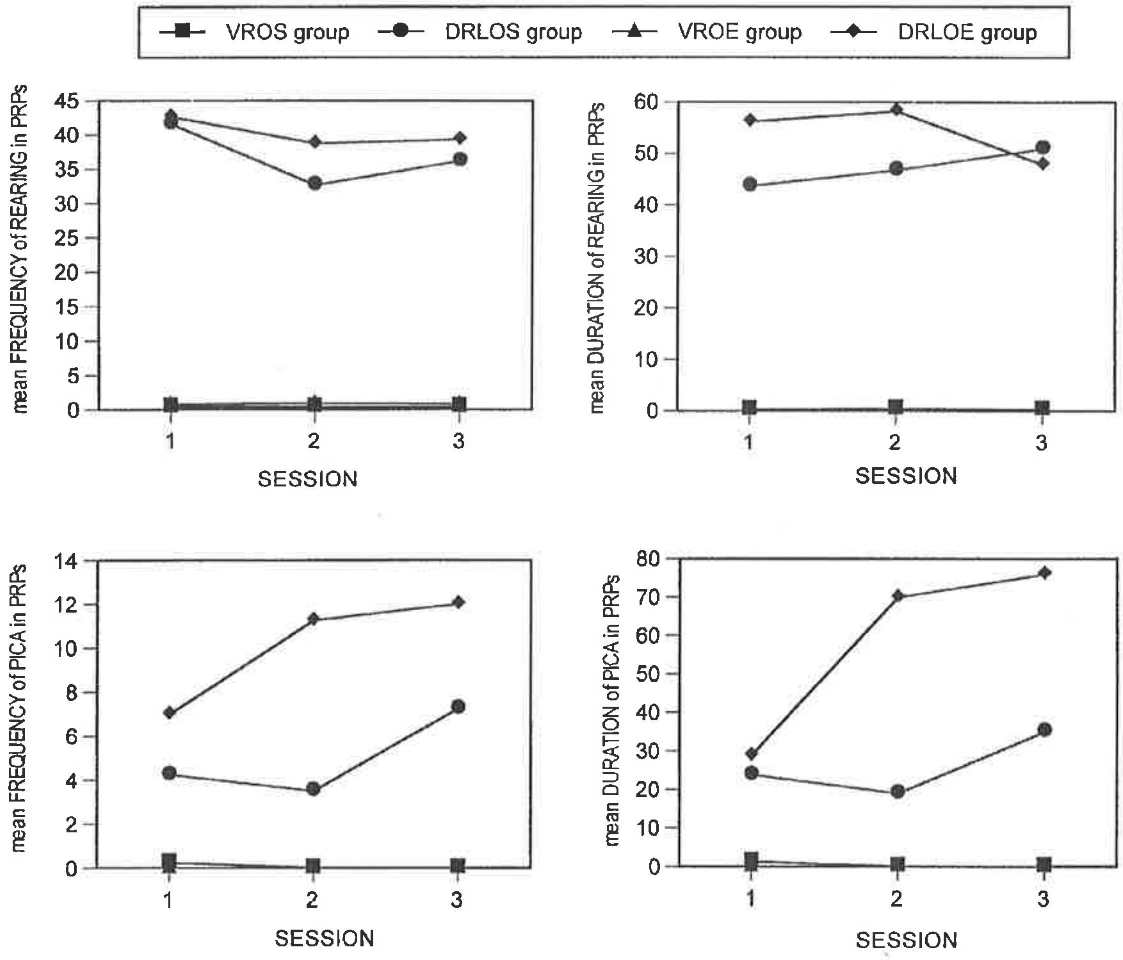


Figure 7.4 (II). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** during the PRPs for all four groups in Experiment 2 (top- ***rearing*** & bottom- ***pica***)

The mean frequency and duration scores of ***pica*** during the PRPs were higher for the ***DRL*** groups across all sessions (Figure 7.4: II). An overall increase in the frequency and duration of both behaviours over sessions was seen for these groups, with scores higher for the DRLOE group in each session. Virtually no ***pica*** occurred during the PRPs for the ***variable-ratio*** groups (in most cases none at all).

7.3.3 CHANGES IN BEHAVIOURS DURING PRPs OVER SCHEDULE SESSIONS, BETWEEN SCHEDULES AND BETWEEN OBJECT CONDITIONS

The previous section presented the mean frequency and duration of the scored behaviours exhibited by the four groups of rats graphically. Since the sample sizes were small, the data have been primarily analysed by description. Bearing this in mind, the data are now analysed by means of statistical testing. As with Experiment 1 (section 6.3.3), a multivariate analysis of variance (MANOVA) was performed for each of the frequency and duration measures, occurring during the PRPs. For each MANOVA there were three independent (or grouping) variables: object (*i.e.*, present or absent), schedule (*i.e.*, ***DRL*** or ***variable-ratio***) and session. In each case there was one dependent variable: the frequency or duration measure of a particular behavioural category.

It should be noted, that there were no objects present in two of the four groups (VROE & DRLOE) during schedule sessions. Therefore, the grouping variable "object" has an obvious effect on ***object-directed behaviours***. If the other independent variables (schedule or session) have a main effect on the frequency or duration of ***object-directed behaviours***, it is only relevant for the two groups with objects present during schedule sessions (VROS & DRLOS).

Two behavioural categories (***jump at lid*** & ***chew/bite object***) were not included in the statistical analysis, since they occurred too infrequently in the four groups.

Main effect of *schedule*

Table 7.5 indicates that the differences between the schedules (***DRL*** or ***variable-ratio***) were statistically significant for all the frequency and duration measures. That is, the schedule that rats were run on clearly affected the frequency and duration of behaviours during the PRPs.

Visual inspection of Figures 7.5 (I) – (III) shows that the frequency and duration scores of behaviours during the PRPs were markedly higher in every session for the ***DRL*** groups. The frequency and duration of ***pica*** and ***digging/burying*** during the PRPs increased steadily over sessions for the ***variable-ratio*** groups, whilst virtually no instances (or indeed none at all) of these behaviours took place during the PRPs in any session for the ***DRL*** groups (Figure 7.5: I). A slight decrease over sessions for the frequency and duration of ***rearing*** and ***propping*** during PRPs was observed for the ***variable-ratio*** groups, whilst these behaviours also tended not to occur during the PRPs for the ***DRL*** groups (Figures 7.5: I & II).

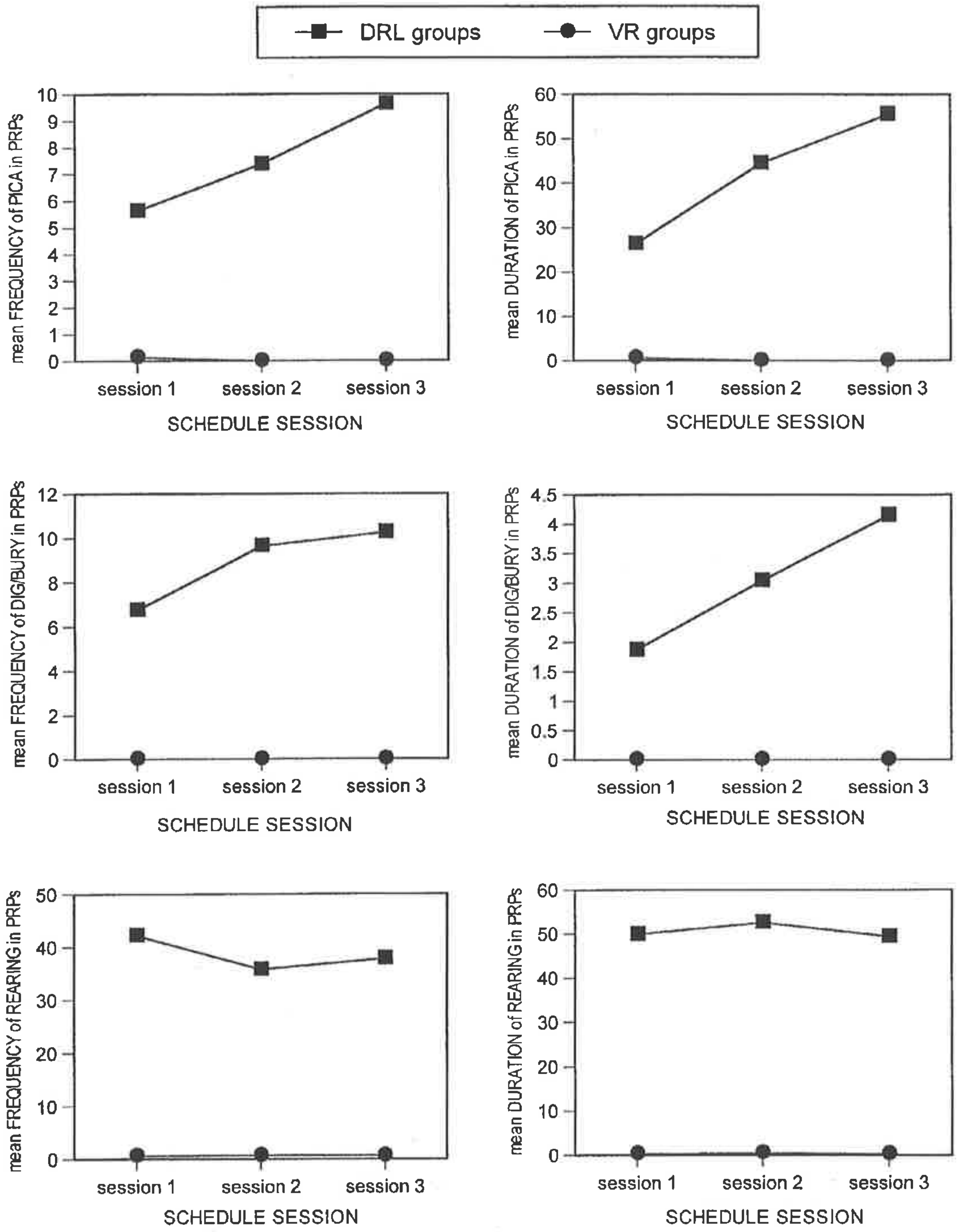


Figure 7.5 (I). Mean frequency (left) and duration (right) of behaviours during the PRPs for the "schedule" grouping variable (top- ***pica***, middle- ***digging/burying*** & bottom- ***rearing***)

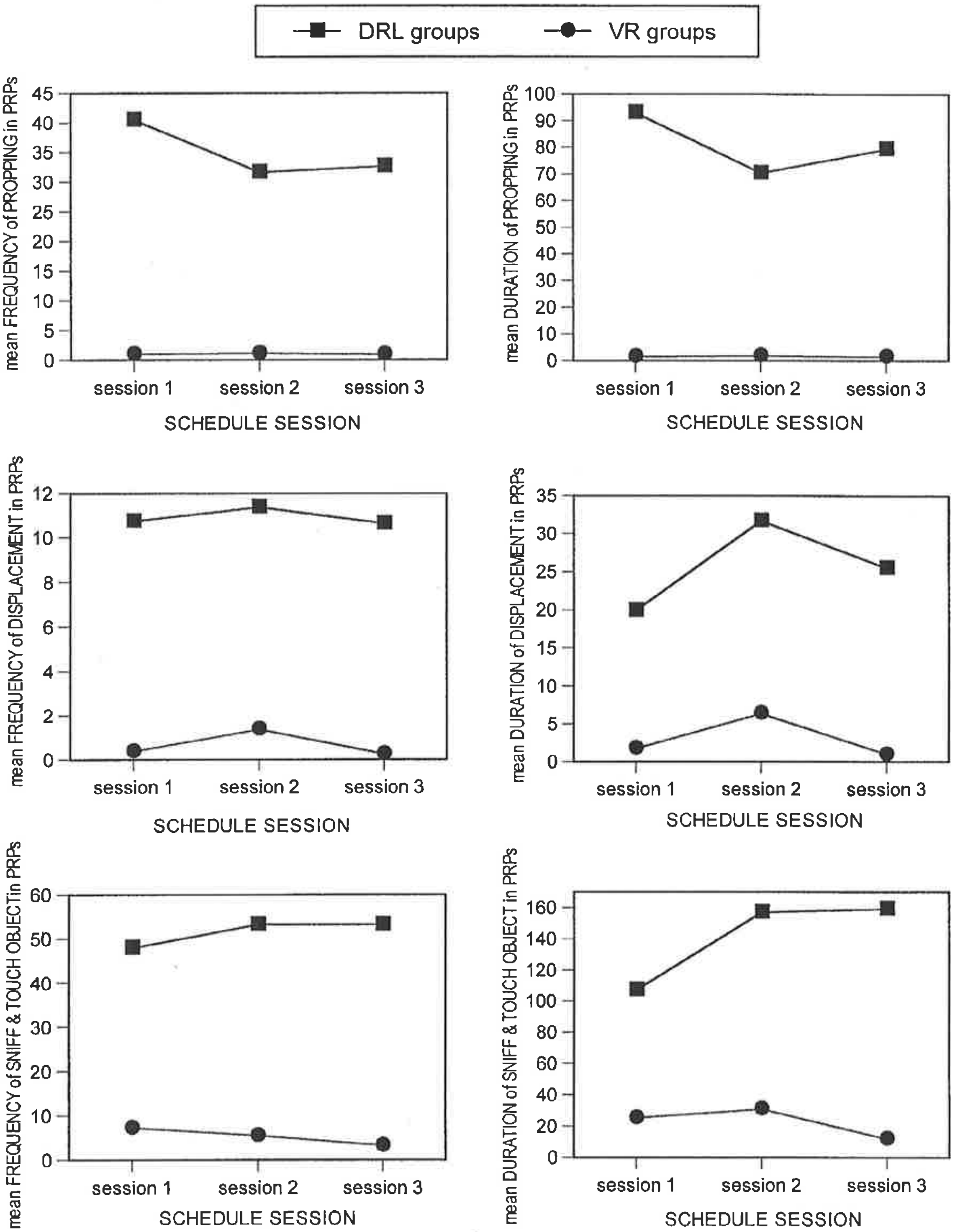


Figure 7.5 (II). Mean frequency (left) and duration (right) of behaviours during the PRPs for the "schedule" grouping variable (top- ***propping***, middle- ***displacement*** & bottom- ***sniff & touch object***)

Table 7.5

Experiment 2 significance levels obtained for measures of behavioural categories during PRP's (***schedule*** main effect).

Variable	*F*(1,12)	Significance level (*p*)
Frequency of ***pica***	11.72	<.01
Duration of ***pica***	12.74	<.01
Frequency of ***digging/burying***	11.03	<.01
Duration of ***digging/burying***	6.01	<.05
Frequency of ***rearing***	29.45	<.001
Duration of ***rearing***	27.01	<.001
Frequency of ***propping***	23.77	<.001
Duration of ***propping***	12.88	<.01
Frequency of ***displacement***	8.40	<.05
Duration of ***displacement***	6.47	<.05
Frequency of ***sniff and touch object***	142.35	<.001
Duration of ***sniff and touch object***	68.98	<.001
Frequency of ***sniff object***	360.23	<.001
Duration of ***sniff object***	233.48	<.001
Frequency of ***bar-related behaviour***	68.73	<.001
Duration of ***bar-related behaviour***	13.21	<.005

Note. No objects were present in the FIOE and VIOE groups during schedule sessions.

As shown in Figure 7.5 (II), the frequency of ***displacement*** and ***sniff and touch object*** during the PRPs increased slightly over sessions for the ***DRL*** groups, whilst the duration measures increased more noticeably. By contrast, a miniscule overall decrease (all the scores were extremely low) over sessions was observed for the same measures in the ***variable-ratio*** groups.

The frequency and duration of ***sniff object*** during the PRPs decreased steadily over sessions for the ***variable-ratio*** groups (Figure 7.5: III). A similar pattern was observed for the ***DRL*** groups, although the scores were much lower. Visual inspection of Figure 7.5 (III) indicates that frequency of ***bar-related behaviour*** during the PRPs increased slightly overall in ***variable-ratio*** and ***DRL*** groups. The duration of this behaviour during PRPs, however, increased slightly for the ***DRL*** groups, but decreased slightly for the ***variable-ratio*** groups (although the scores were all much lower for the ***variable-ratio*** groups in every session).

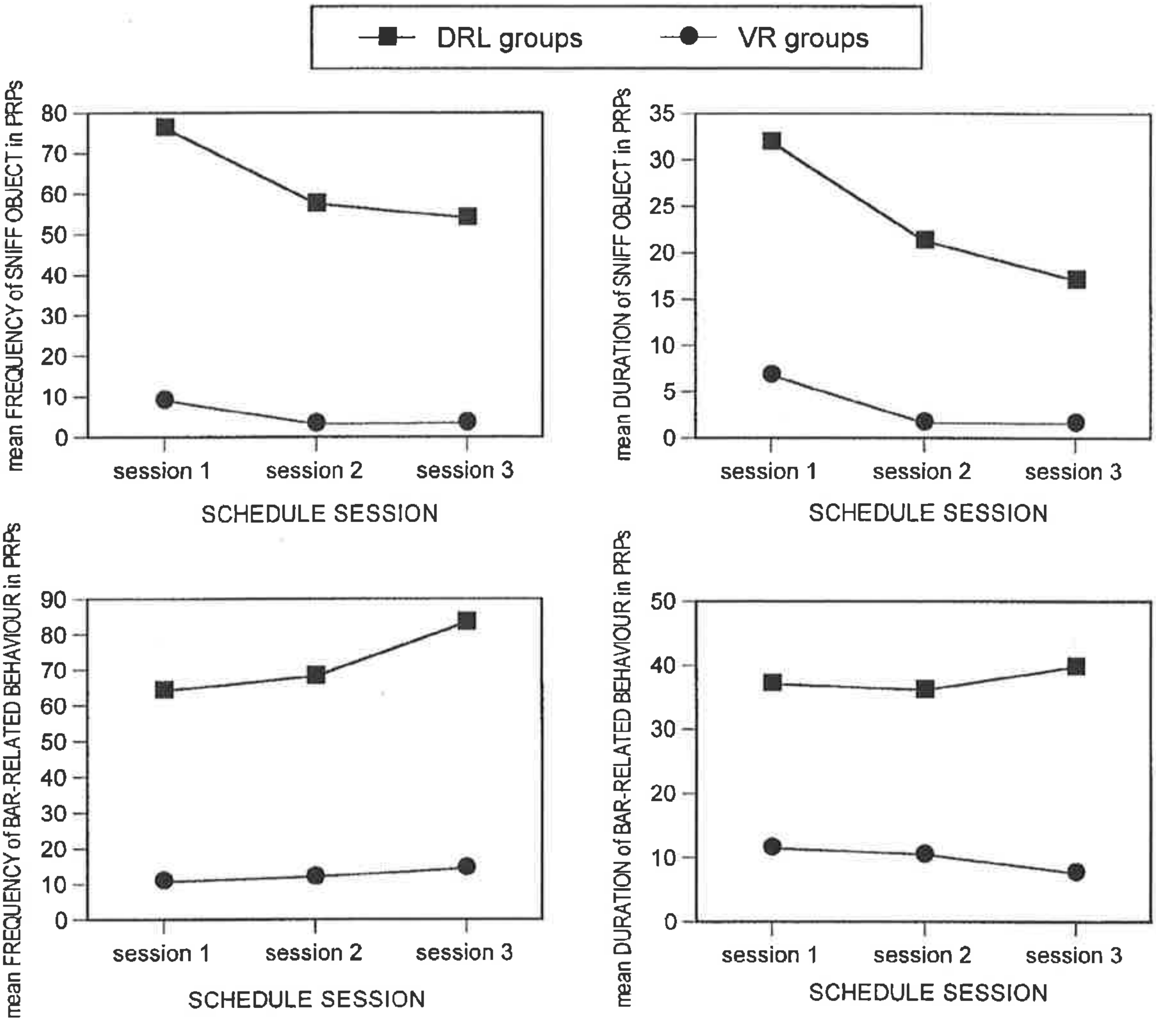


Figure 7.5 (III). Mean frequency (left) and duration (right) of behaviours during the PRPs for the "schedule" grouping variable (top- ***sniff object*** & bottom- ***bar-related behaviour***)

Main effect of *session*

Statistically significant differences over the three schedule sessions (*i.e.*, a session main effect) were reflected in only one measure, namely the duration of ***sniff object*** [*F* (2,24)=10.86, *p*<.001] during the PRPs. Again, it should be noted that objects were only present in the DRLOS and VROS groups. Although the mean duration of ***sniff object*** scores during the PRPs was low (<20 seconds), there was a clear decrease over sessions (Figure 7.5: IV).

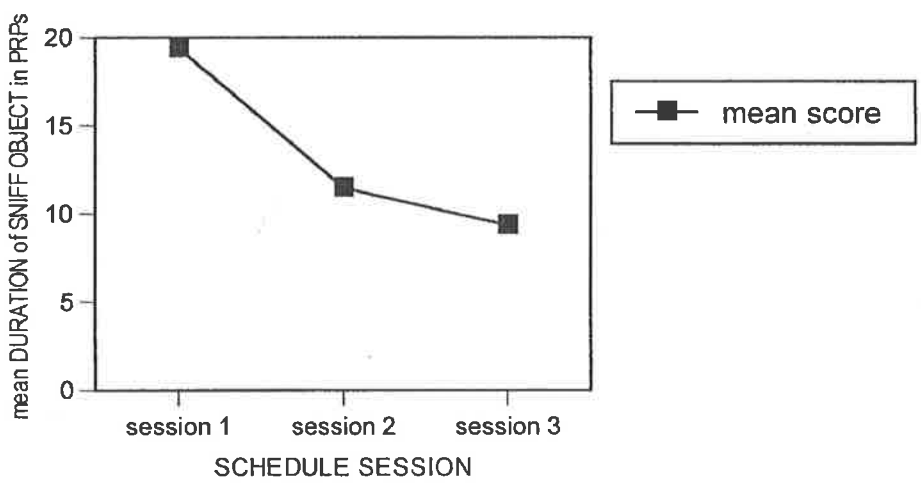


Figure 7.5 (IV). Mean duration of ***sniff object*** during the PRPs for the "session" grouping variable

Object x session **interaction effect**

The MANOVAs for the frequency of ***displacement*** [F (2,24)=3.70, $p<.05$] and duration of ***bar-related behaviour*** [F (2,24)=3.51, $p<.05$] yielded statistically significant ***object*** x ***session*** interactions. That is, these measures were *jointly* affected by the object (*i.e.*, objects present or absent) *and* session grouping variables during schedule sessions.

Although the duration of ***bar-related behaviour*** showed virtually no change over sessions (slight decrease overall), the patterns were different for the "OS" and "OE" groups (Figure 7.5: V). If objects were present during schedule sessions ("OS" groups), then less time was spent engaged in this behaviour during the PRPs over sessions. The opposite pattern was observed if objects were absent ("OE" groups).

The frequency of ***displacement*** during PRPs also showed little change over sessions, but with a slight increase in the second session (Figure 7.5: V). If objects were present during these sessions ("OS" groups), there was an increase in the second session. However, if objects were absent ("OE" groups), fewer bouts of ***displacement*** took place during the PRPs of the second session (*i.e.*, the opposite effect).

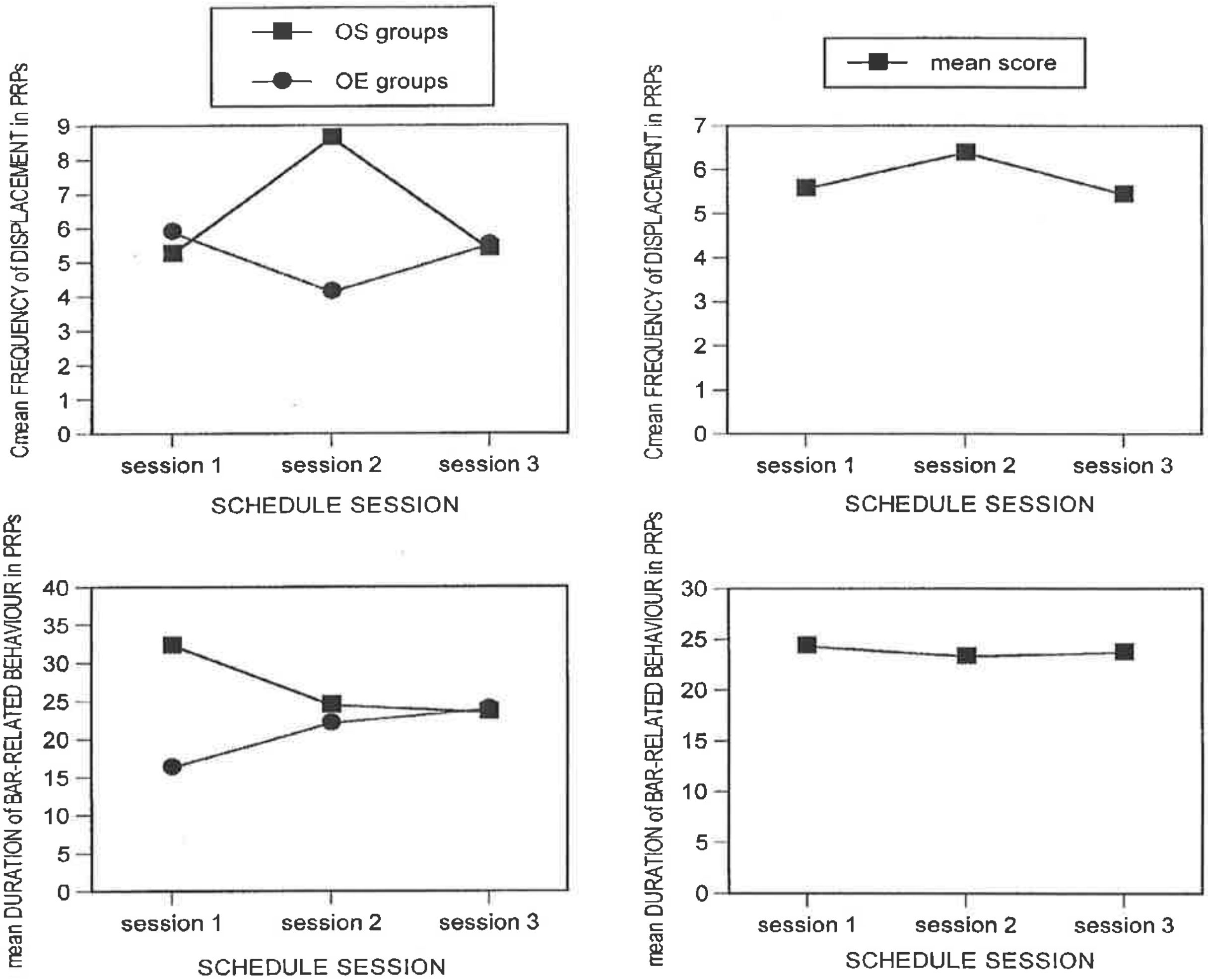


Figure 7.5 (V). Mean frequency of ***displacement*** (top) and duration of ***bar-related behaviour*** (bottom) during the PRPs were jointly affected by the "object" (left) and "session" (right) grouping variables

7.3.4 THE MOST FREQUENTLY OCCURRING BEHAVIOURS, AND ONES OF LONGEST DURATION IN SCHEDULE AND EXTINCTION SESSIONS

In order to test Hypotheses 9 - 12, it was necessary to determine which behavioural events occurred most frequently in each group, for the ***schedule*** (***DRL*** or ***variable-ratio***) and ***extinction*** sessions (separately). The mean values for each frequency measure were summed over the three ***schedule*** sessions, and summed over the three ***extinction*** sessions (separately). Similarly, the mean values for each duration measure were summed over the three ***schedule*** and ***extinction*** sessions (separately), and then used to determine which behavioural measures were of longest duration in each group during ***schedule*** and ***extinction*** sessions. These values are presented in separate tables for the ***DRL*** and ***variable-ratio*** groups, in the current section. The raw data can be found in Appendix B.

7.3.4.1 HYPOTHESIS NINE: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING DRL15s AND VR30 SCHEDULES

If objects are absent during ***differential reinforcement of low rates*** *and* ***variable-ratio*** *sessions, more time and effort can be devoted to behaviours that are not object-directed. Thus, it is expected that higher frequencies and durations of non-object behaviours will be observed in the* ***DRLOE*** *and* ***VROE*** *groups during schedule sessions, when compared to their same schedule counterparts. In addition, without objects present to "distract" them during schedule sessions, the frequency and duration of* ***bar pressing*** *scores is expected to be higher in the* ***DRLOE*** *and* ***VROE*** *groups (****DRLOE*** *compared to* ***DRLOS*** *&* ***VROE*** *compared to* ***VROS****), with the schedule able to exert maximal control.*

The frequency measures for the *DRL* groups

In increasing order, the mean frequency of each behavioural category for the DRLOS group, summed over the three ***DRL*** sessions was: ***chew/bite object***; ***pica***; ***digging/burying***; ***displacement***; ***rearing***; ***propping***; ***sniff and touch object***; ***bar pressing***; ***sniff object***; and ***bar-related behaviour*** (Table 7.6). These values ranged from 22 to 708.5. ***Bar-related behaviour*** was the most frequently occurring behaviour, followed by ***sniff object*** and ***bar pressing***. No instances of ***jump at lid*** occurred during ***DRL*** sessions.

In increasing order, the mean frequency of each behavioural category for the DRLOE group, summed over the three ***DRL*** sessions was: ***jump at lid***; ***displacement***; ***pica***; ***digging/burying***; ***propping***; ***rearing***; ***bar-related behaviour***; and ***bar pressing*** (Table 7.6). These values ranged from 4.25 to 891. After ***bar pressing***, ***bar-related behaviour*** was most frequent, followed by ***rearing*** and ***propping***.

The duration measures for the *DRL* groups

In increasing order of duration, for the DRLOS group over the three ***DRL*** sessions, these measures were: ***digging/burying***; ***chew/bite object***; ***bar pressing***; ***sniff object***; ***pica***; ***rearing***; ***bar-related behaviour***; ***displacement***; ***propping***; and ***sniff and touch object*** (Table 7.6). The values ranged from 23.1 seconds to 1254.58 seconds. Most time was spent engaged in ***sniff and touch object***, followed by ***propping***. Apart from ***digging/burying*** and ***chew/bite object***, ***bar pressing*** took up less time than all other behaviours.

Table 7.6
The mean frequency and duration of behaviours for the DRLOS and DRLOE groups, summed over the three ***DRL*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR SCHEDULE SESSIONS * DRLOS GROUP	SUM OF MEANS FOR SCHEDULE SESSIONS * DRLOE GROUP
FREQUENCIES		
Pica	54	94.75
Digging/Burying	65.25	114
Rearing	259.5	461.75
Propping	270.5	460.25
Displacement	124.5	90
Bar-related Behaviour	708.5	832.5
Sniff object	591.5	no
Sniff & Touch object	467.25	objects
Chew/Bite object	22	present
Jump at Lid	0	4.25
Bar pressing	563.25	891
DURATIONS (in seconds)		
Pica	235.46	443.56
Digging/Burying	23.1	34.31
Rearing	353.81	574.89
Propping	665.21	919.86
Displacement	368.71	282.03
Bar-related Behaviour	362.01	477.61
Sniff object	234.93	no
Sniff & Touch object	1254.58	objects
Chew/Bite object	51.46	present
Jump at Lid	0	1.14
Bar pressing	119.91	159.23

For the DRLOE group, in increasing order of duration for the ***DRL*** sessions, the behavioural measures were: ***jump at lid***; ***digging/burying***; ***bar pressing***; ***displacement***; ***pica***; ***bar-related behaviour***; ***rearing***; and ***propping*** (Table 7.6). The values ranged from 1.14 seconds to 919.86 seconds. Most time was spent engaged in ***propping***, followed by ***rearing***. Only ***jump at lid*** and ***digging/burying*** took up less time than ***bar pressing***.

The frequency measures for the *variable-ratio* groups

The mean frequency of each behavioural category for rats in the VROS group, summed over the three ***variable-ratio*** sessions, in increasing order was: ***chew/bite object***; ***digging/burying***; ***pica***; ***displacement***; ***rearing***; ***propping***; ***sniff and touch object***; ***sniff object***; ***bar-related behaviour***; and ***bar pressing*** (Table 7.7). These values ranged from 14 to 2850. The behaviour to occur most frequently (apart from ***bar pressing***) was ***bar-related behaviour***, followed by ***sniff object***. No instances of ***jump at the lid*** were observed.

Table 7.7
The mean frequency and duration of behaviours for the VROS and VROE groups, summed over the three ***variable-ratio*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR SCHEDULE SESSIONS * VROS GROUP**	**SUM OF MEANS FOR SCHEDULE SESSIONS * VROE GROUP**
FREQUENCIES		
Pica	28.75	45
Digging/Burying	21.5	30.75
Rearing	141	333.5
Propping	223.75	385
Displacement	73.25	121.5
Bar-related Behaviour	646.75	992
Sniff object	329	no objects present
Sniff & Touch object	284.5	
Chew/Bite object	14	
Jump at Lid	0	3
Bar pressing	2850	1028.25
DURATIONS (in seconds)		
Pica	281.7	400.61
Digging/Burying	6.79	8.83
Rearing	217.76	528.48
Propping	472.73	992.23
Displacement	327.36	341.03
Bar-related Behaviour	519.76	875.13
Sniff object	159.21	no objects present
Sniff & Touch object	1132.34	
Chew/Bite object	20.51	
Jump at Lid	0	0.81
Bar pressing	513.13	212.26

The behavioural events that occurred most frequently in the VROE group (during ***variable-ratio*** sessions) were: ***jump at lid***; ***digging/burying***; ***pica***; ***displacement***; ***rearing***; ***propping***; ***bar-related behaviour***; and ***bar pressing*** (in increasing order). The values ranged from 3 to 1028.25 (Table 7.7). After ***bar pressing***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***propping***.

The duration measures for the *variable-ratio* groups

For the VROS group, in increasing order of duration for the ***variable-ratio*** sessions, the measures were: ***digging/burying***; ***chew/bite object***; ***sniff object***; ***rearing***; ***pica***; ***displacement***; ***propping***; ***bar pressing***; ***bar-related behaviour***; and ***sniff and touch object*** (Table 7.7). The values ranged from 6.79 seconds to 1132.34 seconds. Most time was spent engaged in ***sniff and***

touch object, followed by ***bar-related behaviour*** and ***bar pressing***. No instances of ***jump at lid*** were observed.

For the VROE group, in increasing order of duration for the ***variable-ratio*** sessions, the measures were: ***jump at lid***; ***digging/burying***; ***bar pressing***; ***displacement***; ***pica***; ***rearing***; ***bar-related behaviour***; and ***propping*** (Table 7.7). The values ranged from 0.81 seconds to 992.23 seconds. Most time was spent engaged in ***propping***, followed by ***bar-related behaviour***. In addition, ***rearing***, ***pica*** and ***displacement*** took up more time than ***bar pressing***.

Summary

Hypothesis nine was supported, with respect to the frequency and duration measures of all behaviours that were not ***object-directed***, apart from ***bar pressing***, for the ***DRL*** and ***variable-ratio*** groups (with a couple of exceptions). Without objects to "distract" them during ***DRL*** and ***variable-ratio*** sessions, the DRLOE and VROE groups were able to engage in more non ***object-directed behaviours*** (than the DRLOS & VROS rats). As expected, the DRLOE rats also engaged in more ***bar pressing*** (than the DRLOS rats). However, unexpectedly, the VROE rats did not engage in more ***bar pressing*** (than the VROS rats).

The frequency and duration of non ***object-directed behaviours*** were markedly higher in the group without objects (DRLOE group) during ***DRL*** sessions. The only exceptions were frequency and duration of ***displacement***. ***Jump at lid*** only occurred (a few times, for a brief period) if objects were absent.

The frequency and duration of non ***object-directed behaviours*** were markedly higher in the group without objects (VROE) group during ***variable-ratio*** sessions, especially frequency and duration of ***pica***, ***rearing***, ***propping***, and ***bar-related behaviour*** (& frequency of ***displacement***). The only exceptions were the frequency and duration of ***bar pressing***, which were much higher (>50%) in the VROS group. ***Jump at lid*** only occurred (a few times & very briefly) if objects were absent.

7.3.4.2 HYPOTHESIS TEN: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

For rats previously run on the ***DRL*** *schedule, when objects are first encountered during* ***extinction****, it is expected that* <u>*higher*</u> *frequencies and durations of object-directed behaviours will be observed. That is, the DRLOE group will direct more behaviours towards novel stimulus objects during* ***extinction*** *sessions than the DRLOS group. No firm expectations are held for the other behavioural categories.*

Since ***extinction*** *is less readily discriminated after a* ***variable-ratio*** *schedule, and the* ***VROE*** *group are more likely to be under the "control of the schedule", less behaviour will be directed towards novel stimulus objects (*<u>*lower*</u> *frequencies & durations) during* ***extinction*** *sessions (than for the* ***VROS*** *group). No firm expectations are held for the other behavioural categories.*

<u>The frequency measures for the *DRL* groups</u>

For the DRLOS group, in increasing order, the mean frequency of each behavioural category summed over the ***extinction*** sessions was: ***jump at lid***; ***digging/burying***; ***pica***; ***displacement***; ***chew/bite object***; ***rearing***; ***propping***; ***bar pressing***; ***bar-related behaviour***; ***sniff object***; and ***sniff and touch object*** (Table 7.8). The values ranged from 0.5 to 400. The most frequently occurring behaviour was ***sniff and touch object***, followed by ***sniff object*** and ***bar-related behaviour***.

For the DRLOE group, in increasing order, the mean frequency of each behavioural category summed over the ***extinction*** sessions was: ***chew/bite object***; ***digging/burying***; ***pica***; ***displacement***; ***rearing***; ***bar pressing***; ***propping***; ***sniff and touch object***; ***bar-related behaviour***; and ***sniff object*** (Table 7.8). The values ranged from 30 to 448. There were no instances of ***jump at lid***. The most frequently occurring behaviour was ***sniff object***, followed by ***bar-related behaviour***, ***sniff and touch object*** and ***propping***.

<u>The duration measures for the *DRL* groups</u>

In increasing order of duration, for the DRLOS group during the ***extinction*** sessions, the behaviours were: ***jump at lid***; ***digging/burying***; ***bar pressing***; ***sniff object***; ***rearing***; ***bar-related behaviour***; ***chew/bite object***; ***pica***; ***displacement***; ***propping***; and ***sniff and touch object*** (Table 7.8). The values ranged from 0.15 seconds to 1377.26 seconds. Most time was spent engaged in ***sniff and touch object***, followed by ***propping*** and ***displacement***. Only ***jump at lid*** and ***digging/burying*** took up less time than ***bar pressing***.

Table 7.8
The mean frequency and duration of behaviours for the DRLOS and DRLOE groups, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR EXTINCTION SESSIONS * DRLOS GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS * DRLOE GROUP**
FREQUENCIES		
Pica	79	68.5
Digging/Burying	41	61.5
Rearing	191.25	193.75
Propping	254.25	283.75
Displacement	94	98.75
Bar-related Behaviour	340.5	412.5
Sniff object	378.25	448
Sniff & Touch object	400	367
Chew/Bite object	102.75	30
Jump at Lid	0.5	0
Bar pressing	262.75	257.75
DURATIONS (in seconds)		
Pica	393.83	424.88
Digging/Burying	9.38	19.71
Rearing	301.43	246.69
Propping	851.58	894.73
Displacement	504.84	559.03
Bar-related Behaviour	372.68	458.46
Sniff object	160.23	212.25
Sniff & Touch object	1377.26	1269.43
Chew/Bite object	379.54	58.63
Jump at Lid	0.15	0
Bar pressing	54.54	50.88

In increasing order of duration for the DRLOE group during the ***extinction*** sessions, the behavioural measures were: ***digging/burying***; ***bar pressing***; ***chew/bite object***; ***sniff object***; ***rearing***; ***pica***; ***bar-related behaviour***; ***displacement***; ***propping***; and ***sniff and touch object*** (Table 7.8). The values ranged from 19.71 seconds to 1269.43 seconds. Most time was spent engaged in ***sniff and touch object***, followed by ***propping*** and ***displacement***. No time was spent engaged in ***jump at lid***. Only ***digging/burying*** took up less time than ***bar pressing***.

The frequency measures for the *variable-ratio* groups

Table 7.9 provides the mean values for each frequency measure summed over the three ***extinction*** sessions for the VROS group. In increasing order, the categories were: ***jump at lid***; ***digging/burying***; ***pica***; ***chew/bite object***; ***displacement***; ***rearing***; ***propping***; ***sniff object***; ***sniff and touch object***; ***bar-related behaviour***; and ***bar pressing***. The values ranged from 0.75 to

1380.5. Apart from ***bar pressing***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***sniff and touch object*** and ***sniff object***.

Table 7.9
The mean frequency and duration of behaviours for the VROS and VROE groups, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR EXTINCTION SESSIONS * VROS GROUP	SUM OF MEANS FOR EXTINCTION SESSIONS * VROE GROUP
FREQUENCIES		
Pica	39.5	68.75
Digging/Burying	31.25	38.5
Rearing	186	106.75
Propping	212.75	227.5
Displacement	84.25	93
Bar-related Behaviour	590.75	407.75
Sniff object	320.5	417
Sniff & Touch object	325.5	341.5
Chew/Bite object	71.25	33
Jump at Lid	0.75	0.5
Bar pressing	1380.5	404.25
DURATIONS (in seconds)		
Pica	259.71	547.31
Digging/Burying	6.91	11.38
Rearing	239.03	122.23
Propping	452.88	748.88
Displacement	490.71	405.38
Bar-related Behaviour	642.66	552.03
Sniff object	146.83	257.26
Sniff & Touch object	1107.19	1425.26
Chew/Bite object	320.18	71.16
Jump at Lid	0.95	0.18
Bar pressing	244.43	86.06

In increasing order, the mean frequency of each behavioural category for the VROE group, summed over the three ***extinction*** sessions was: ***jump at lid***; ***chew/bite object***; ***digging/burying***; ***pica***; ***displacement***; ***rearing***; ***propping***; ***sniff and touch object***; ***bar pressing***; ***bar-related behaviour***; and ***sniff object*** (Table 7.9). The values ranged from 0.5 to 417. The behaviour to occur most frequently was ***sniff object***, followed by ***bar-related behaviour*** and ***bar pressing***.

The duration measures for the *variable-ratio* groups

In increasing order of duration for the VROS group during the ***extinction*** sessions, the behavioural measures were: ***jump at lid***; ***digging/burying***; ***sniff object***; ***rearing***; ***bar pressing***; ***pica***; ***chew/bite object***; ***propping***; ***displacement***; ***bar-related behaviour***; and ***sniff and touch***

object (Table 7.9). The values ranged from 0.95 seconds to 1107.19 seconds. Most time was spent engaged in ***sniff and touch object***, followed by ***bar-related behaviour*** and ***displacement***. In addition, ***propping***, ***chew/bite object*** and ***pica*** took up more time than ***bar pressing***.

In increasing order of duration for the VROE group during the ***extinction*** sessions, the behavioural measures were: ***jump at lid***; ***digging/burying***; ***chew/bite object***; ***bar pressing***; ***rearing***; ***sniff object***; ***displacement***; ***pica***; ***bar-related behaviour***; ***propping***; and ***sniff and touch object*** (Table 7.9). The values ranged from 0.18 seconds to 1425.26 seconds. Most time was spent engaged in ***sniff and touch object***, followed by ***propping*** and ***bar-related behaviour***. In addition, ***pica***, ***displacement***, ***sniff object*** and ***rearing*** took up more time than ***bar pressing***.

Summary

There was ***partial support for Hypothesis 11***, with respect to the frequency and duration measures during ***extinction***, for rats previously run on the ***DRL*** schedule (Table 7.8). That is, there was some support for the prediction that the frequency and duration of ***object-directed behaviours*** would be higher in the DRLOE group during ***extinction*** (when objects were first encountered). No firm expectations were held for the other non ***object-directed behaviours***.

When objects were first encountered during ***extinction*** (DRLOE group), the frequency and duration of ***sniff object*** was higher. However, frequency and duration of ***sniff and touch object*** and ***chew/bite object*** were lower (especially the latter). With respect to the other behaviours, the frequency of ***rearing***, ***displacement*** and frequency and duration of ***bar pressing*** were similar in the two groups (<6% difference). The frequency and duration of ***digging/burying***, ***propping***, ***bar-related behaviour*** and duration of ***pica*** and ***displacement*** were higher in the DRLOE group, whereas the frequency of ***pica*** and duration of ***rearing*** were lower. ***Jump at lid*** did not occur in the DRLOE group, and only a few times in the DRLOS group (the reverse of ***DRL*** sessions).

There was also ***partial support for Hypothesis 11***, with respect to the frequency and duration measures during ***extinction***, for rats previously run on the ***variable-ratio*** schedule (Table 7.9). That is, there was some support for the prediction that the frequency and duration of ***object-directed behaviours*** would be lower in the VROE group during ***extinction*** (when objects were first encountered). No firm expectations were held for the other non ***object-directed behaviours***.

When objects were first encountered during ***extinction*** (VROE group), the frequency of ***sniff object*** was lower, whilst the frequency and duration of ***chew/bite object*** were markedly lower. However, the frequency and duration of ***sniff and touch object*** were higher and the duration of

sniff object was markedly higher. With respect to the other behaviours, the frequency and duration of ***pica***, ***digging/burying***, ***propping*** and frequency of ***displacement*** were higher in the VROE group, whereas the frequency and duration of ***rearing***, ***bar-related behaviour***, ***jump at lid*** and duration of ***displacement*** were lower. Unexpectedly, the frequency (>150%) and duration (>60%) of ***bar pressing*** were far lower in the VROE group during ***extinction***.

7.3.4.3 HYPOTHESIS ELEVEN: FREQUENCY AND DURATION OF BEHAVIOURS DURING DRL15-s AND VR30 SCHEDULES

*Rats run on the more predictable **DRL** schedule (which evokes low rates of instrumental responding) should demonstrate lower frequency and duration of **bar pressing** and higher frequency and duration of other behaviours than their counterpart rats run on the less predictable **variable-ratio** schedule (**DRLOS** compared to **VROS** & **DRLOE** compared to **VROE**).*

Table 7.10 provides a summary of the mean frequency and duration of behaviours for all groups summed over the three ***schedule*** sessions (Table 7.6 & 7.7 combined).

The frequency measures

With respect to the frequency measures, ***Hypothesis 11 was supported***. It was predicted that lower frequency of ***bar pressing*** would be observed in the ***DRL*** groups. This was indeed the case. Hypothesis 11 also predicted that higher frequency of other behaviours would be observed in the ***DRL*** groups. The frequency scores of all the other behaviours were higher for the DRLOS group when compared to the VROS group. For the DRLOE group, the frequency of all behaviours (except ***displacement*** & ***bar-related behaviour***) was higher than for the VROE group. ***Jump at lid*** was not observed if objects were present during ***schedule*** sessions, irrespective of type of schedule (Table 7.10).

Thus, the presence or absence of objects as well as the predictability or unpredictability of the schedule appeared to have an effect upon the frequency measures.

Table 7.10
The mean frequency and duration of behaviours for all groups summed over the three ***schedule*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR SCHEDULE SESSIONS * DRLOS GROUP	SUM OF MEANS FOR SCHEDULE SESSIONS * VROS GROUP	SUM OF MEANS FOR SCHEDULE SESSIONS * DRLOE GROUP	SUM OF MEANS FOR SCHEDULE SESSIONS * VROE GROUP
FREQUENCIES				
Pica	54	28.75	94.75	45
Digging/Burying	65.25	21.5	114	30.75
Rearing	259.5	141	461.75	333.5
Propping	270.5	223.75	460.25	385
Displacement	124.5	73.25	90	121.5
Bar-related Behaviour	708.5	646.75	832.5	992
Sniff object	591.5	329	no	no
Sniff & Touch object	467.25	284.5	objects	objects
Chew/Bite object	22	14	present	present
Jump at Lid	0	0	4.25	3
Bar pressing	563.25	2850	891	1028.25
DURATIONS (in seconds)				
Pica	235.46	281.7	443.56	400.61
Digging/Burying	23.1	6.79	34.31	8.83
Rearing	353.81	217.76	574.89	528.48
Propping	665.21	472.73	919.86	992.23
Displacement	368.71	327.36	282.03	341.03
Bar-related Behaviour	362.01	519.76	477.61	875.13
Sniff object	234.93	159.21	no	no
Sniff & Touch object	1254.58	1132.34	objects	objects
Chew/Bite object	51.46	20.51	present	present
Jump at Lid	0	0	1.14	0.81
Bar pressing	119.91	513.13	159.23	212.26

The duration measures

With respect to the duration measures, there was ***partial support for Hypothesis 11.*** It was predicted that lower duration of ***bar pressing*** would be observed in the ***DRL*** groups. Indeed, this was found to be the case. It was also predicted that higher duration of other behaviours would be observed in the ***DRL*** groups. The duration of ***digging/burying*** and ***rearing*** were higher for both ***DRL*** groups. For the DRLOS group, the duration of ***propping***, ***displacement*** and the three ***object-directed behaviours*** were also higher than for the VROS group. However, for the DRLOE group, only the duration of ***pica*** and ***jump at lid*** were higher than in the VROE group (Table 7.10).

Again, the presence or absence of objects as well as the predictability or unpredictability of the schedule appeared to have an effect upon the duration measures.

7.3.4.4 HYPOTHESIS TWELVE: FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

*During extinction, the **DRL** rats should more readily discriminate between the previous **DRL** schedule and new **extinction** sessions, than their counterpart rats previously run on the **variable-ratio** schedule (**DRLOS** compared to **VROS** & **DRLOE** compared to **VROE**). Thus, **DRL** groups should demonstrate lower frequency and duration of **bar pressing** and higher frequency and duration of other behaviours (since there is even more time available to engage in other activities).*

Table 7.11 provides a summary of the mean frequency and duration of behaviours for all groups summed over the three ***extinction*** sessions (Tables 7.8 & 7.9 combined).

The frequency measures

With respect to the frequency measures, ***Hypothesis 12 was supported*** (with a couple of exceptions). It was predicted that the frequency of ***bar pressing*** would be lower for the ***DRL*** groups. Indeed, this measure was much lower. Hypothesis 12 also predicted that higher frequency scores of other behaviours would be found for the ***DRL*** groups. The frequency of most of the behavioural categories was indeed higher for the ***DRL*** groups (Table 7.11). However, if objects were first encountered during ***schedule*** sessions (DRLOS group), the frequency of ***bar-related behaviour*** was lower (than for the VROS group). If objects were first encountered during ***extinction*** (DRLOE group), the frequency of ***pica*** and ***chew/bite object*** was marginally lower (than in the VROE group). The frequency scores of ***jump at lid*** were almost negligible in all groups (although slightly higher in the ***variable-ratio*** groups).

Thus, whether objects were first encountered during ***schedule*** or ***extinction*** sessions, as well as the ease or difficulty of the discrimination between the previous ***schedule*** and new ***extinction*** conditions appeared to have an effect upon the frequency measures.

Table 7.11
The mean frequency and duration of behaviours for all groups summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR EXTINCTION SESSIONS** * **DRLOS GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS** * **VROS GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS** * **DRLOE GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS** * **VROE GROUP**
FREQUENCIES				
Pica	79	39.5	68.5	68.75
Digging/Burying	41	31.25	61.5	38.5
Rearing	191.25	186	193.75	106.75
Propping	254.25	212.75	283.75	227.5
Displacement	94	84.25	98.75	93
Bar-related Behaviour	340.5	590.75	412.5	407.75
Sniff object	378.25	320.5	448	417
Sniff & Touch object	400	325.5	367	341.5
Chew/Bite object	102.75	71.25	30	33
Jump at Lid	0.5	0.75	0	0.5
Bar pressing	262.75	1380.5	257.75	404.25
DURATIONS (in seconds)				
Pica	393.83	259.71	424.88	547.31
Digging/Burying	9.38	6.91	19.71	11.38
Rearing	301.43	239.03	246.69	122.23
Propping	851.58	452.88	894.73	748.88
Displacement	504.84	490.71	559.03	405.38
Bar-related Behaviour	372.68	642.66	458.46	552.03
Sniff object	160.23	146.83	212.25	257.26
Sniff & Touch object	1377.26	1107.19	1269.43	1425.26
Chew/Bite object	379.54	320.18	58.63	71.16
Jump at Lid	0.15	0.95	0	0.18
Bar pressing	54.54	244.43	50.88	86.06

The duration measures

There was ***partial support for Hypothesis 12***, with respect to the duration measures. It was predicted that duration of ***bar pressing*** would be lower for the ***DRL*** groups. This was indeed the case.

Hypothesis 12 also predicted that higher duration scores of other behaviours would be observed in the ***DRL*** groups. However, the duration scores were not higher for all behaviours in the ***DRL*** groups (Table 7.11). If objects were first present during ***schedule*** sessions (DRLOS group), the duration of ***bar-related behaviour*** was lower (than for the VROS group). If objects were first present during ***extinction*** (DRLOE group), the duration of ***pica***, ***bar-related behaviour***, and all three ***object-directed behaviours*** was lower (than in the VROE group). The duration of ***jump at lid*** was almost negligible in all groups (although slightly higher in the ***variable-ratio*** groups).

Again, whether objects were first encountered during ***schedule*** or ***extinction*** sessions, as well as the ease or difficulty of the discrimination between the previous ***schedule*** and new ***extinction*** conditions appeared to have an effect upon the duration measures.

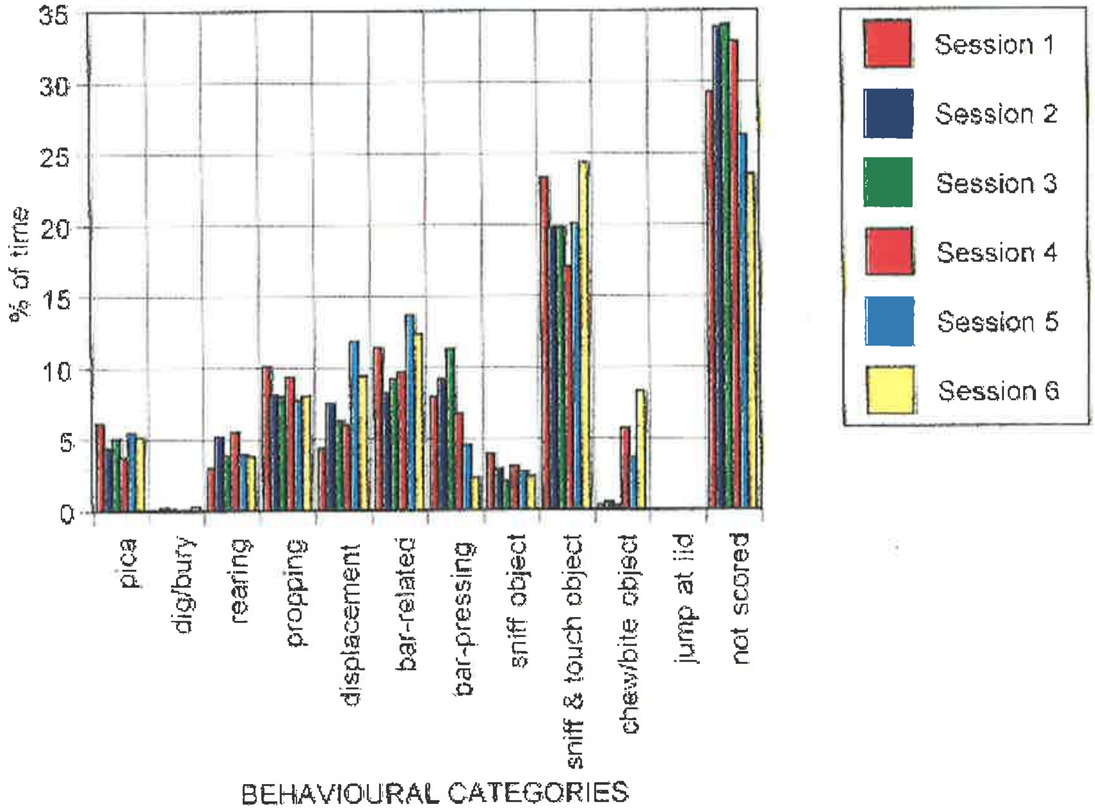
7.3.5 PERCENTAGE OF TOTAL SESSION TIME SPENT ENGAGED IN EACH BEHAVIOURAL CATEGORY, OVER SESSIONS, AND BETWEEN GROUPS

Graphical representations for the mean percentage of time spent engaged in each behavioural category are provided in Figures 7.6 (I) and (II). It should be noted that a substantial percentage of "not scored" exists for each group. As shown in Table 7.12, between 15% and 51% of session time was spent engaged in behavioural categories that were ***not scored*** despite the wide range of behavioural categories included (eleven in all). Most of this ***not scored*** category was likely to have been ***general ambulatory behaviour***. That is, the rats' movement between the bar area, objects, and peripheral areas of the box.

Table 7.12
The percentage of total session time (1800 seconds) spent engaged in behaviour that was ***not scored.***

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
VROS	29.26 %	33.86 %	34.03 %	32.85 %	26.31 %	23.54 %
DRLOS	31.33 %	33.14 %	31.69 %	22.64 %	17.19 %	15.43 %
VROE	34.61 %	41.86 %	36.9 %	26.17 %	22.37 %	16.62 %
DRLOE	50.26 %	45.14 %	43.91 %	26.96 %	22.25 %	17.75 %

Overall, the percentage of total session time spent engaged in behaviours that were ***not scored*** decreased across the six sessions for all groups (Table 7.12). Percentages decreased over ***extinction*** sessions for all groups, whereas they increased over ***schedule*** sessions for all but the



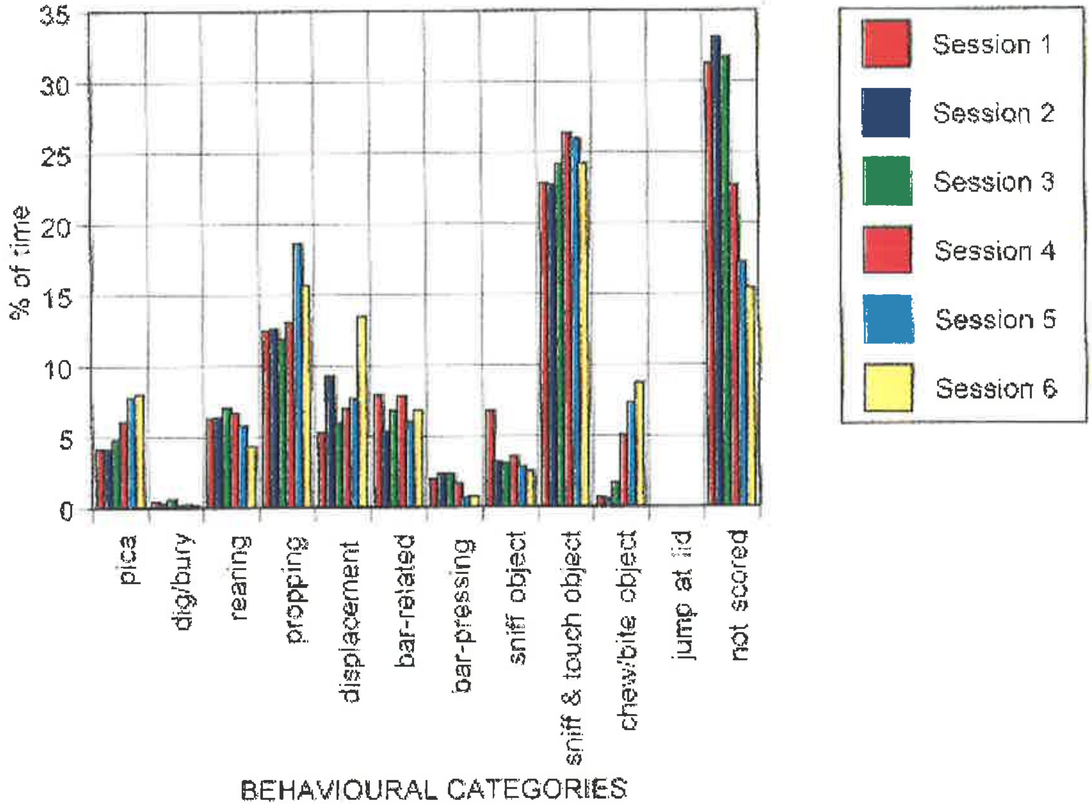
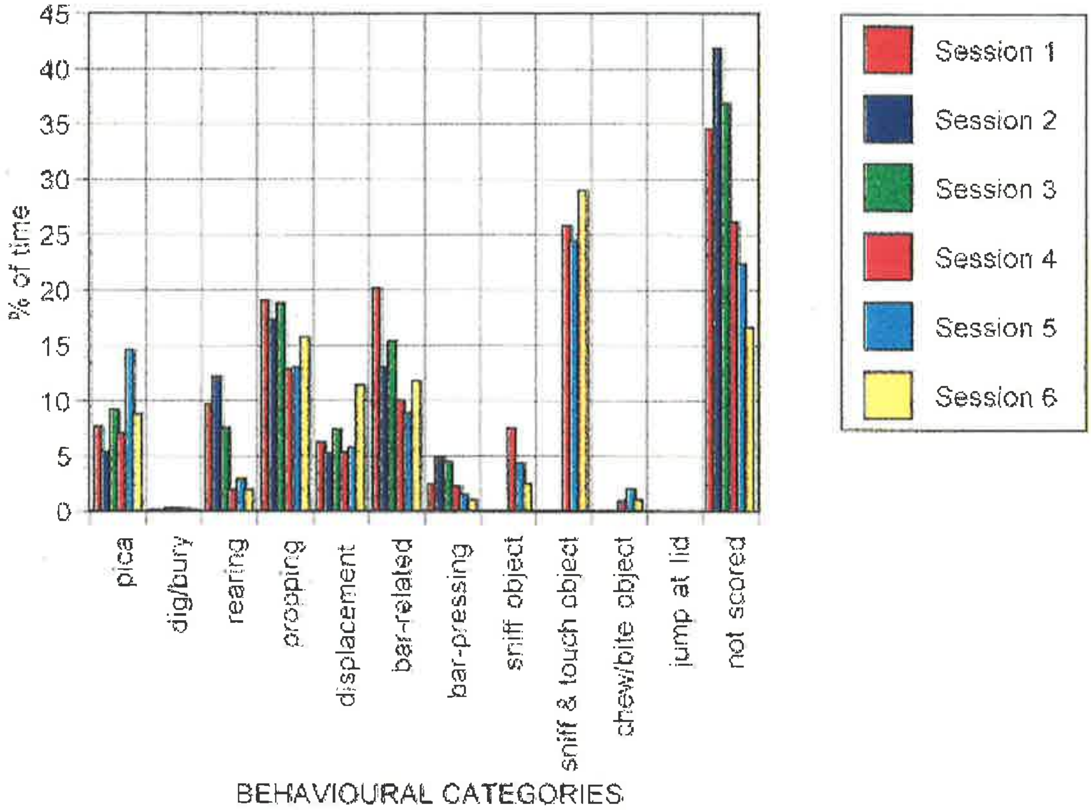


Figure 7.6 (I). Mean percentage of time spent engaged in each behavioural category for the VROS (top) and DRLOS (bottom) groups in Experiment 2, for each session. (Calculated as mean time in seconds spent engaged in behaviour, as a percentage of total session time, i.e., 1800 seconds).



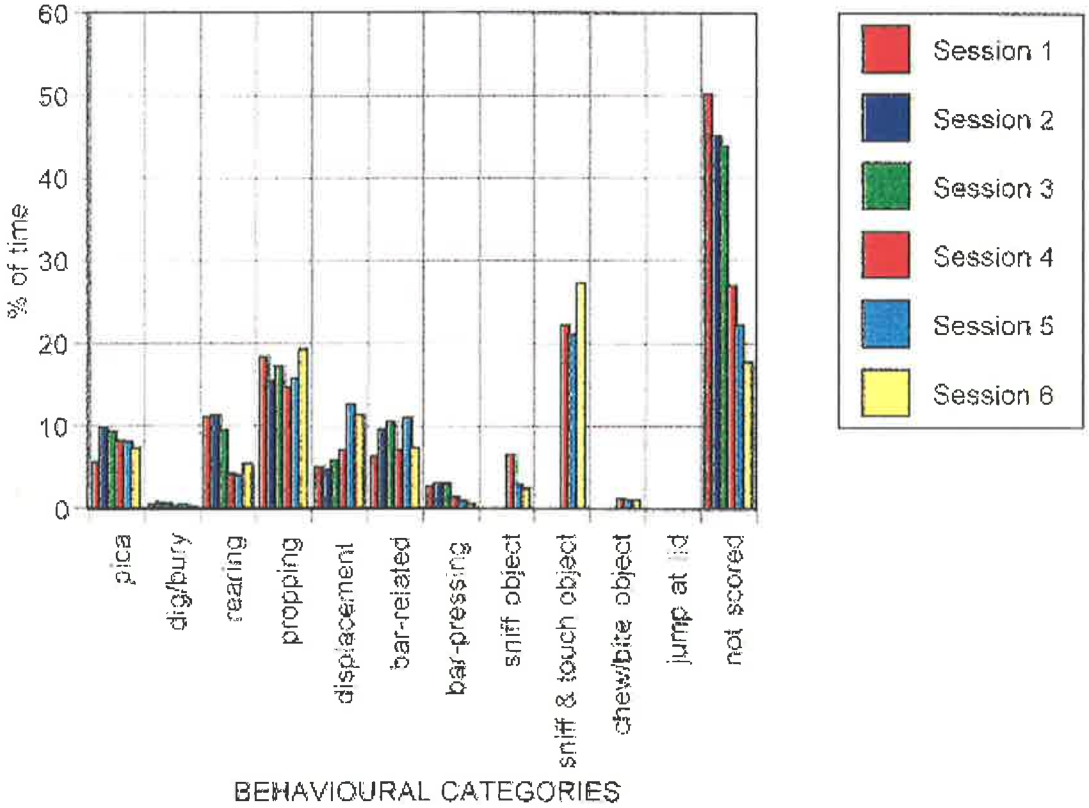


Figure 7.6 (II). Mean percentage of time spent engaged in each behavioural category for the VROE (top) and DRLOE (bottom) groups in Experiment 2, for each session. (Calculated as mean time in seconds spent engaged in behaviour, as a percentage of total session time, i.e., 1800 seconds).

DRLOE group. If objects were first present during ***schedule*** sessions, the scores for the ***variable-ratio*** group (VROS) were higher in all but session 1. However, if objects were first present during ***extinction*** sessions, this trend was reversed, with scores for the ***variable-ratio*** group (VROE) lower in all but session 5 (where scores were almost identical).

7.3.5.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

During ***schedule*** sessions, the ***DRL*** groups spent between 9.04% and 13.63% of total session time engaged in ***behaviour directed at the bar and food-trough area*** (Table 7.13). By contrast, these behaviours represented between 17.5% and 22.6% of total session time for the ***variable-ratio*** groups. Thus, ***behaviour directed at the bar and food-trough area*** took up less than 23% of total session time in all cases, but never represented less than 9% of total session time during ***schedule*** sessions.

During ***extinction*** sessions, the ***DRL*** groups spent between 10.33% and 18.21% of total session time engaged ***in behaviour directed at the bar and food-trough area*** (Table 7.13). The ***variable-ratio*** groups spent between 6.69% and 12.02% of ***extinction*** sessions engaged in these behaviours. ***Behaviour directed at the bar and food-trough area*** took up less than 19% of total session time, but never represented less than 6% of total session time during ***extinction***.

Table 7.13
The percentage of total session time (1800 seconds) spent engaged in ***behaviour directed at the bar and food-trough area*** (***bar-pressing*** + ***bar-related behaviour***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
VROS	19.4 %	17.50 %	20.49 %	16.47 %	18.21 %	14.60 %
DRLOS	9.89 %	7.72 %	9.16 %	9.47 %	6.69 %	7.57 %
VROE	22.60 %	17.94 %	19.87 %	12.32 %	10.33 %	12.80 %
DRLOE	9.04 %	12.72 %	13.63 %	8.45 %	12.02 %	7.83 %

Although the percentage of total session time spent engaged in ***behaviour directed at the bar and food-trough area*** demonstrated an overall decrease across the six sessions for all groups, the patterns of change across ***schedule*** and ***extinction*** sessions varied between groups. The percentages showed an overall increase across ***schedule*** sessions for the VROS and DRLOE groups, and an overall decrease for the other groups. Then the percentage decreased in the first ***extinction*** session for all but the DRLOS group. A decrease across ***extinction*** sessions was observed for all but the VROE group.

7.3.5.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

During ***schedule*** sessions, the DRLOS group spent between 26.43% and 30.25% of total session time engaged in ***behaviour directed at the stimulus objects*** (Table 7.14). These percentages were slightly lower for the VROS group (between 22.1% & 27.61%). Thus, between 22% and 31% of total session time was spent engaged in ***object-directed behaviours*** in all cases.

During ***extinction*** sessions, between 34.93% and 36.15% of the DRLOS group's time was spent engaged in these behaviours, whereas the percentages ranged from 24.89% to 30.77% for the DRLOE group (Table 7.14). The VROS group spent between 25.98% and 35.06% of its total session time engaged in ***object-directed behaviours*** during ***extinction***. For the VROE group the percentages ranged from 30.8% to 34.13% during these sessions. In ***extinction***, between 24% and 37% of total session time was spent engaged in ***object-directed behaviours*** in all instances.

Table 7.14
The percentage of total session time (1800 seconds) spent engaged in ***object-directed behaviours*** (***sniff object*** + ***sniff and touch object*** + ***chew/bite object***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
VROS	27.61 %	23.18 %	22.10 %	25.98 %	26.41 %	35.06 %
DRLOS	30.25 %	26.43 %	28.94 %	34.93 %	36.15 %	35.42 %
VROE	no objects present	no objects present	no objects present	34.13 %	30.80 %	32.50 %
DRLOE	no objects present	no objects present	no objects present	29.92 %	24.89 %	30.77 %

Overall, high percentages of total session time (between 22.1% & 36.15%) were spent engaged in ***behaviour directed at the stimulus objects*** (whenever objects were present) by all groups. When objects were present during ***schedule*** sessions (VROS & DRLOS groups), the percentages showed an overall decrease across ***schedule*** sessions. When a different set of objects was introduced to these groups during ***extinction***, the opposite effect was observed over sessions.

That is, the percentage increased in the first ***extinction*** sessions, and an overall increase across ***extinction*** occurred. If objects were first encountered during ***extinction*** (VROE & DRLOE groups), there was also an overall increase in percentage of total session time spent engaged in ***object-directed behaviours*** over sessions.

For groups with objects present during ***schedule*** sessions (DRLOS & VROS), the ***chew/bite object*** category (which might be ***object-directed aggression***) took up less than 2% of total session time (see Appendix B for raw data). However, by the third ***extinction*** session the percentages increased to over 8% of total session time in both of these groups. For the other two groups (DRLOE & VROE), less than 2% of total session time during ***extinction*** was spent engaged in ***chew/bite object***.

7.3.5.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

The ***jump at lid*** category took up less than 1% of total session time in all cases (see Appendix B for raw data). For groups with objects first present during ***schedule*** sessions (DRLOS & VROS), the behaviour was first recorded in the last ***extinction*** session. Similar (very low) scores were observed in the other two groups during ***schedule*** sessions, and during ***extinction*** the behaviour was only observed in one session (in the VROE group). Thus, most of the ***behaviour directed at the peripheral areas of the box*** was comprised of ***propping*** (Table 7.15).

During ***schedule*** sessions, the ***DRL*** groups spent between 11.87% and 18.36% of total session time engaged in ***behaviour directed at the peripheral areas of the box*** (Table 7.15). The ***variable-ratio*** groups spent between 8.03% and 19.02% of ***schedule*** time engaged in these behaviours. The percentages were higher in every session for groups with objects absent in ***schedule*** sessions (VROE & DRLOE).

During ***extinction*** sessions, between 13.07% and 19.27% of both the ***DRL*** groups' time was spent engaged in these behaviours (Table 7.15). The ***variable-ratio*** groups spent less total session time (between 7.71% & 15.78%) engaged in ***behaviour directed at the peripheral areas of the box***. The percentages were higher in the ***DRL*** groups than their counterparts (DRLOS compared with VROS & DRLOE compared to VROE), and also higher for groups with objects first present during ***extinction*** (VROE & DRLOE).

Table 7.15
The percentage of total session time (1800 seconds) spent engaged in ***behaviour directed at the peripheral areas of the box (propping + jump at lid)***.

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
VROS	10.13 %	8.11 %	8.03 %	9.39 %	7.71 %	8.11 %
DRLOS	12.46 %	12.62 %	11.87 %	13.07 %	18.58 %	15.67 %
VROE	19.02 %	17.33 %	18.82 %	12.80 %	13.03 %	15.78 %
DRLOE	18.36 %	15.49 %	17.33 %	14.67 %	15.76 %	19.27 %

Overall, all groups showed a slight decrease over ***schedule*** sessions (Table 7.15). An overall increase across ***extinction*** sessions was observed for all but the VROS group. Across the six sessions, the ***DRL*** percentages increased overall, whereas the ***variable-ratio*** percentages decreased. When objects were first present during ***schedule*** sessions, the percentages were higher for the ***DRL*** group (DRLOS) in every session. If, however, objects were first present during ***extinction*** sessions, the ***DRL*** group (DRLOE) percentages were lower during ***schedule*** sessions but higher during ***extinction*** sessions.

7.3.5.4 OTHER BEHAVIOURAL CATEGORIES

During ***schedule*** sessions, the ***DRL*** groups spent between 4.82% and 9.29% of total session time engaged in ***displacement***. The percentages were slightly lower for the ***variable-ratio*** groups, ranging from 4.36% to 7.52% (Table 7.16). During ***extinction*** sessions, between 6.94% and 13.45% of the ***DRL*** groups' session time was spent in ***displacement***. For the ***variable-ratio*** groups, the percentages ranged from 5.33% to 11.84%.

The percentage of total session time spent engaged in ***displacement*** increased across ***schedule*** sessions for all groups (Table 7.16). The percentages then decreased in the first ***extinction*** session for the ***variable-ratio*** groups. There was an overall increase across ***extinction*** sessions for all groups. Overall, there was an increase across all six sessions for all groups.

All groups spent less than one percent of any session engaged in ***digging/burying*** (Table 7.16). Across ***schedule*** sessions, there was an overall increase for all groups. By contrast, there was an overall decrease for all but the VROS group across ***extinction***. There was also an overall decrease in percentage of total session spent ***digging/burying*** across all six sessions for all but the VROS group.

Table 7.16
The percentage of total session time (1800 seconds) spent engaged in ***other behavioural categories (displacement, digging/burying, rearing & pica)***.

GROUP	**SESSION 1**	**SESSION 2**	**SESSION 3**	**SESSION 4**	**SESSION 5**	**SESSION 6**
VROS	***displacement*** 4.36 % ***dig/bury*** 0.06% ***rearing*** 3.02% ***pica*** 6.16%	***displacement*** 7.52 % ***dig/bury*** 0.2% ***rearing*** 5.2% ***pica*** 4.43%	***displacement*** 6.30 % ***dig/bury*** 0.12% ***rearing*** 3.88% ***pica*** 5.06%	***displacement*** 6.0 % ***dig/bury*** 0.05% ***rearing*** 5.53% ***pica*** 3.73%	***displacement*** 11.84% ***dig/bury*** 0.07% ***rearing*** 3.93% ***pica*** 5.52%	***displacement*** 9.42 % ***dig/bury*** 0.26% ***rearing*** 3.82% ***pica*** 5.18%
DRLOS	***displacement*** 5.27 % ***dig/bury*** 0.4% ***rearing*** 6.27% ***pica*** 4.14%	***displacement*** 9.29 % ***dig/bury*** 0.31% ***rearing*** 6.37% ***pica*** 4.13%	***displacement*** 5.93 % ***dig/bury*** 0.58% ***rearing*** 7.02% ***pica*** 4.81%	***displacement*** 6.94 % ***dig/bury*** 0.19% ***rearing*** 6.69% ***pica*** 6.07%	***displacement*** 7.66 % ***dig/bury*** 0.2% ***rearing*** 5.75% ***pica*** 7.78%	***displacement*** 13.45 % ***dig/bury*** 0.13% ***rearing*** 4.31% ***pica*** 8.03%
VROE	***displacement*** 6.28 % ***dig/bury*** 0.15% ***rearing*** 9.66% ***pica*** 7.67%	***displacement*** 5.26 % ***dig/bury*** 0.1% ***rearing*** 12.15% ***pica*** 5.36%	***displacement*** 7.40 % ***dig/bury*** 0.24% ***rearing*** 7.55% ***pica*** 9.22%	***displacement*** 5.33 % ***dig/bury*** 0.29% ***rearing*** 1.92% ***pica*** 7.04%	***displacement*** 5.78 % ***dig/bury*** 0.2% ***rearing*** 2.91% ***pica*** 14.59%	***displacement*** 11.41 % ***dig/bury*** 0.14% ***rearing*** 1.96% ***pica*** 8.78%
DRLOE	***displacement*** 5.05 % ***dig/bury*** 0.54% ***rearing*** 11.15% ***pica*** 5.62%	***displacement*** 4.82 % ***dig/bury*** 0.8% ***rearing*** 11.29% ***pica*** 9.75%	***displacement*** 5.80 % ***dig/bury*** 0.57% ***rearing*** 9.50% ***pica*** 9.27%	***displacement*** 7.18 % ***dig/bury*** 0.35% ***rearing*** 4.26% ***pica*** 8.21%	***displacement*** 12.57 % ***dig/bury*** 0.48% ***rearing*** 4.01% ***pica*** 8.03%	***displacement*** 11.31 % ***dig/bury*** 0.26% ***rearing*** 5.44% ***pica*** 7.37%

During ***schedule*** sessions, the ***DRL*** groups spent between 6.27% and 11.29% of total session time engaged in ***rearing***, whilst the percentages ranged from 3.03% to 12.15% for the ***variable-ratio*** groups (Table 7.16). If objects were present (DRLOS & VROS groups), less time was spent engaged in ***rearing***. The ***DRL*** groups spent more time ***rearing*** than their counterparts (except DRLOE group in session 2). During ***extinction***, the ***DRL*** groups spent between 4.01% and 6.69% of time engaged in this behaviour. These percentages ranged from 1.92% to 5.53% for the ***variable-ratio*** groups during ***extinction***. The ***DRL*** percentages were higher in every session (except DRLOE in session 4), and more time was spent ***rearing*** than their counterparts. If objects were first present during ***extinction*** (DRLOE & VROE groups), the percentages were lower (except for the DRLOE group in session 6) than for their counterparts.

The percentage of total session time spent engaged in ***rearing*** showed an overall decrease across the six sessions for all but the VROS group (Table 7.16). For groups with objects present during ***schedule*** sessions (DRLOS & VROS groups), the percentages increased over ***schedule*** sessions, and decreased over ***extinction***. The opposite pattern was observed for the groups that first encountered objects during ***extinction***. For these groups there was a noticeable decrease in ***rearing*** when objects were present. The percentage of total session time spent ***rearing*** decreased in the first ***extinction*** session in all but the VROS group.

All groups spent less than 10% of total session time (>3.5%) engaged in ***pica*** in every session (except session 5 for the VROE group). For groups with objects first present during ***schedule*** sessions (DRLOS & VROS groups), less time was spent engaged in ***pica*** in every session than their counterparts (Table 7.16). The DRLOS group percentages were lower during ***schedule*** sessions, but higher during ***extinction*** sessions than for the VROS group. The percentages were higher for the DRLOE group than for the VROE group in all but session 1. Overall, the percentage of total session time spent engaged in ***pica*** increased across ***schedule*** sessions, as well as the six sessions for all but the VROS group. The percentages decreased in the first ***extinction*** session for all groups, except the DRLOS group. An overall increase across ***extinction*** was observed in all but the DRLOE group.

7.3.6 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE OVER SESSIONS, AND BETWEEN GROUPS

The changes in each behavioural measure (frequency & duration) over the three ***schedule*** sessions (sessions 1 - 3), and three ***extinction*** sessions (sessions 4 - 6) are presented graphically in Figures 7.7 - 7.10: II (inclusive). The scores for all four groups are plotted on each graph, allowing a visual comparison of trends across the six sessions.

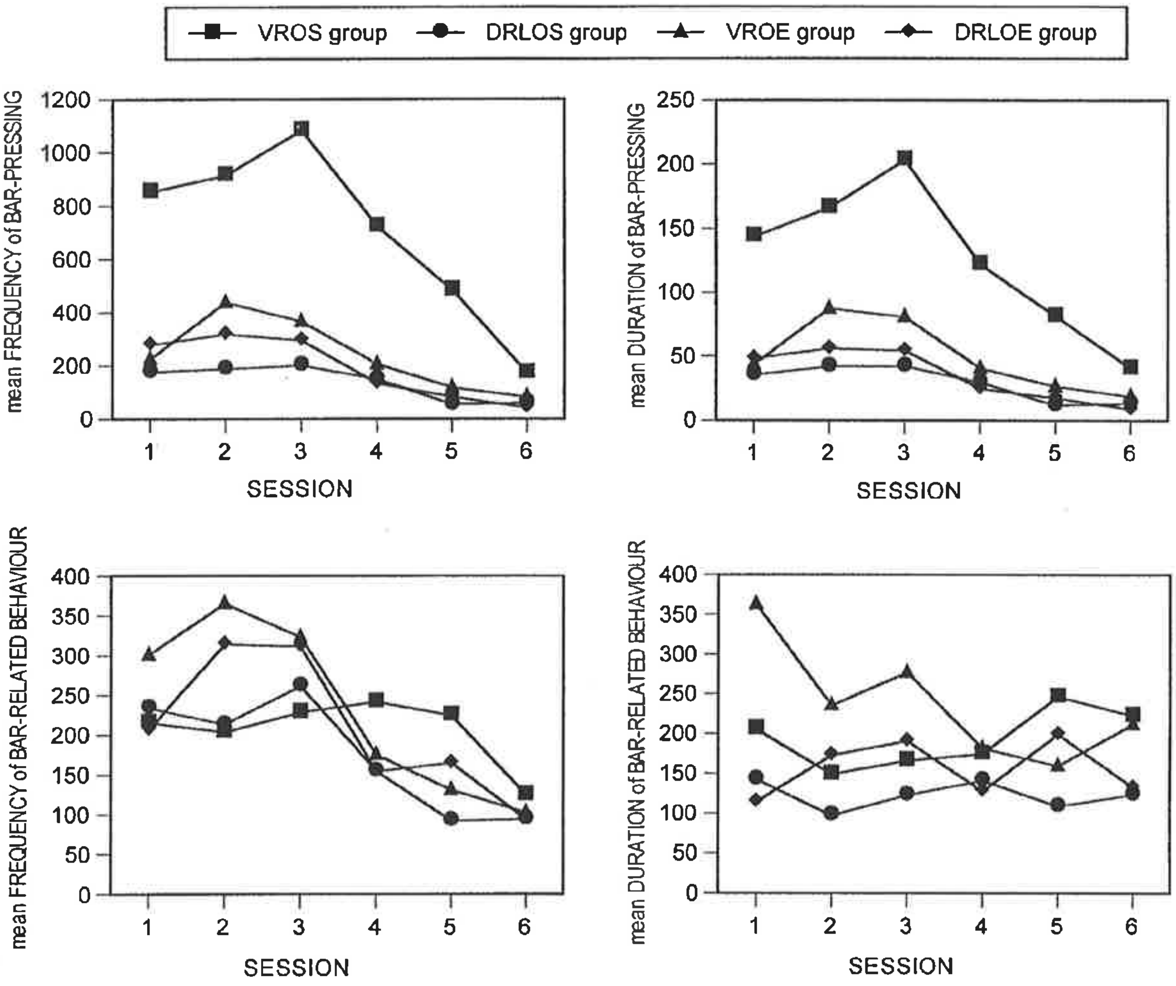


Figure 7.7. Mean frequency (left) and duration (right) scores of ***behaviour directed at the bar and food-trough area*** for all four groups in Experiment 2 (top- ***bar pressing*** & bottom- ***bar-related behaviour***)

7.3.6.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

All four groups showed a similar trend in ***bar pressing*** scores across all six sessions (Figure 7.7). The frequency and duration scores increased over the three ***schedule*** sessions, and decreased over the three ***extinction*** sessions. The pattern was accentuated in the VROS group, which had markedly higher frequency and duration scores in every session. The VROE scores were next highest in all but the first session. The frequency and duration scores were very similar for the

DRL groups during ***extinction***. The highest frequency and duration scores were obtained in session 3 for the VROS and DRLOS groups and in session 2 for the VROE and DRLOE groups.

An overall increase in the frequency of ***bar-related behaviour*** was seen for all four groups over the three ***schedule*** sessions (Figure 7.7). Overall decreases in duration scores were seen in all but the DRLOE group over these same sessions. This trend was reversed over the ***extinction*** sessions, with an overall decrease in frequency scores and an overall increase in duration scores (except for the DRLOS group). The highest frequency score was seen in session 2 for the VROE and DRLOE groups, and in session 3 for the DRLOS group. For the VROS group, the highest frequency score was observed in the first ***extinction*** session. The highest duration score was obtained in session 1 for the VROE and DRLOS groups and in session 5 for the VROS and DRLOE groups.

7.3.6.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

The frequency and duration of ***sniff object*** scores decreased over the ***schedule*** sessions for the DRLOS and VROS groups, with DRLOS scores higher in every session (Figure 7.8). For the VROS group, the frequency and duration scores increased in the first ***extinction*** session. For the DRLOS group, the frequency increased in the first ***extinction*** session, whereas the duration decreased. The frequency and duration of ***sniff object*** decreased over the three ***extinction*** sessions in all four groups. The lowest frequency and duration scores for the VROS group were found in session 3, whilst the lowest scores for these measures were found during ***extinction*** (session 5 or 6) in the other groups. The highest scores were obtained in the first session in which objects were encountered for all groups.

For the DRLOS group there was an overall decrease in frequency and slight overall increase in duration of ***sniff and touch object*** over the six sessions (Figure 7.8). Both measures showed a slight overall increase over the six sessions for the VROS group. The frequency scores for the DRLOS and VROS groups decreased over ***schedule*** sessions, whilst the duration decreased for the VROS group and increased for the DRLOS group over these same sessions. The frequency and duration scores of ***sniff and touch object*** showed an overall increase over ***extinction*** in all but the DRLOS group. The highest frequency and duration scores were seen in the last ***extinction*** session for all but the DRLOS group. The measures for the VROS group were lowest in most sessions. Overall, the duration scores were high in all groups.

Few instances of ***chew/bite object*** were observed in the DRLOS and VROS groups during ***schedule*** sessions (Figure 7.8). There was a slight overall decrease in frequency for both groups over these sessions, whilst the duration increased for the DRLOS group and decreased slightly for the VROS group. Both groups showed a sharp increase in both measures in the first ***extinction*** session and the frequency and duration scores continued to increase over ***extinction***, with the highest overall scores obtained in the last session. The frequency and duration of ***chew/bite object*** scores indicated minimal overall change over ***extinction*** sessions, but both measures peaked in the session 5 for the VROE group.

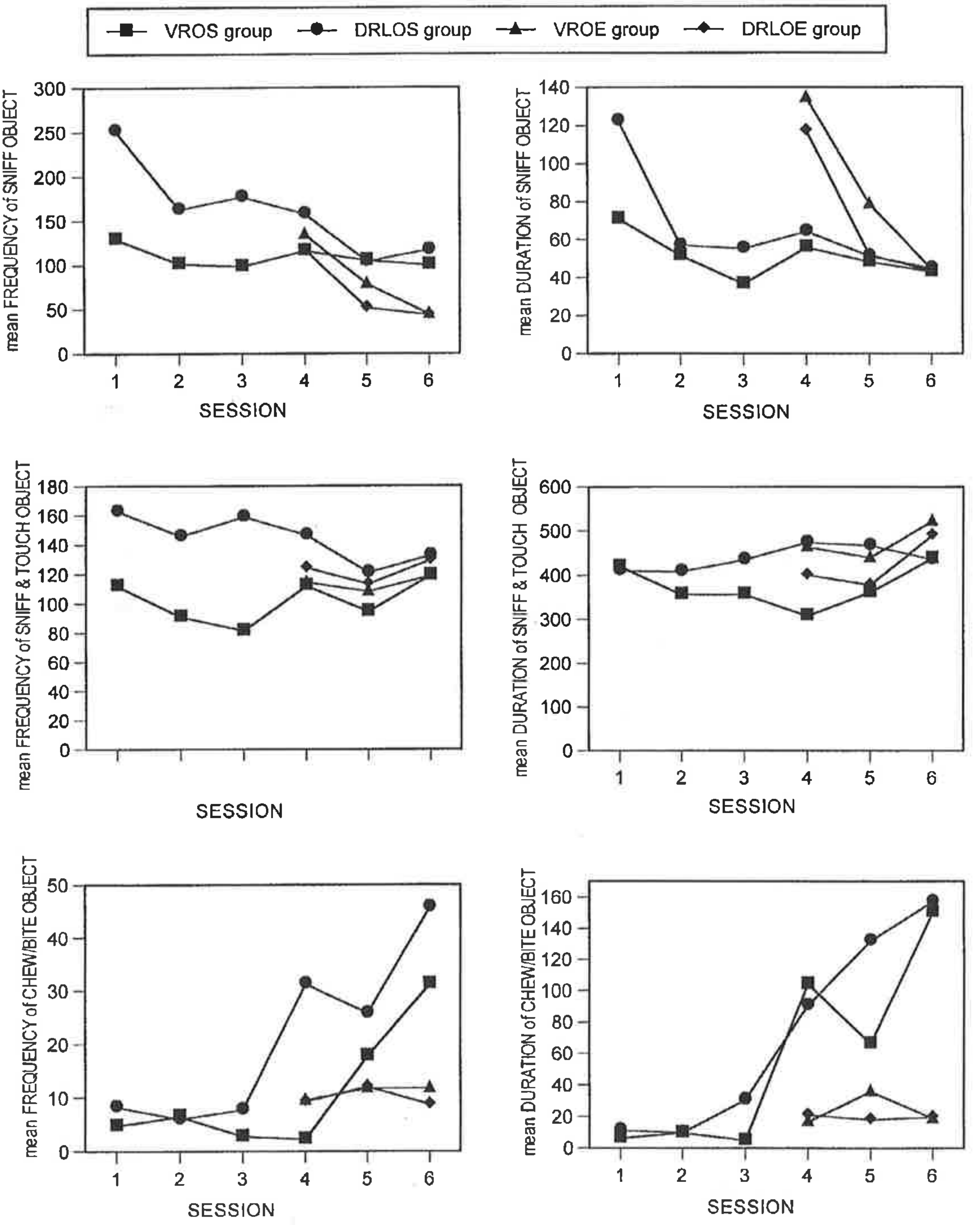


Figure 7.8. Mean frequency (left) and duration (right) scores of ***behaviour directed at the stimulus objects*** for all four groups in Experiment 2 (top- ***sniff object***, middle- ***sniff & touch object*** & bottom- ***chew/bite object***)

7.3.6.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

The frequency of ***propping*** scores decreased over ***schedule*** sessions for all but the VROE group, whilst the duration scores showed a slight overall decrease for all groups (Figure 7.9). Over ***extinction***, the frequency and duration scores increased for all but the VROS group. The lowest frequency and duration scores were observed in the VROS group in all sessions (except frequency in session 4). The DRLOE group showed the highest frequency scores in all sessions and highest duration scores during ***schedule*** sessions.

For the DRLOS and VROS groups, ***jump at lid*** was only observed during the last ***extinction*** session (Figure 7.9). Thus, this category of behaviour was only observed during ***schedule*** sessions if objects were absent. For the DRLOE and VROE groups, the frequency and duration scores of ***jump at lid*** decreased once objects were present (*i.e.*, during ***extinction***). Over ***schedule*** sessions both measures of ***jump at lid*** increased for these groups.

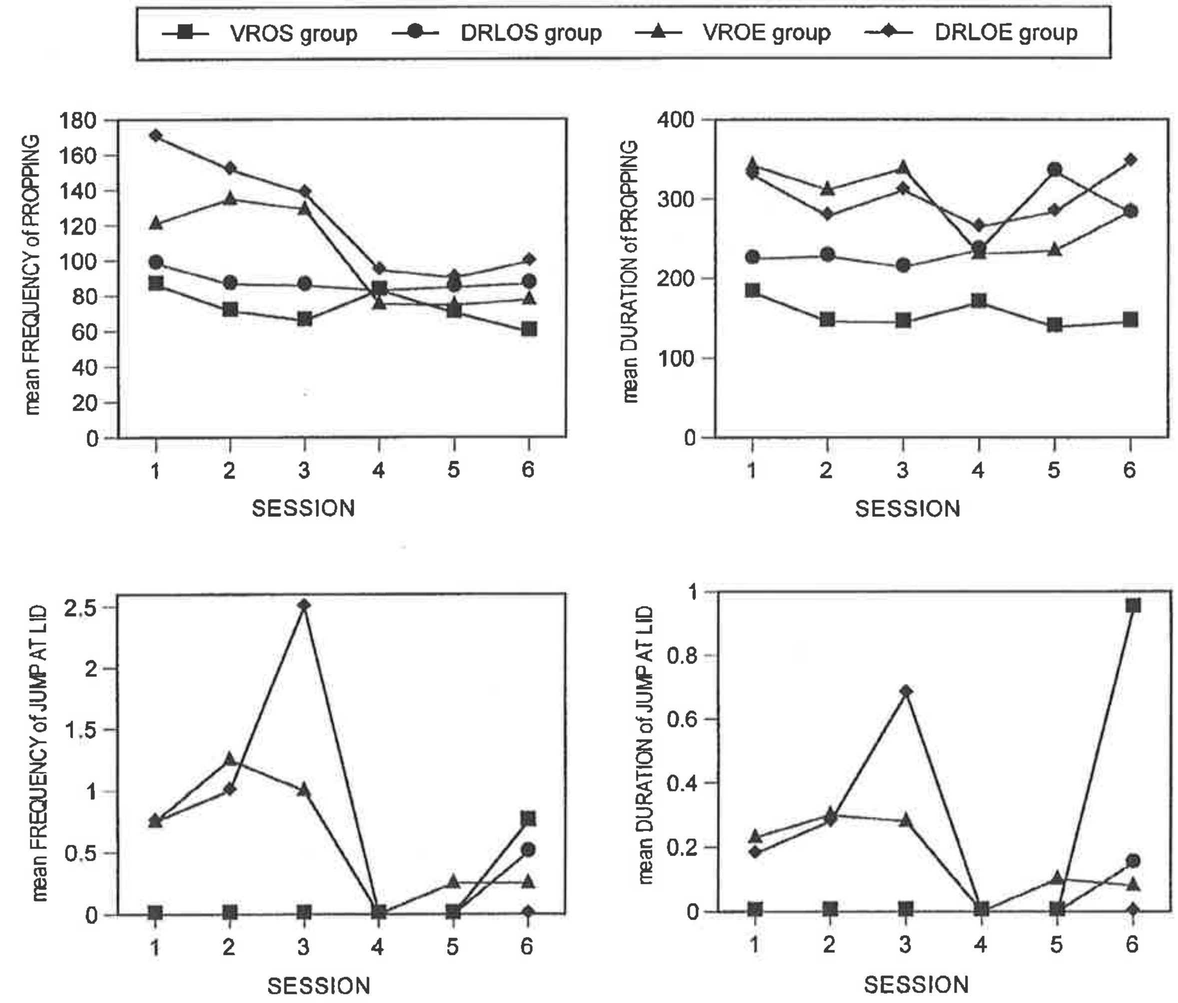


Figure 7.9. Mean frequency (left) and duration (right) scores of ***behaviour directed at the peripheral areas of the box*** for all four groups in Experiment 2 (top- ***propping*** & bottom- ***jump at lid***)

7.3.6.4 OTHER BEHAVIOURAL CATEGORIES

As Figure 7.10 (I) indicates, the frequency and duration scores of ***displacement*** increased over the three ***schedule*** sessions in all groups (except frequency for the DRLOE group, which showed an almost negligible decrease). The frequency scores decreased in the first ***extinction*** session, before increasing over the remaining sessions for all but the DRLOE group. The duration scores demonstrated a marked increase across the three ***extinction*** sessions for all groups, with highest overall duration scores obtained in the last two sessions.

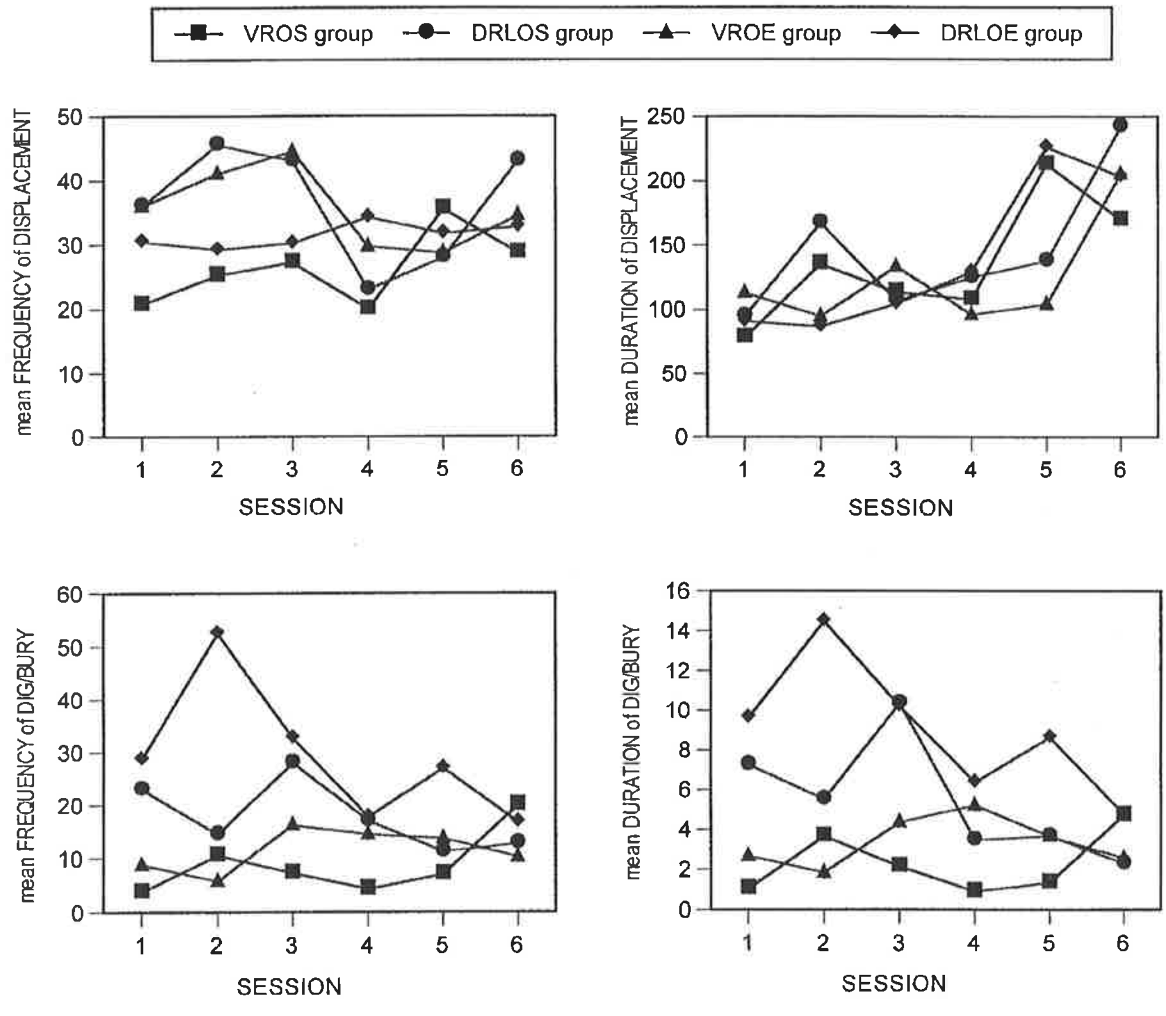


Figure 7.10 (I). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** for all four groups in Experiment 2 (top- ***displacement*** & bottom- ***digging/burying***)

For the ***digging/burying*** category, an overall increase in frequency scores was seen in the ***variable-ratio*** groups, whereas an overall decrease in this measure was seen for the ***DRL*** groups over the six sessions (Figure 7.10: I). The duration scores decreased over the six sessions for all but the VROS group. Over the three ***schedule*** sessions, the frequency and duration scores showed an overall increase for all groups. Over ***extinction***, an overall decrease in frequency and duration was seen for all but the VROS group. Except for the DRLOE group, the highest frequency score was observed during ***extinction*** and the lowest during a ***schedule*** session. The lowest duration score was seen during ***schedule*** running for all but the VROS group. The highest duration occurred during ***extinction*** in the DRLOS and VROE groups.

An overall decrease in frequency of ***rearing*** scores was seen in all groups over the three ***schedule*** sessions (Figure 7.10: II). The duration scores during ***schedule*** sessions were noticeably higher for the groups that did not have objects present (DRLOE & VROE groups). These scores showed an overall decrease for these groups over ***schedule*** sessions, whereas the duration scores increased for the DRLOS and VROS groups. Over ***extinction***, the frequency scores decreased for all but the DRLOE group. The duration scores decreased over ***extinction*** for the groups that had objects present during ***schedule*** sessions (DRLOS & VROS). The lowest frequency and duration scores were observed in the ***variable-ratio*** groups (VROS during ***schedule*** & VROE during ***extinction***).

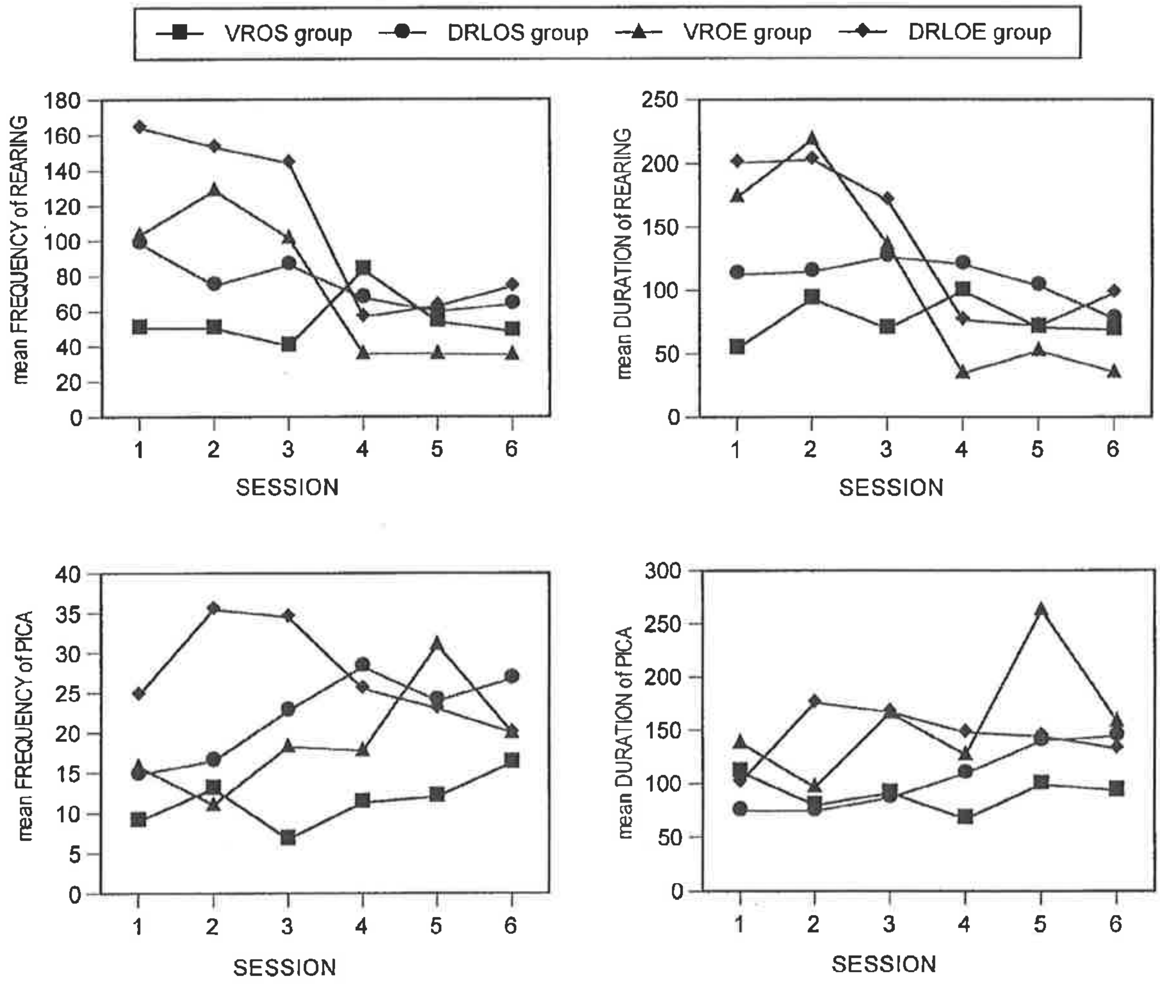


Figure 7.10 (II). Mean frequency (left) and duration (right) scores of ***other behavioural categories*** for all four groups in Experiment 2 (top- ***rearing*** & bottom- ***pica***)

The frequency and duration of ***pica*** scores increased overall during ***schedule*** sessions for all but the VROS group (Figure 7.10: II). For the ***variable-ratio*** groups, the frequency and duration scores increased over ***extinction***. For the DRLOE group, both measures decreased over ***extinction***, whereas for the DRLOS group, the frequency decreased and the duration increased. The frequency and duration scores were highest for the DRLOE group during ***schedule*** sessions (except duration in session 1). The frequency scores were lowest for the VROS group in all sessions except session 2. The duration scores were lowest for the DRLOS group during ***schedule*** sessions and the VROS group during ***extinction***.

7.3.7 CHANGES IN BEHAVIOURS OVER SESSIONS, BETWEEN SCHEDULES, AND BETWEEN OBJECT CONDITIONS

The previous section presented the mean frequency and duration of the scored behaviours exhibited by the four groups of rats graphically. Since the sample sizes were small, the data have been primarily analysed by description. Bearing this in mind, the data are now analysed by means of statistical testing. As with Experiment 1 (section 6.3.7), a multivariate analysis of variance (MANOVA) was performed for each of the frequency and duration measures, during the three ***schedule*** sessions (section 7.3.7.1), three ***extinction*** sessions (section 7.3.7.2) and all six sessions (section 7.3.7.3). For each MANOVA there were three independent (or grouping) variables: object (*i.e.*, objects first present during ***schedule*** or ***extinction***), schedule (*i.e.*, ***DRL*** or ***variable-ratio***) and session. In each case there was one dependent variable: the frequency or duration measure of a particular behavioural category.

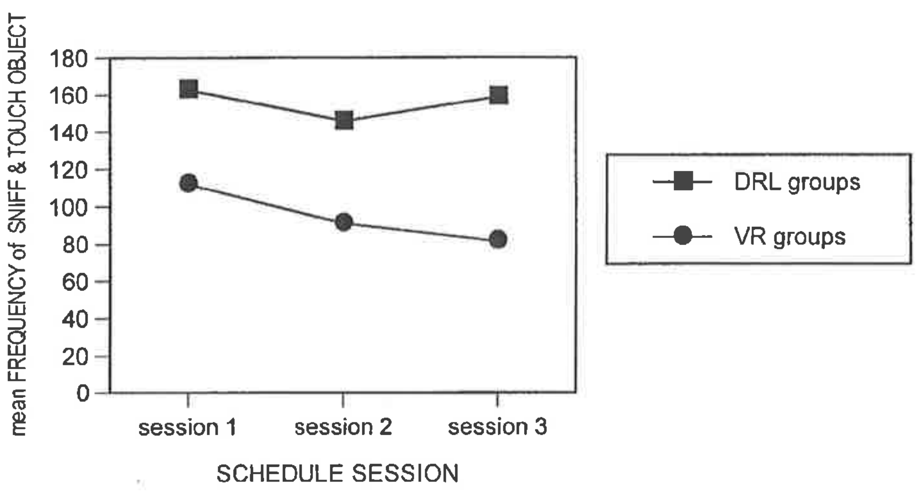
It should be noted, that objects were absent in two of the four groups (VROE & DRLOE) during ***schedule*** sessions. Therefore, the grouping variable "object" has an obvious effect on ***object-directed behaviours*** in those three sessions. If the other independent variables (schedule or session) have a main effect on the frequency or duration of ***object-directed behaviours***, it is only relevant for the two groups with objects present during ***schedule*** sessions (VROS & DRLOS).

7.3.7.1 SCHEDULE SESSIONS

Main effect of *schedule*

The differences between the schedules (***DRL*** or ***variable-ratio***) were statistically significant for only one measure, namely the frequency of ***sniff and touch object*** [F (1,12)=7.25, p<.05]. It should be noted that objects were only present in the DRLOS and DRLOE groups. As shown in Figure 7.11 (I), the scores were noticeably higher in every session for the ***DRL*** groups. The

variable-ratio scores decreased steadily over sessions, whereas the ***DRL*** scores showed little overall change, but with a slight decrease in the second session.



<u>**Figure 7.11 (I).**</u> Mean frequency of ***sniff and touch object*** for the "schedule" grouping variable during the ***schedule*** sessions

<u>Main effect of *object*</u>

A statistically significant main effect of ***object*** was found for the frequency of ***rearing*** [*F* (1,12)=8.36, *p*<.05], the duration of ***rearing*** [*F* (1,12)=4.88, *p*<.05] and the frequency of ***propping*** [*F* (1,12)=9.14, *p*<.05]. Thus, the presence or absence of objects affected only three measures of behaviour (Figure 7.11: II). If objects were <u>absent</u> ("OE" groups), the mean scores of these measures were much higher in every session. The mean frequency of ***rearing*** and ***propping*** showed an overall decrease over sessions, irrespective of whether objects were present or absent. The mean duration of ***rearing*** scores, however, decreased over sessions if objects were <u>absent</u>, but increased over sessions when objects were <u>present</u>.

<u>Main effect of *session*</u>

The differences between sessions were only statistically significant for the measures of one behavioural category. That is, the session number affected the frequency of ***bar pressing*** [*F* (2,24)=3.90, *p*<.05] and the duration of ***bar pressing*** [*F* (2,24)=5.69, *p*<.05]. Visual inspection of Figure 7.11 (III) indicates that the frequency of ***bar pressing*** increased noticeably over the three ***schedule*** sessions.

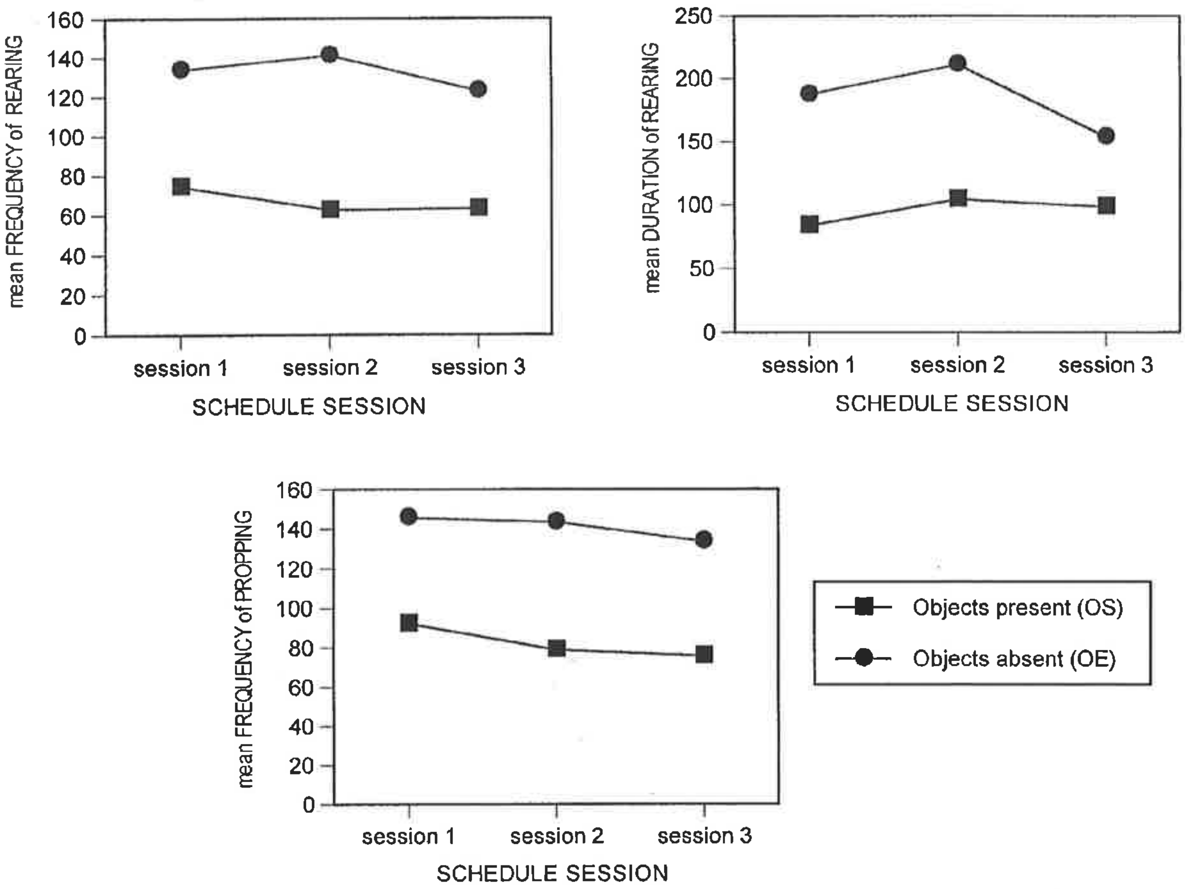


Figure 7.11 (II). Mean frequency of ***rearing*** (top left), duration of ***rearing*** (top right) and frequency of ***propping*** (bottom) for the "object" grouping variable during ***schedule*** sessions

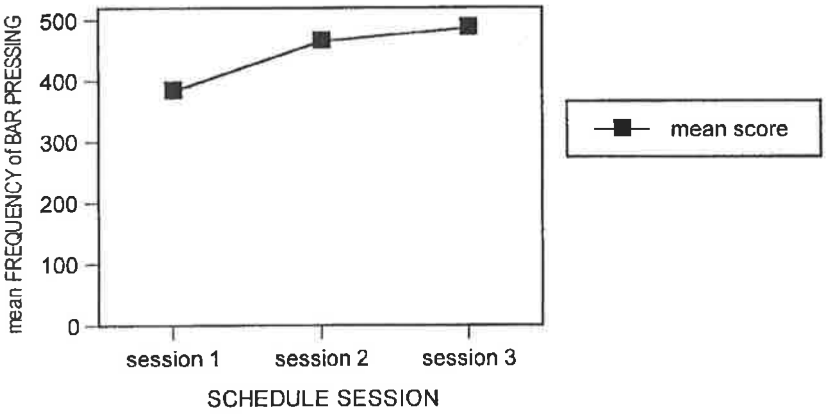


Figure 7.11 (III). Mean frequency of ***bar pressing*** for the "session" grouping variable during ***schedule*** sessions

Object x session interaction effect

A statistically significant ***object*** x ***session*** interaction was obtained for the frequency of ***bar-related behaviour*** [*F* (2,24)=4.43, *p*<.05] and the duration of ***displacement*** [*F* (2,24)=4.35, *p*<.05]. Thus, these two measures were *jointly* affected by the object (objects present or absent) *and* session grouping variables.

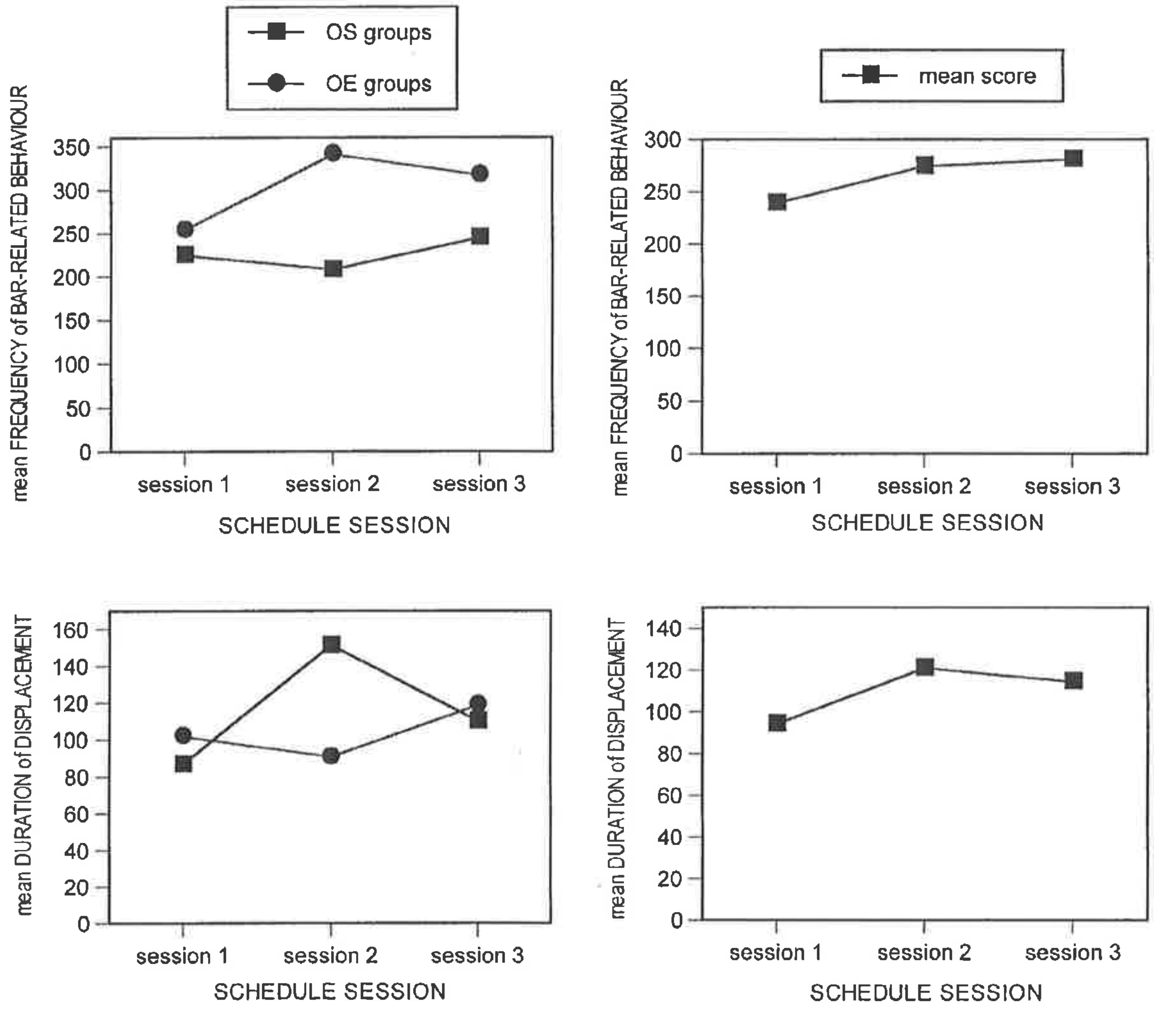


Figure 7.11 (IV). Mean frequency of ***bar-related behaviour*** (top) and duration of ***displacement*** (bottom) were jointly affected by the "object" (left) and "session" (right) grouping variables during ***schedule*** sessions

The frequency of ***bar-related behaviour*** increased gradually over sessions (Figure 7.11: IV). However, the scores were higher in every session if objects were absent ("OE" groups), and the increase over sessions was most pronounced for these groups. There was little change over sessions if objects were present.

As demonstrated in Figure 7.11 (IV), the duration of ***displacement*** showed an overall increase across sessions. Whilst there was an overall increase irrespective of presence or absence of objects, the patterns for the second session were very different depending on the object condition. If objects were absent ("OE" groups), the scores decreased slightly in the second session, whereas a sharp increase (to the highest score obtained overall) was observed if objects were present.

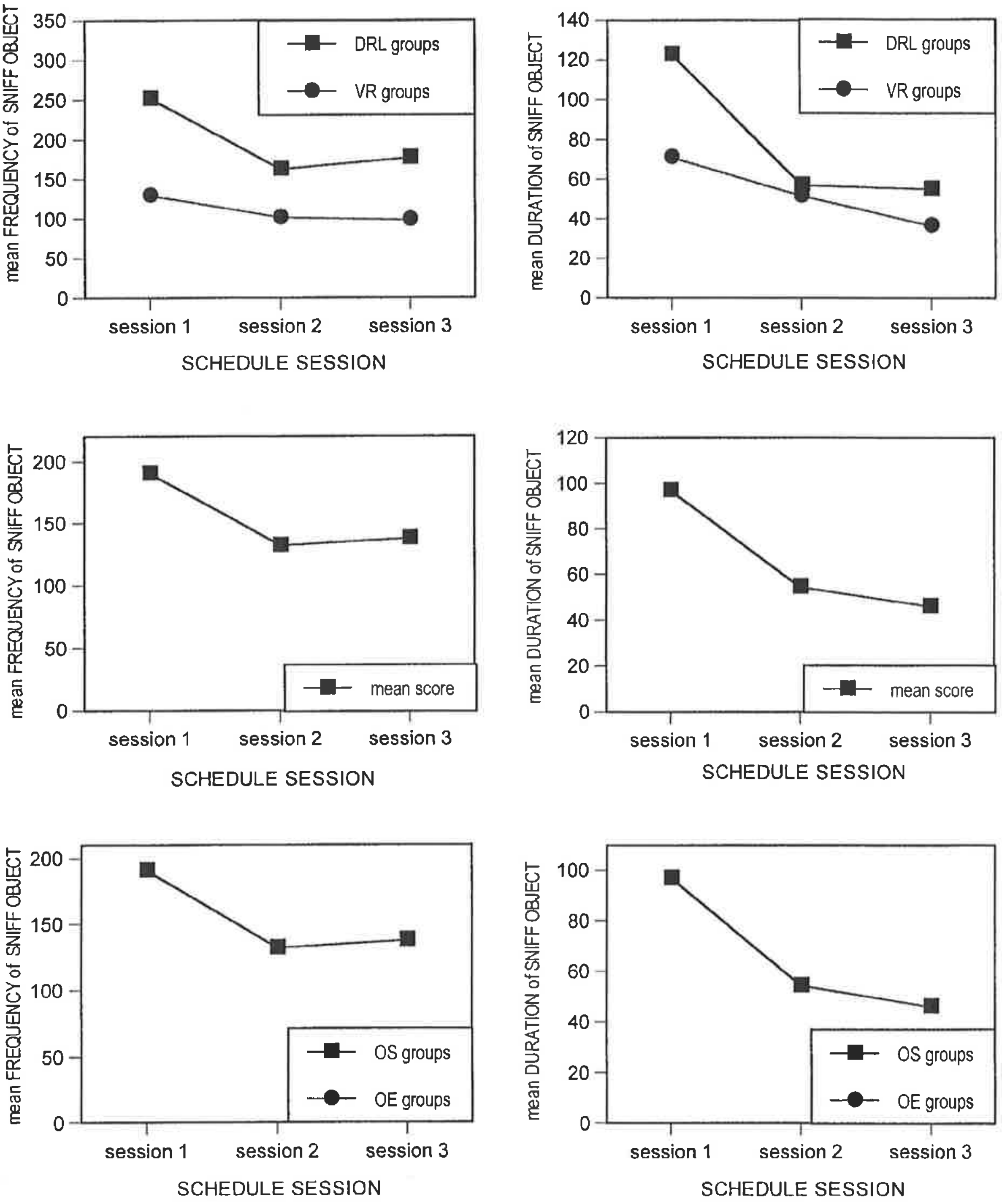


Figure 7.11 (V). Mean frequency (left) and duration (right) of ***sniff object*** was affected by all three grouping variables during ***schedule*** sessions (top- "schedule" grouping variable, middle- "session" grouping variable, & bottom- "object" grouping variable)

Object x schedule x session interaction effect

A statistically significant ***object*** x ***schedule*** x ***session*** interaction was found for three measures. The frequency of ***digging/burying*** [*F* (2,24)=5.55, *p*<.05], and the frequency of ***sniff object*** [*F* (2,24)=4.67, *p*<.05] and duration of ***sniff object*** [*F* (2,24)=10.09, *p*<.005] were affected by all three grouping variables.

Visual inspection of Figure 7.11 (V) shows that there was an overall decrease across sessions for the frequency and duration of ***sniff object***. This decrease was more pronounced in the ***DRL*** groups, which obtained the highest scores in every session. There was an obvious effect of "object" (bottom graphs), since objects were absent in these sessions for the "OE" groups.

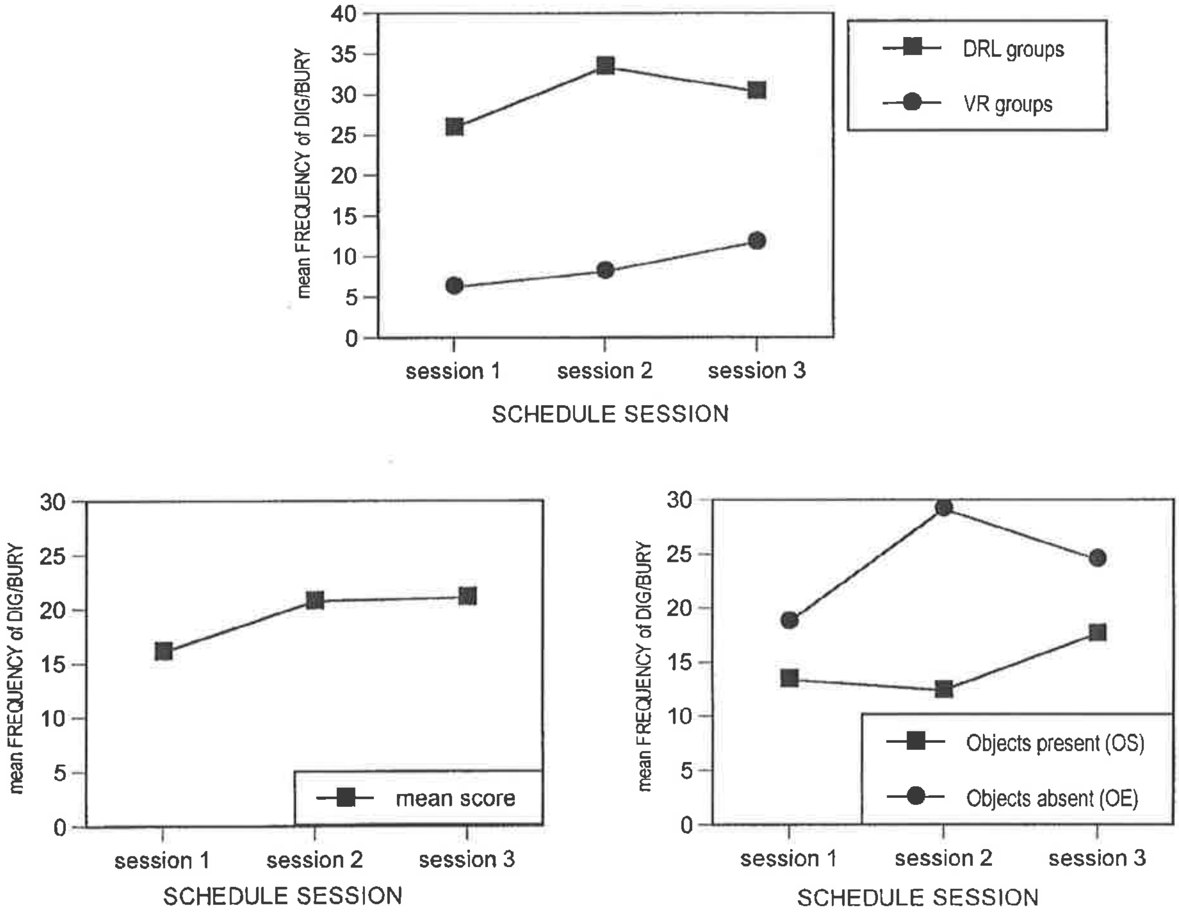


Figure 7.11 (VI). Mean frequency of ***digging/burying*** was affected by all three grouping variables during ***schedule*** sessions (top- "schedule" grouping variable, bottom left- "session" grouping variable & bottom right- "object" grouping variable)

The frequency of ***digging/burying*** increased slightly over sessions, but the scores were markedly higher in every session for rats in the ***DRL*** groups (Figure 7.11: VI). Scores were also higher in every session if objects were absent ("OE" groups). If objects were absent ("OE" groups), the frequency of ***digging/burying*** increased in the second session, whereas the score decreased in this session if objects were present.

7.3.7.2 EXTINCTION SESSIONS

Main effect of *session*

The differences between ***extinction*** sessions were statistically significant for measures of four behavioural categories (Table 7.17). That is, the session number affected three frequency measures and two duration measures.

Table 7.17
Experiment 2 significance levels obtained for measures of behavioural categories during the three ***extinction*** sessions (***session*** main effect).

Variable	***F*(2,24)**	**Significance level (*p*)**
Duration of ***pica***	4.07	<.05
Frequency of ***sniff and touch object***	4.23	<.05
Frequency of ***bar-related behaviour***	11.82	<.001
Frequency of ***bar pressing***	5.99	<.01
Duration of ***bar pressing***	4.78	<.05

The frequency and duration of ***bar pressing*** decreased markedly (almost linear) over sessions (Figure 7.12: I). The frequency of ***bar-related behaviour*** also showed a steady decrease over sessions (Figure 7.12: I). An overall slight increase in the mean duration of ***pica*** occurred over sessions, with a noticeable increase to the highest score in session 5 (Figure 7.12: I). The frequency of ***sniff and touch object*** showed little overall change across sessions, although there was a noticeable decline in this measure during the second ***extinction*** session.

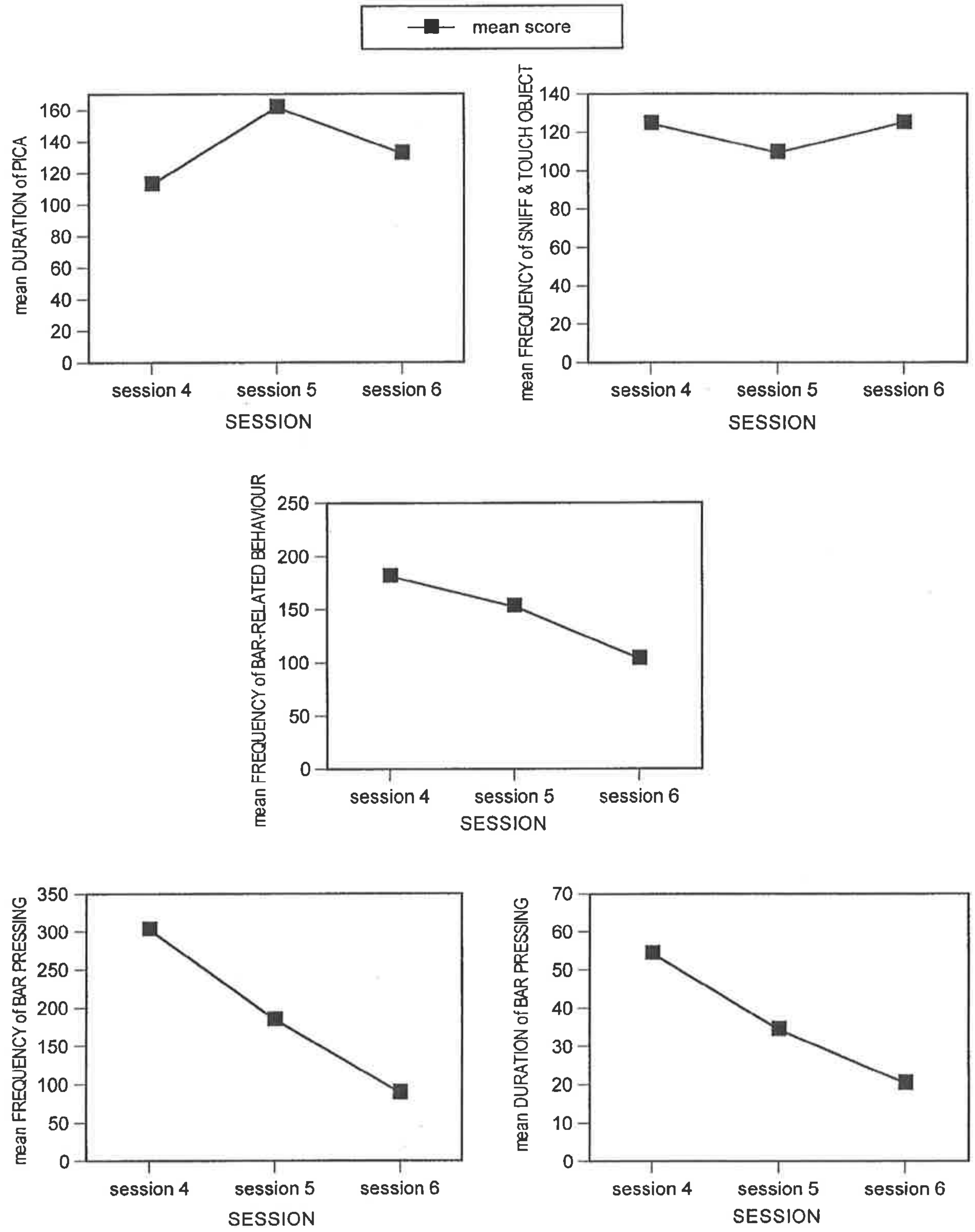


Figure 7.12 (I). Mean frequency and duration of behaviours for the "session" grouping variable during ***extinction*** (top- duration of ***pica*** & frequency of ***sniff & touch object***, middle- frequency of ***bar-related behaviour***, & bottom- frequency & duration of ***bar pressing***)

Main effect of *object*

Whether objects were first encountered during ***schedule*** or ***extinction*** sessions affected only one behavioural category. That is, a statistically significant main effect of ***object*** was found for the frequency of ***chew/bite object*** [*F* (1,12)=18.53, *p*<.005] and the duration of ***chew/bite object*** [*F* (1,12)=29.67, *p*<.001]. The mean scores of both measures were noticeably higher in every session for the "OS" groups (Figure 7.12: II). That is, if objects were first encountered during ***extinction***, fewer bouts of ***chew/bite object*** occurred, and less time was spent in this behaviour. In addition, for the "OE" groups, there was little change over sessions, whereas an overall increase in frequency and duration of ***chew/bite object*** took place across ***extinction*** in the "OS" groups.

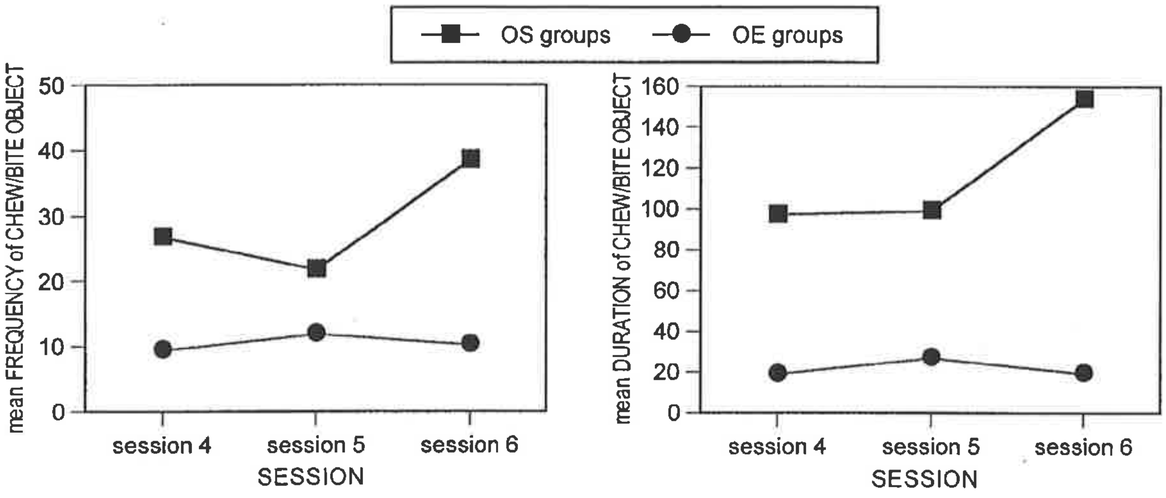


Figure 7.12 (II). Mean frequency (left) and duration (right) of ***chew/bite object*** for the "object" grouping variable during ***extinction***

Object x session interaction effect

A statistically significant ***object*** x ***session*** interaction was found for the duration of ***sniff object*** [*F* (2,24)=23.28, *p*<.001]. This measure was *jointly* affected by the object (first present during ***schedule*** or ***extinction*** sessions) *and* session grouping variables. A steady decrease in this measure took place over the three ***extinction*** sessions (Figure 7.12: III). However, this decrease was only slight for the "OS" groups. The mean duration of ***sniff object*** was lower in the first two ***extinction*** sessions if objects had first been encountered during ***schedule*** sessions ("OS" groups).

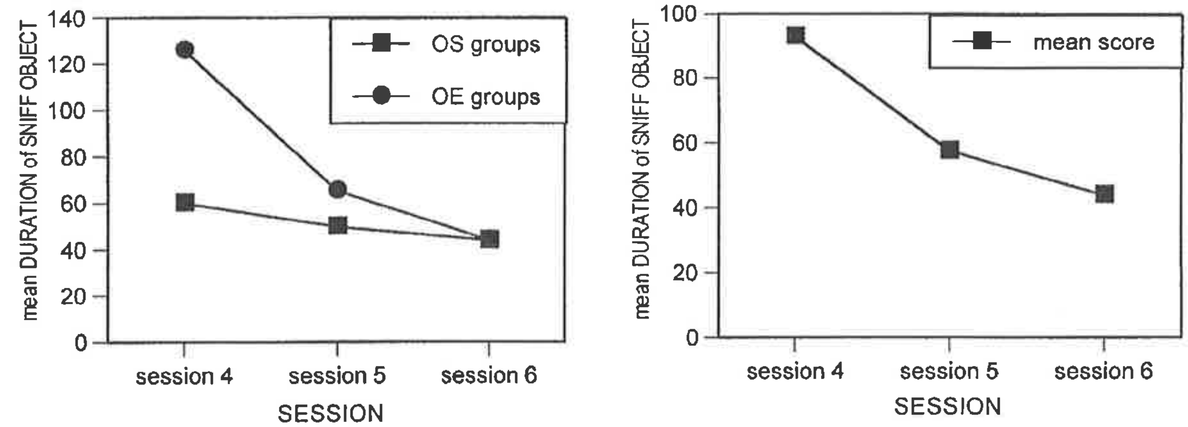


Figure 7.12 (III). Mean duration of ***sniff object*** was jointly affected by the "object" (left) and "session" (right) grouping variables during ***extinction***

Schedule x session interaction effect

The MANOVA for the frequency of ***sniff object*** yielded a statistically significant ***schedule*** x ***session*** interaction [*F* (2,24)=4.99, *p*<.05]. Thus, the frequency of ***sniff object*** was *jointly* affected by the schedule (***DRL*** or ***variable-ratio***) *and* session grouping variables. As shown in Figure 7.12 (IV), there was an overall decrease in the frequency of ***sniff object*** over ***extinction***, although there was little change between the scores in the last two ***extinction*** sessions (a slight increase). This decrease was gradual for the rats previously run on the ***variable-ratio*** schedule, with lowest scores for two of the three ***extinction*** sessions. For rats previously run on the ***DRL*** schedule, there was an overall decrease in frequency of ***sniff object*** over sessions, but the score dropped noticeably in the second ***extinction*** session, before increasing again.

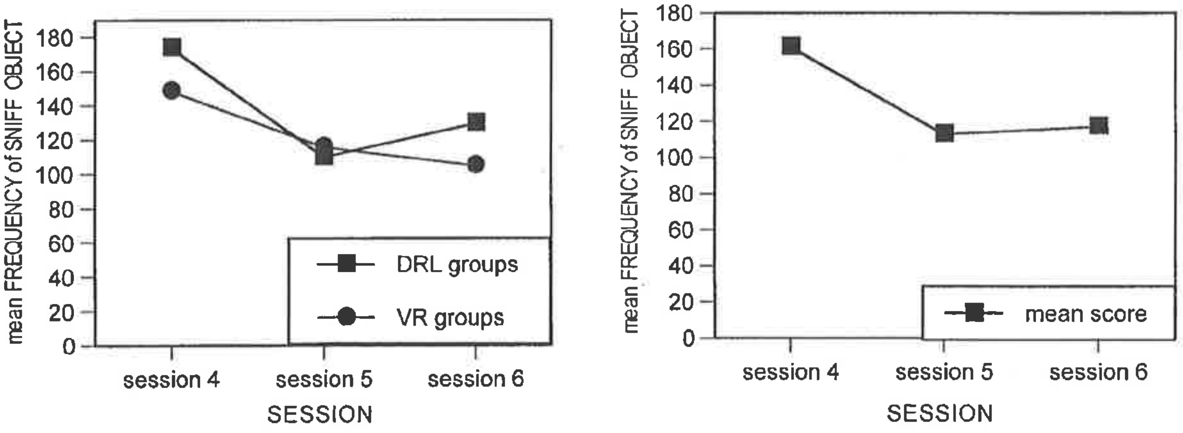


Figure 7.12 (IV). Mean frequency of ***sniff object*** was jointly affected by the "schedule" (left) and "session" (right) grouping variables during ***extinction***

Object x schedule x session **interaction effect**

A statistically significant ***object*** x ***schedule*** x ***session*** interaction was found for one measure. The duration of ***displacement*** [*F* (2,24)=5.06, *p*<.05] was affected by all three grouping variables during ***extinction*** sessions. Visual inspection of Figure 7.12 (V) indicates that the duration of ***displacement*** increased markedly over the three ***extinction*** sessions. However, the scores were slightly lower in every session if objects were first encountered during ***extinction*** ("OE" groups). Scores were more noticeably lower in every session if rats were previously run on the ***variable-ratio*** schedule.

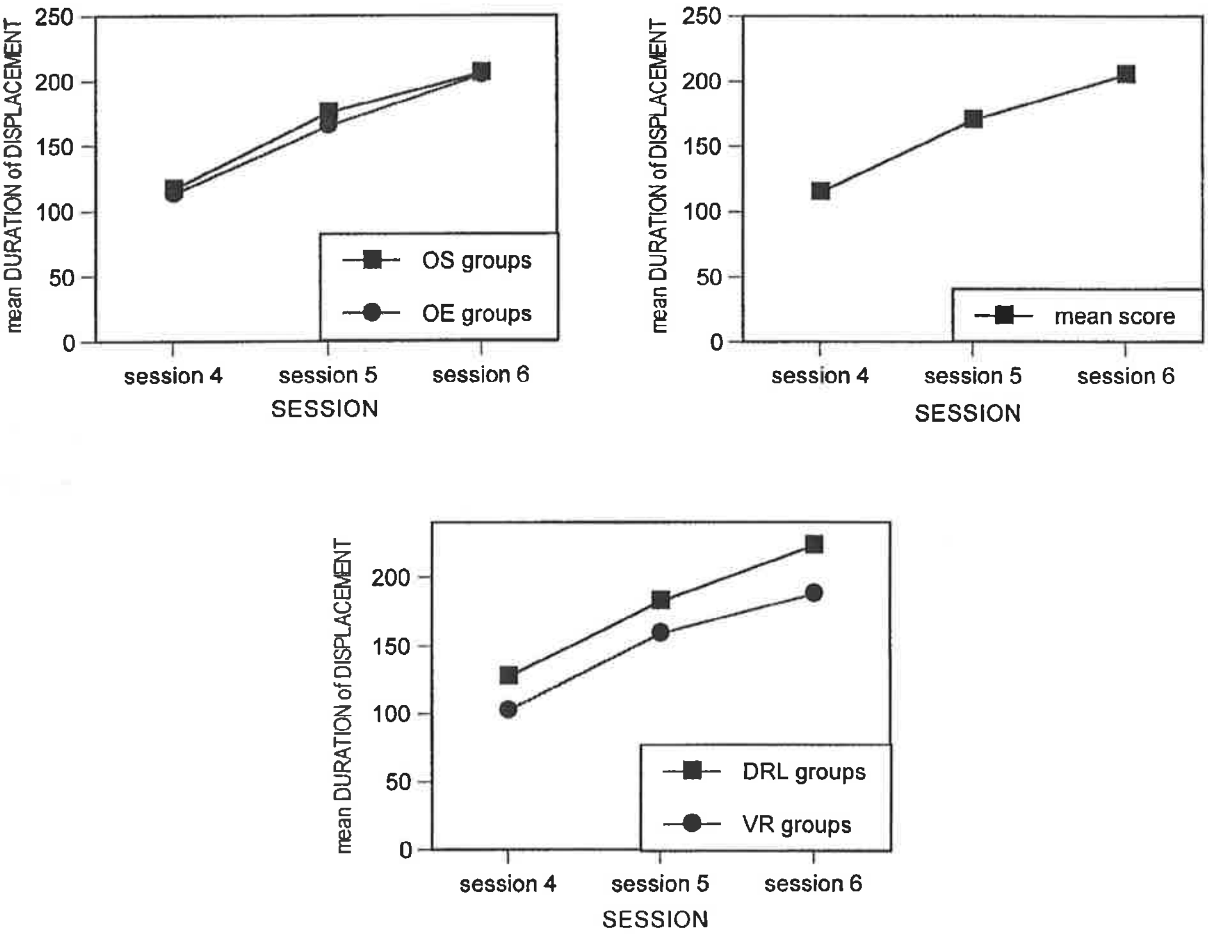


Figure 7.12 (V). Mean duration of ***displacement*** was affected by all three grouping variables during ***extinction*** (top left- "object" grouping variable, top right- "session" grouping variable & bottom- "schedule" grouping variable)

7.3.7.3 ALL SIX SESSIONS

Main effect of *session*

The differences between sessions were statistically significant for three behavioural measures. That is, the session number affected the duration of ***pica*** [*F* (5,60)=2.46, *p*<.05], frequency of ***bar-pressing*** [*F* (5,60)=8.03, *p*<.001] and the duration of ***bar-pressing*** [*F* (5,60)=7.97, *p*<.001]. The frequency and duration scores of ***bar pressing*** increased steadily over ***schedule*** sessions, dropped noticeably in the first ***extinction*** session and continued to decrease steadily over the remaining ***extinction*** sessions (Figure 7.13: I). The highest mean score of frequency and duration of ***bar pressing*** occurred in session 3 (***schedule*** session). The duration of ***pica***, on the other hand, showed a slight overall increase over ***schedule*** sessions, decreased slightly in the first ***extinction*** session, and then increased overall across ***extinction***. The highest mean score of duration of ***pica*** occurred in session 5 (***extinction*** session).

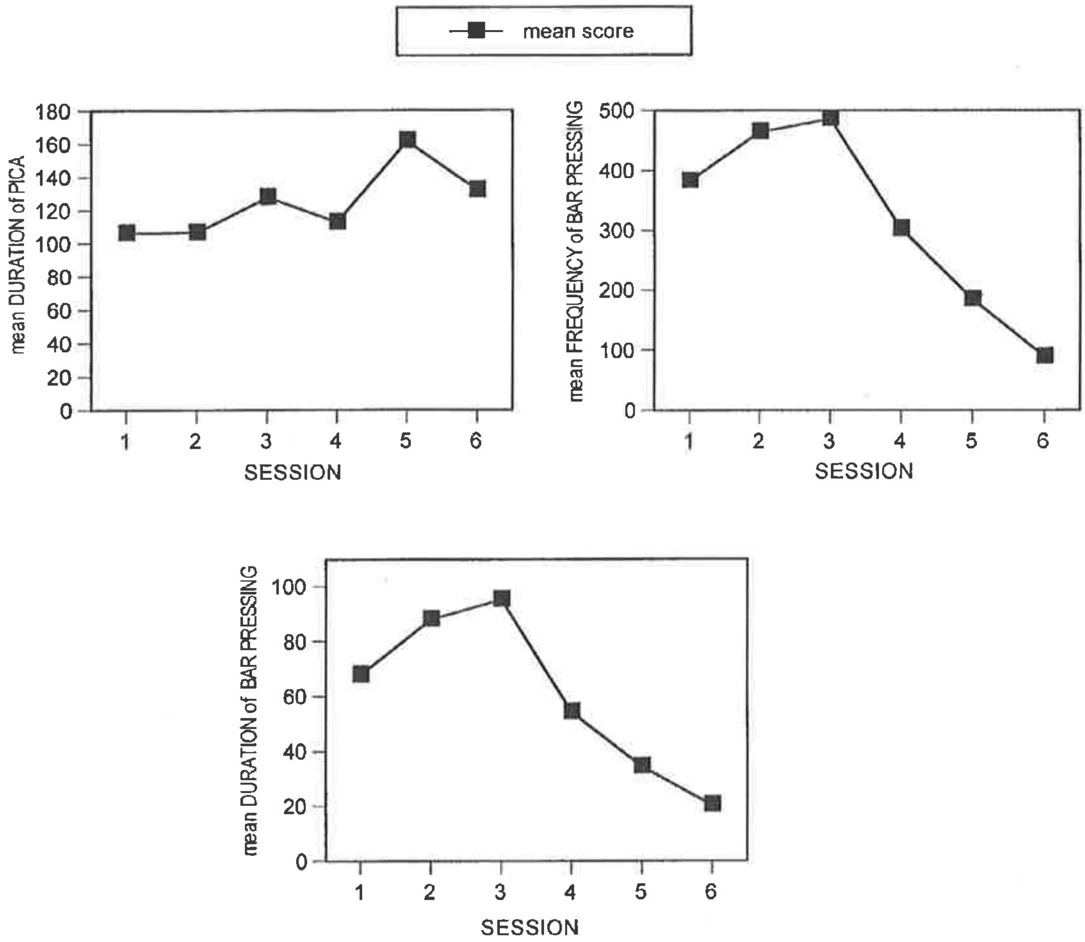


Figure 7.13 (I). Mean duration of ***pica*** (top left), frequency (top right) and duration (bottom) of ***bar pressing*** for the "session" grouping variable over the six sessions

Object x session **interaction effect**

A statistically significant ***object*** x ***session*** interaction was found for measures of six behavioural categories (Table 7.18). Thus, these measures were *jointly* affected by the object (*i.e.*, objects first present during ***schedule*** or ***extinction***) *and* session grouping variables over the six sessions.

Table 7.18
Experiment 2 significance levels obtained for measures of behavioural categories during all six sessions (***object*** **x** ***session*** interaction).

Variable	***F*(5,60)**	**Significance level (*p*)**
Duration of ***rearing***	6.15	<.001
Frequency of ***propping***	4.51	<.005
Frequency of ***chew/bite object***	3.32	<.05
Duration of ***chew/bite object***	6.93	<.001
Frequency of ***sniff and touch object***	56.69	<.001
Duration of ***sniff and touch object***	28.21	<.001
Duration of ***sniff object***	61.66	<.001
Frequency of ***bar-related behaviour***	3.42	<.01

Overall, there was a slight decrease in duration of ***rearing*** over ***schedule*** sessions, a noticeable decrease in the first ***extinction*** session, followed by a small decrease over the remaining ***extinction*** sessions (Figure 7.13: II). However, the patterns differed depending upon when objects were first encountered. If objects were first encountered during ***schedule*** sessions ("OS" groups), there was little change over the six sessions, although an overall increase over ***schedule*** sessions and overall decrease over ***extinction*** was observed. If objects were absent during ***schedule*** sessions ("OE" groups), the duration of ***rearing*** was markedly higher during those sessions and showed an overall decrease over sessions. Once objects were present during ***extinction***, the scores for the "OE" groups were noticeably lower during the first two ***extinction*** sessions and there was a slight overall increase across ***extinction***.

As shown in Figure 7.13 (II), the frequency of ***propping*** decreased gradually over ***schedule*** sessions, declined more noticeably in the first ***extinction*** session and changed little over the remaining sessions (slight overall decrease). However, if objects were absent during ***schedule*** sessions ("OE" groups), the number of bouts of ***propping*** was markedly higher in those three sessions. The scores dropped noticeably for the "OE" groups in the first ***extinction*** session, whereas they increased slightly for the "OS" groups. In every ***extinction*** session, frequency of

propping was slightly lower for the "OS" groups. Over ***extinction***, there was a slight increase for the "OE" groups, but a slight decrease for the "OS" groups.

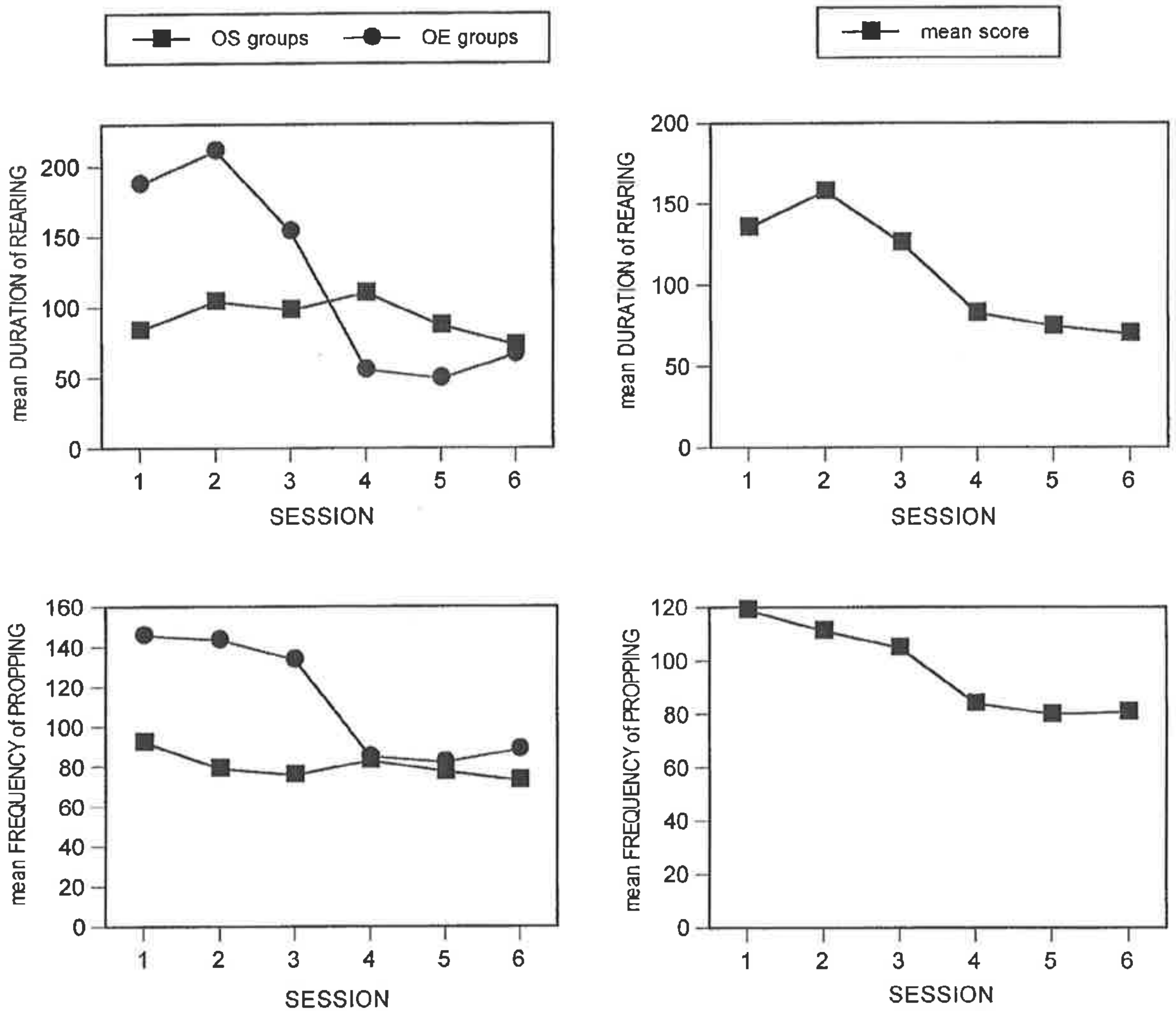


Figure 7.13 (II). Mean duration of ***rearing*** (top) and frequency of ***propping*** (bottom) were jointly affected by the "object" (left) and "session" (right) grouping variables over the six sessions

Visual inspection of Figure 7.13 (III) indicates, that frequency of ***chew/bite object*** decreased slightly over ***schedule*** sessions, whilst the duration of this behaviour increased slightly. Objects were only present in the "OS" groups during these sessions. Both measures increased noticeably over ***extinction***. The frequency and duration of ***chew/bite object***, however, was markedly lower in every ***extinction*** session for the rats that first encountered objects during those sessions ("OE" groups). For these groups, there was little change in these measures over ***extinction***.

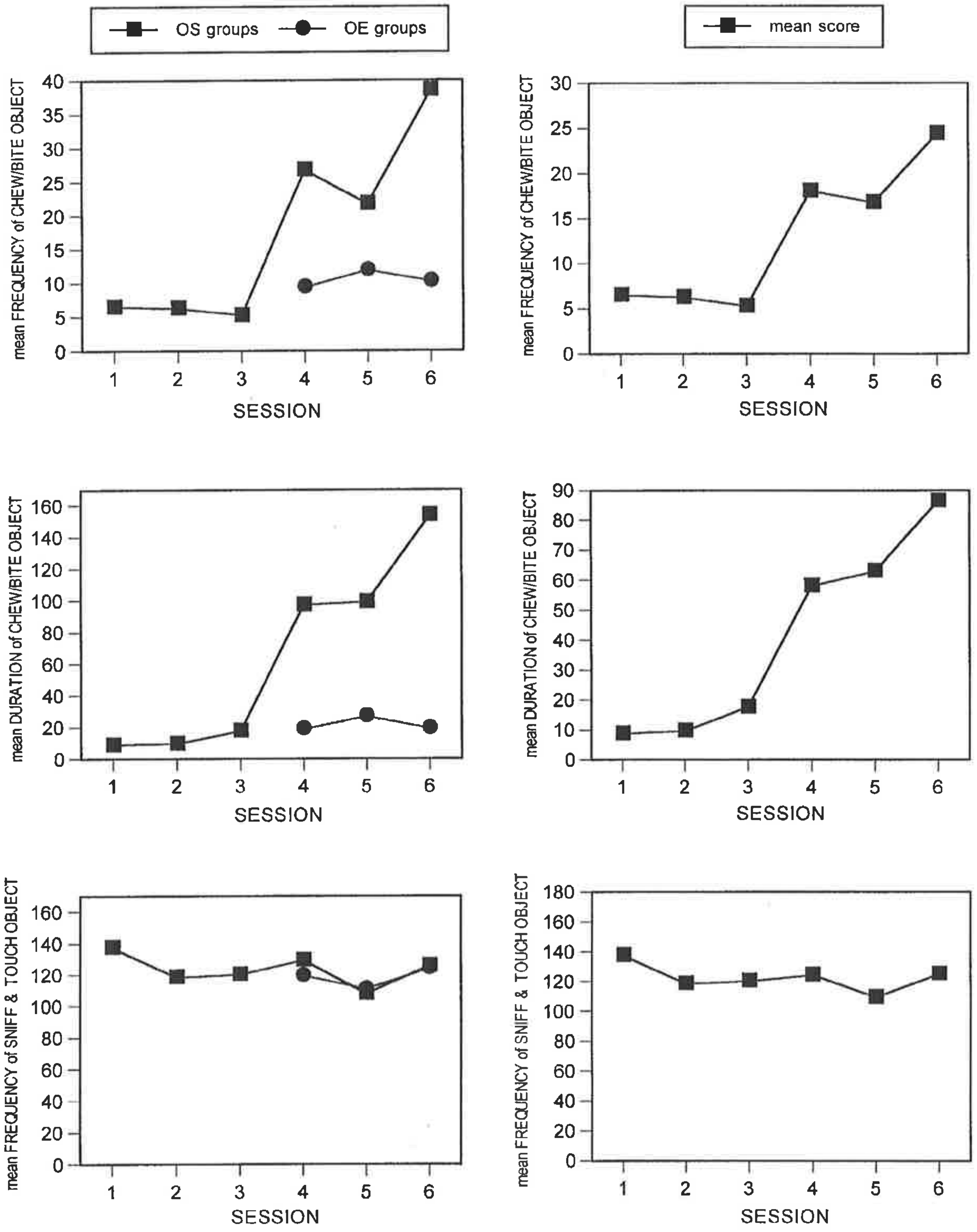


Figure 7.13 (III). Mean frequency of ***chew/bite object*** (top), duration of ***chew/bite object*** (middle) and frequency of ***sniff and touch object*** (bottom) were jointly affected by the "object" (left) and "session" (right) grouping variables over the six sessions

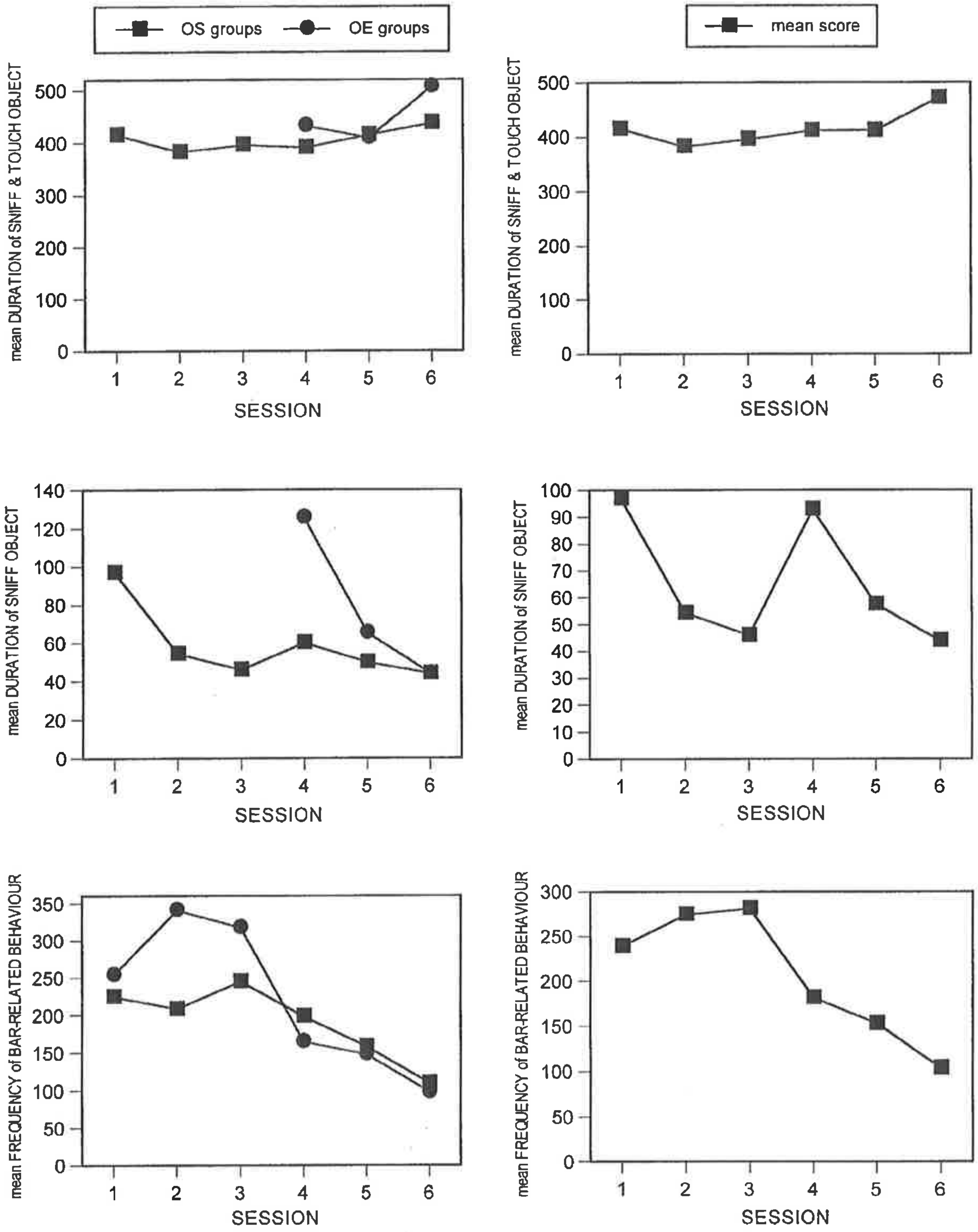


Figure 7.13 (IV). Mean duration of ***sniff & touch object*** (top), duration of ***sniff object*** (middle) and frequency of ***bar-related behaviour*** (bottom) were jointly affected by the "object" (left) and "session" (right) grouping variables over the six sessions

The frequency and duration of ***sniff and touch object*** decreased slightly over ***schedule*** sessions if objects were present ("OS" groups). During ***extinction***, there was a marginal increase in the frequency measure over sessions for the "OE" groups, but a slight decrease for the "OS" groups (Figure 7.13:III). The duration scores of ***sniff and touch object*** increased over ***extinction*** (Figure 7.13: IV). The scores tended to be lower for the "OS" groups, and showed a gradual increase over ***extinction***. For the "OE" groups, overall there was a more marked increase in this measure across ***extinction***, although there was actually a slight decrease in session 5.

The duration of ***sniff object*** decreased sharply over ***schedule*** sessions, when objects were present ("OS" groups). This was followed by an equally sharp increase in the first ***extinction*** session, followed by a steep decrease over the remaining sessions (Figure 7.13: IV). However, for the "OS" groups, the increase in the first ***extinction*** session was not pronounced, and the decrease over ***extinction*** was steady (not sharp). If objects were first encountered during ***extinction*** ("OE" groups), the duration of ***sniff object*** was much higher (more than double) in the first ***extinction*** session. Although this measure was still higher during the second ***extinction*** session, by the last session it was almost identical. The duration of ***sniff object*** decreased very sharply over ***extinction*** for the "OE" group.

As shown in Figure 7.13 (IV), the frequency of ***bar-related behaviour*** increased over ***schedule*** sessions, decreased markedly in the first ***extinction*** session and then continued to decrease steadily over the remaining sessions. If objects were absent during ***schedule*** sessions ("OE" groups), the scores were noticeably higher in those sessions and the increase in frequency of ***bar-related behaviour*** over sessions was more pronounced (especially in the second session). The decrease in the first ***extinction*** session was much sharper for the "OE" groups, who encountered objects for the first time in that session. The scores were slightly lower in every ***extinction*** session for the "OE" groups.

Schedule x session interaction effect

Statistically significant ***schedule*** x ***session*** interactions were found for the frequency of ***sniff object*** [*F* (5,60)=5.20, *p*<.001] and duration of ***sniff object*** [*F* (5,60)=3.10, *p*<.05]. Thus, both measures of ***sniff object*** were *jointly* affected by the schedule (***DRL*** or ***variable-ratio***) *and* session grouping variables over the six sessions.

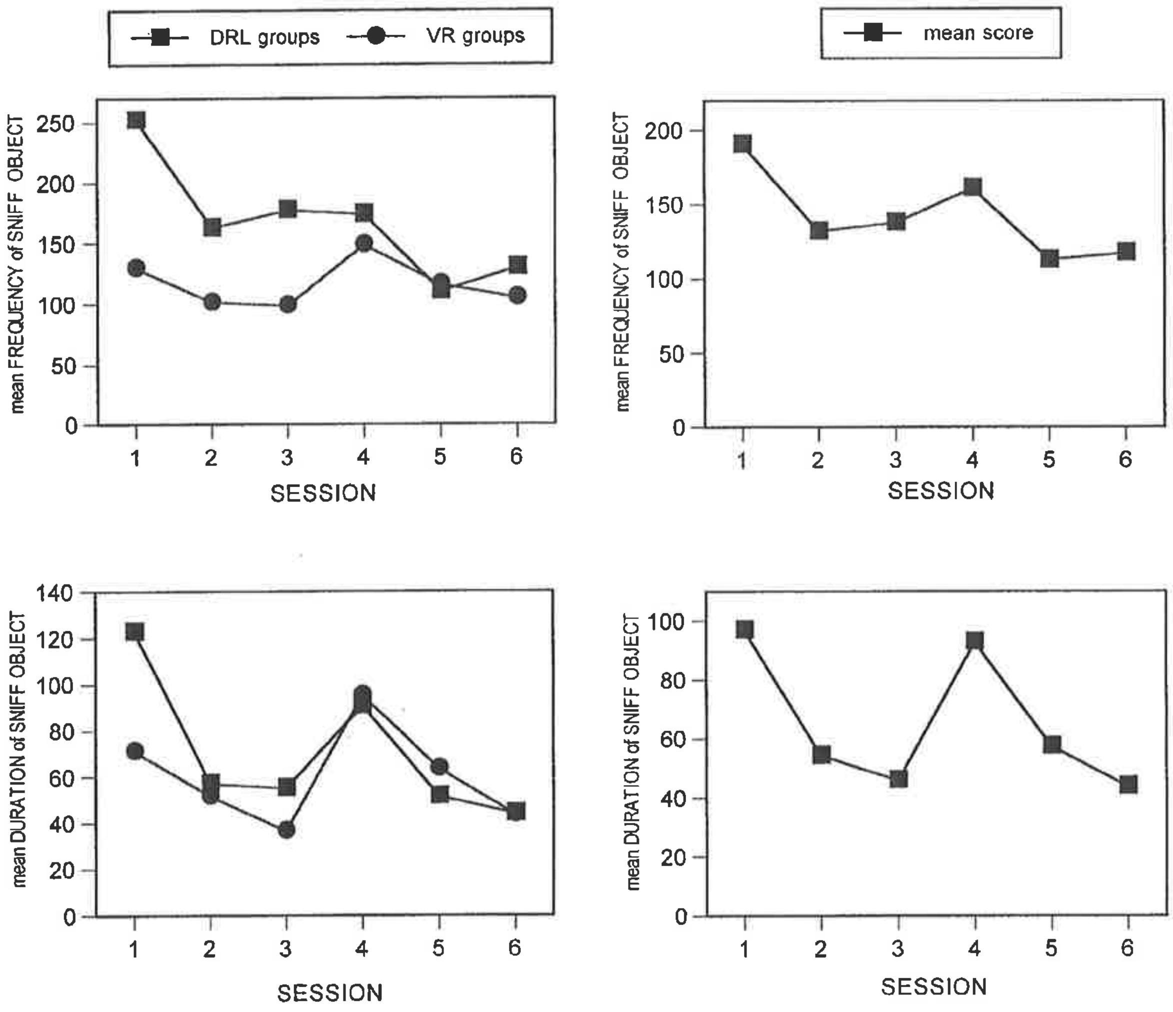


Figure 7.13 (V). Mean frequency (top) and duration (bottom) of ***sniff object*** scores were jointly affected by the "schedule" (left) and "session" (right) grouping variables over the six sessions

Visual inspection of Figure 7.13 (V) shows that the frequency and duration of ***sniff object*** decreased noticeably over ***schedule*** sessions, increased in the first ***extinction*** session and then decreased just as noticeably over the remaining sessions. The frequency and duration scores were higher in the first three sessions for rats run on the ***DRL*** schedule (much higher for the frequency scores), and the decrease over sessions was more marked. The frequency of ***sniff object*** scores tended to be higher during the ***extinction*** sessions for rats previously run on the ***DRL*** schedule, whereas the duration scores tended to be lower.

Object x schedule interaction effect

A statistically significant ***object*** x ***schedule*** interaction was found for the frequency of ***sniff and touch object*** [*F* (1,12)=5.51, *p*<.05] and the duration of ***sniff object*** [*F* (1,12)=5.81, *p*<.05]. Thus, these two measures were *jointly* affected by the object (*i.e.*, objects first present during ***schedule*** or ***extinction*** sessions) and schedule (***DRL*** or ***variable-ratio***) grouping variables over the six sessions.

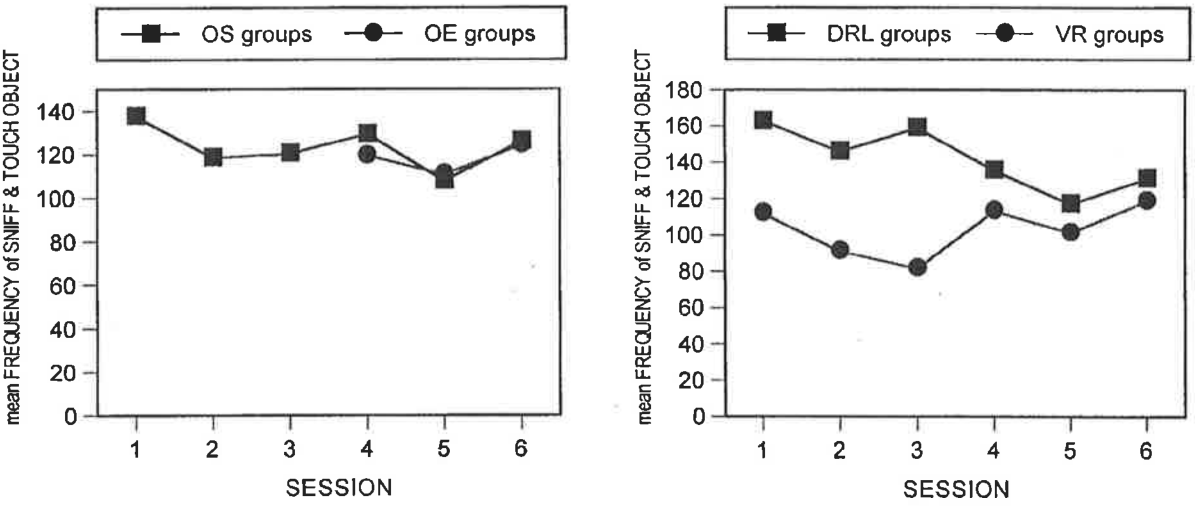


Figure 7.13 (VI). Mean frequency of ***sniff and touch object*** was jointly affected by the "object" (left) and "schedule" (right) grouping variables over the six sessions

If objects were present during ***schedule*** sessions ("OS" groups), the frequency of ***sniff and touch object*** scores demonstrated an overall decrease across the first three sessions (Figure 7.13: VI). The scores, however, were markedly higher in each of those sessions for rats run on the ***DRL*** schedule (DRLOS group). During ***extinction*** there was a slight overall increase in this measure for the "OS" groups and for rats previously run on the ***variable-ratio*** schedule. By contrast, there was slight overall decrease in frequency of ***sniff and touch object*** for the "OE" groups and for rats previously run on the ***DRL*** schedule. For rats previously run on the ***DRL*** schedule, the mean scores for this measure were higher in every ***extinction*** session.

As shown in Figure 7.13 (VII), if objects were present during ***schedule*** sessions ("OS" groups), the duration of ***sniff object*** decreased steadily over the first three sessions. The scores were higher in each of those sessions if rats were run on the ***DRL*** schedule, and the decrease over sessions was more marked for these rats. The frequency of ***sniff object*** scores also tended to be higher during the ***extinction*** sessions for rats previously run on the ***DRL*** schedule. For the "OS" groups, the decrease in this measure over ***extinction*** was steady, whereas the decline was sharp for the "OE" groups. If objects were first encountered during ***extinction*** ("OE" groups), the duration of ***sniff object*** was much higher (more than double) in the first ***extinction*** session, but almost identical by the last session (a sharp decline over extinction for the "OE" groups).

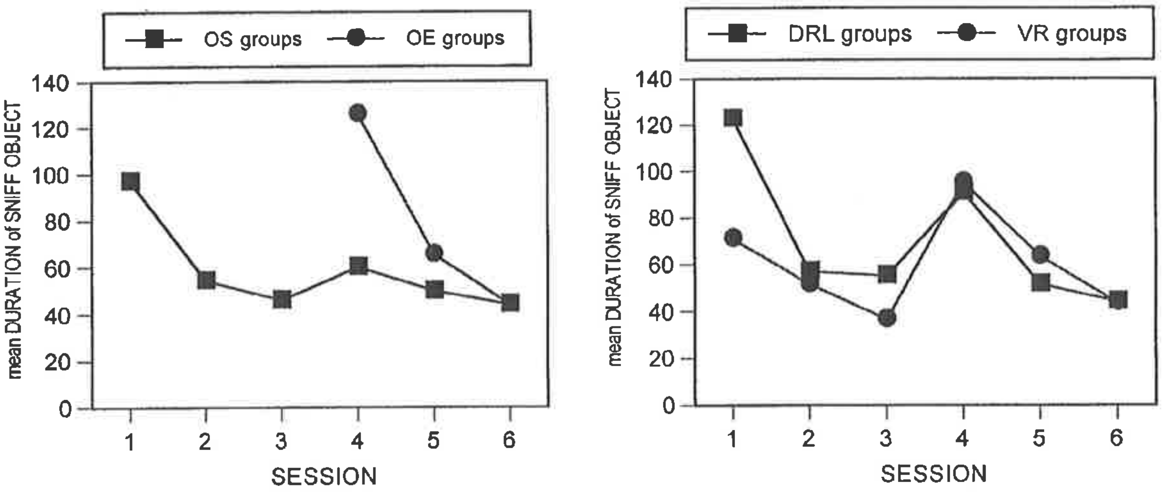


Figure 7.13 (VII). Mean duration of ***sniff object*** was jointly affected by the "object" (left) and "schedule" (right) grouping variables over the six sessions

Object x schedule x session **interaction effect**

As can be seen in Table 7.19, a statistically significant ***object*** x ***schedule*** x ***session*** interaction was found for measures of six behavioural categories. These frequency and duration measures were affected by all three grouping variables over the six sessions.

Table 7.19
Experiment 2 significance levels obtained for measures of behavioural categories during all six sessions (***object*** **x** ***schedule*** **x** ***session*** interaction).

Variable	***F*(5,60)**	**Significance level (*p*)**
Frequency of ***pica***	2.49	<.05
Frequency of ***digging/burying***	3.22	<.05
Duration of ***digging/burying***	2.59	<.05
Duration of ***displacement***	2.71	<.05
Frequency of ***rearing***	2.42	<.05
Frequency of ***sniff object***	6.79	<.001
Duration of ***bar-related behaviour***	3.66	<.01

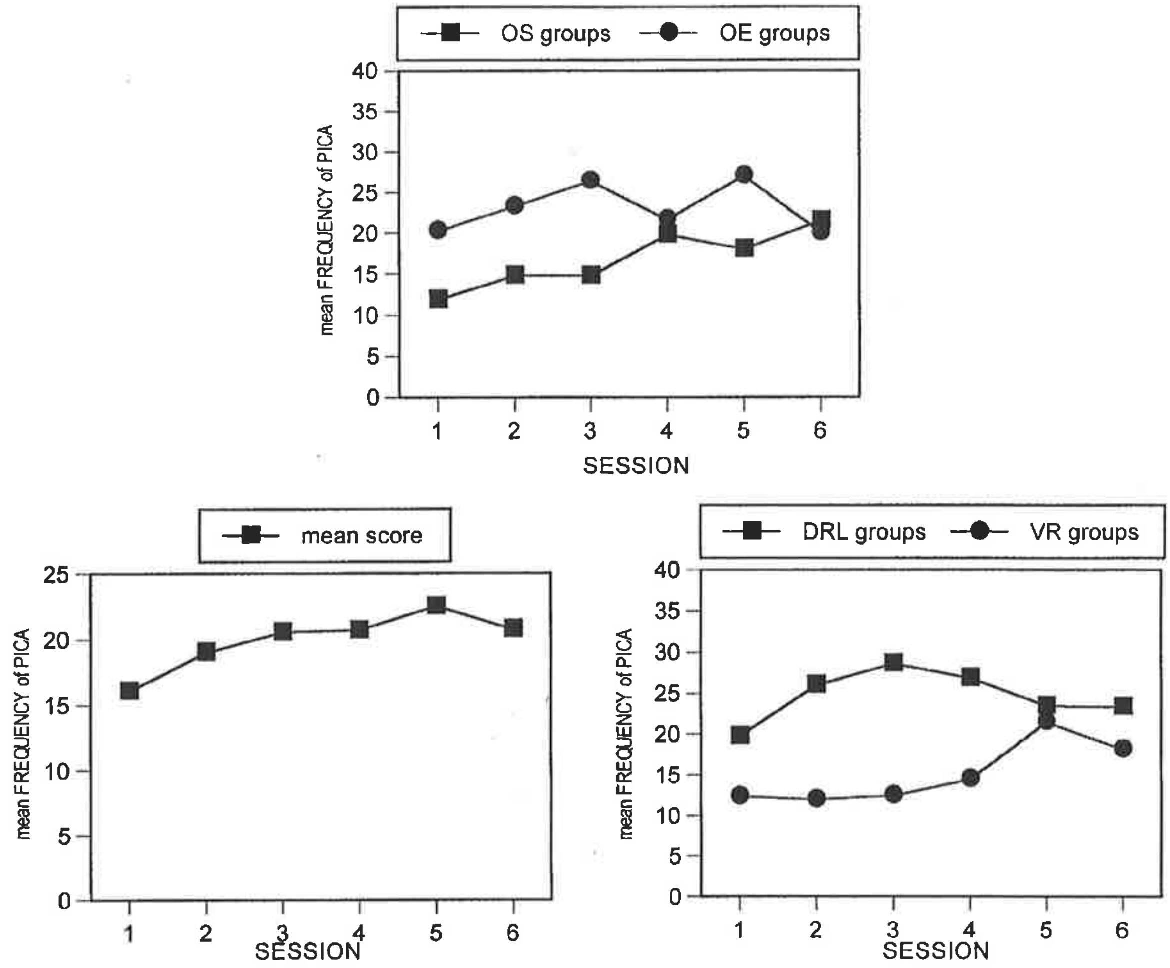


Figure 7.13 (VIII). Mean frequency of ***pica*** was affected by all three grouping variables over the six sessions (top- "object" grouping variable, bottom left- "session" grouping variable, & bottom right- "schedule" grouping variable)

The frequency of ***pica*** increased gradually over ***schedule*** sessions, remained stable during the first ***extinction*** session and then showed a slight overall increase over the remaining sessions (Figure 7.13: VIII). The scores were higher in every session for the ***DRL*** groups, as well as the "OE" groups (except in the last session). In the first ***extinction*** session, the scores increased for the "OS" groups, as well as for rats previously run on the ***variable-ratio*** schedule. Similarly, there was an overall increase in frequency of ***pica*** across ***extinction*** for these same groups. The opposite effects were observed for the "OE" groups and ***DRL*** groups.

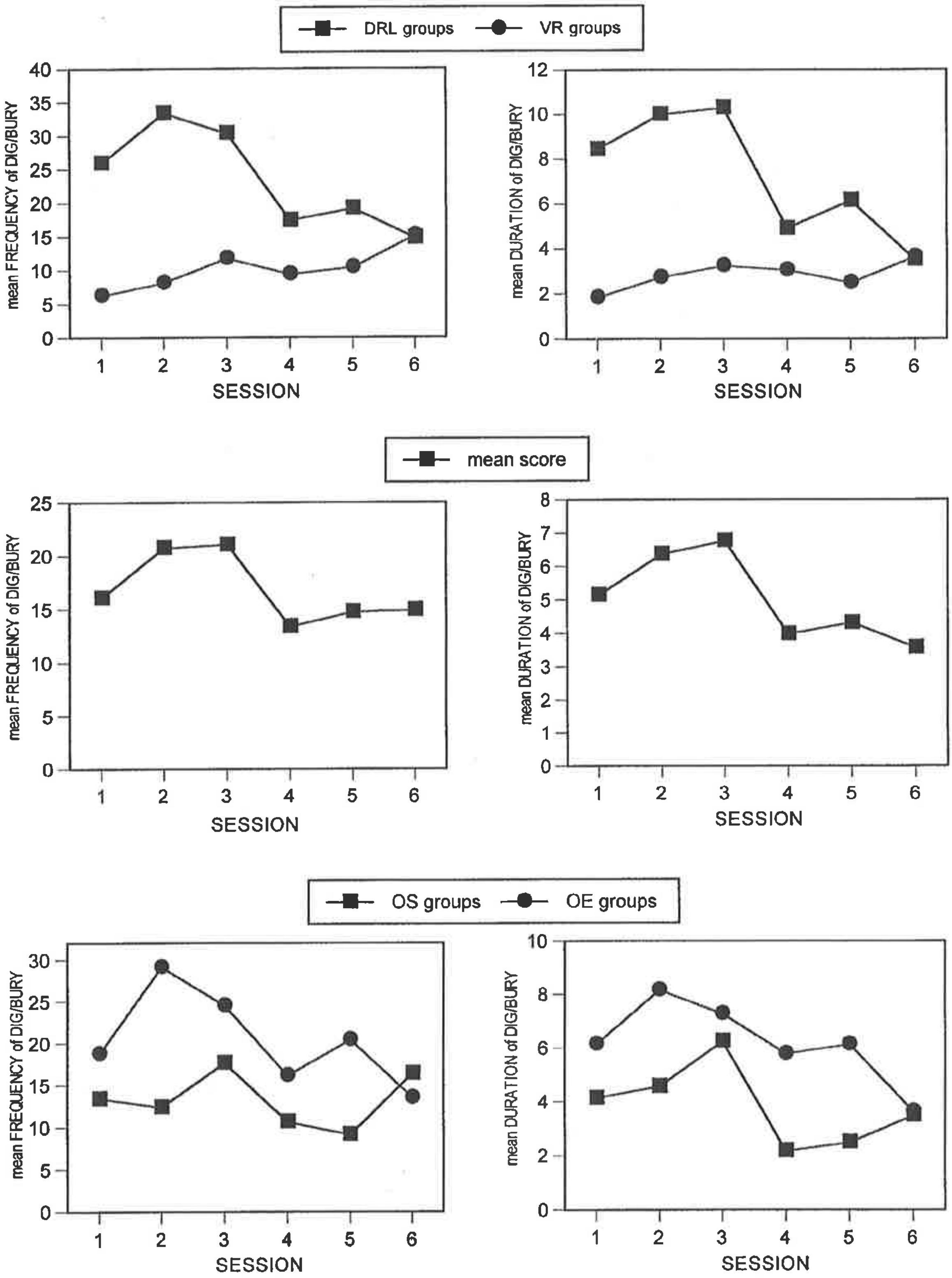


Figure 7.13 (IX). Mean frequency (left) and duration (right) of ***digging/burying*** scores were affected by all three grouping variables over the six sessions (top- "schedule" grouping variable, middle- "session" grouping variable, & bottom- "object" grouping variable)

Visual inspection of Figure 7.13 (IX) shows that the frequency and duration of ***digging/burying*** increased slightly over ***schedule*** sessions and decreased in the first ***extinction*** session. Over ***extinction***, there was a slight increase in the frequency measure, whereas the duration measure decreased slightly. The mean scores for both measures were higher in every session for rats in the ***DRL*** groups (although the scores were almost identical in the last session). If objects were first encountered during ***extinction*** ("OE" groups), the mean frequency and duration scores of ***digging/burying*** were also higher in every session (except the last session). Over ***extinction***, the scores only increased for rats previously run on the ***variable-ratio*** schedule or "OS" groups.

The duration of ***displacement*** showed an overall increase across ***schedule*** sessions, remained virtually unchanged in the first ***extinction*** session, before increasing steadily over ***extinction*** (Figure 7.13: X). During ***schedule*** sessions, a noticeable peak in scores was observed, if objects were present ("OS" groups) or rats were run on the ***DRL*** schedule. During ***extinction***, the scores tended to be higher in the groups that first encountered objects during ***schedule*** sessions ("OS" groups), and in rats previously run on the ***DRL*** schedule.

As shown in Figure 7.13 (X), the frequency of ***rearing*** decreased gradually over the first three sessions, declined noticeably in the first ***extinction*** session, and then continued to decrease slightly over the remaining sessions. If objects were absent during ***schedule*** sessions ("OE" groups), the scores were markedly higher during those sessions, and there was a sharp decrease in frequency of ***rearing*** in the first ***extinction*** session. For the "OS" groups, there was relatively little change over the six sessions. The scores were lower in every session for the ***variable-ratio*** groups. A marked decrease in the first ***extinction*** session took place in the groups previously run on the ***DRL*** schedule.

If objects were present during ***schedule*** sessions ("OS" groups), the frequency of ***sniff object*** decreased noticeably in session 2 and then increased slightly in the third session (Figure 7.13: XI). The scores were much higher in every session for rats run on the ***DRL*** schedule (DRLOS group). There was an increase in scores in the first ***extinction*** session, although the "OS" groups and ***DRL*** groups actually showed little change. The noticeable decline in session 5 was most pronounced in the "OE" groups and ***DRL*** groups. The overall decrease across ***extinction*** was observed in all groups, although the lowest score in every session occurred in the "OS" groups and ***variable-ratio*** groups (except session 5).

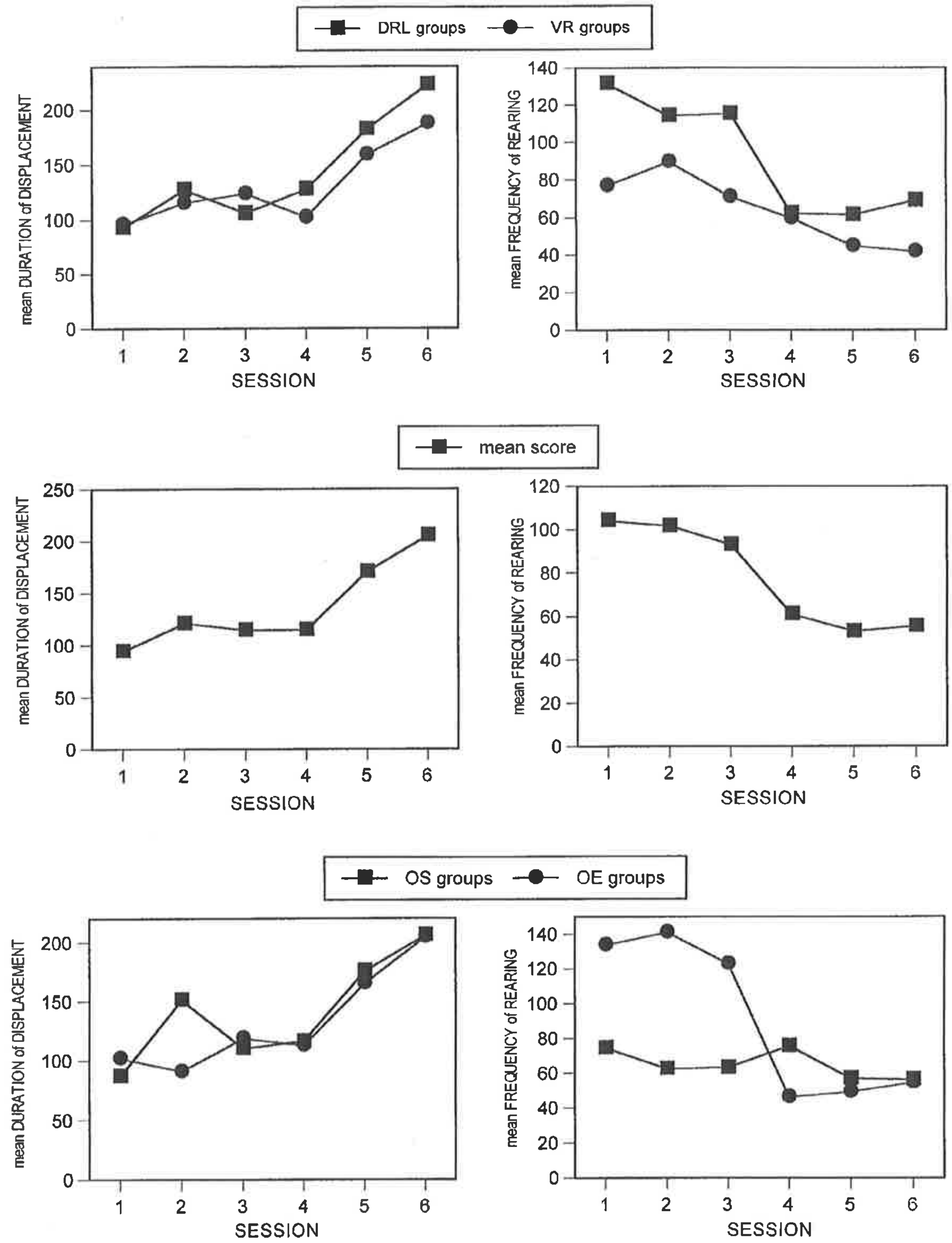


Figure 7.13 (X). Mean duration of ***displacement*** (left) and frequency of ***rearing*** (right) scores were affected by all three grouping variables over the six sessions (top- "schedule" grouping variable, middle- "session" grouping variable, & bottom- "object" grouping variable)

Figure 7.13 (XI) illustrates that the duration of ***bar-related behaviour*** decreased over ***schedule*** sessions, decreased in the first ***extinction*** session, and then increased slightly over the remaining sessions. This pattern was reversed for the ***DRL*** groups. The mean scores were much lower in every session for rats in the ***DRL*** groups. During the ***schedule*** sessions, the duration of ***bar-***

related behaviour scores were much lower if objects were present ("OS" groups), but almost identical to the "OE" group scores during ***extinction*** (when objects were present in all groups).

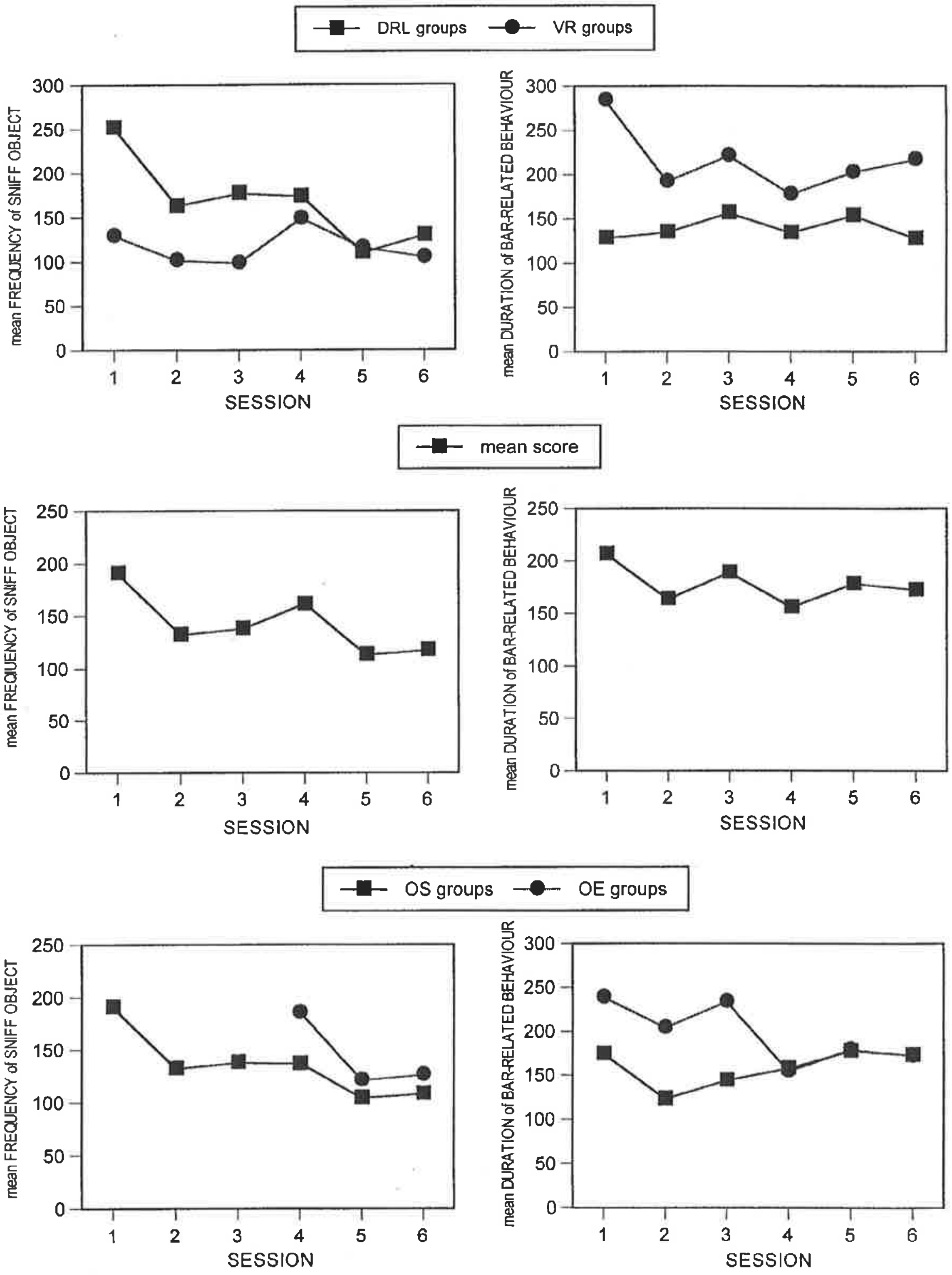


Figure 7.13 (XI). Mean frequency of ***sniff object*** (left) and duration of ***bar-related behaviour*** (right) scores were affected by all three grouping variables over the six sessions (top- "schedule" grouping variable, middle- "session" grouping variable, & bottom- "object" grouping variable)

7.3.7.4 INDEPENDENT JUDGING

As with Experiment 1, the reliability of the experimenter's behavioural measurements and the behavioural criteria were tested via independent judging of an animal chosen at random. Again, two statistical procedures were followed in order to analyse the data obtained from the three independent judges. The first statistical procedure involved the construction of two inter-correlation matrices: one for frequency of behavioural events, and another for the duration of these events. The inter-correlation matrices were used to determine the degree of correlation between the three independent judges and the experimenter.

The probability values pertaining to the frequency of behavioural events were statistically significant for all judges:

	JUDGE 4 (Experimenter)	
JUDGE 1	$r=.782$	$p<.05$
JUDGE 2	$r=.821$	$P<.01$
JUDGE 3	$r=.937$	$p<.001$

The probability values for the duration measures were also statistically significant for all judges:

	JUDGE 4 (Experimenter)	
JUDGE 1	$r=.713$	$p<.05$
JUDGE 2	$r=.765$	$p<.05$
JUDGE 3	$r=.924$	$p<.01$

The second stage of statistical analysis involved the application of Kendall's W coefficient of concordance to the data. This program measured the agreement amongst the judges. A high degree of agreement was found to exist between the judges for the frequency and duration measures of all behavioural categories:

$W=.853$ $p<.001$.

7.4 DISCUSSION FOR EXPERIMENT 2

7.4.1 THE PRESENCE OF EXPLORATORY AND OTHER BEHAVIOURS DURING THE POST-REINFORCEMENT PAUSES

7.4.1.1 HYPOTHESIS SEVEN: PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF DRL15-s AND VR30 SCHEDULES

Hypothesis seven predicted that a larger proportion of each of the scored behaviours would occur during the PRPs for rats run on the ***DRL*** schedule, when compared with the ***variable-ratio*** counterpart, since ***variable-ratio*** schedules are characterised by the absence of PRPs. ***Hypothesis 7 was supported.*** The percentage of total mean frequency and duration of all the behavioural categories occurring during the PRPs was markedly higher for the ***DRL*** groups.

For the groups with objects present during ***schedule*** sessions (DRLOS & VROS), the percentage of total frequency and duration occurring during the PRPs was much higher in the ***DRL*** group for all categories of behaviour. No ***digging/burying*** and almost negligible amounts of ***pica*** and ***rearing*** (<1%) took place during PRPs for the ***variable-ratio*** group. For the other measures, less than 11% occurred during the PRPs for this same group. By contrast, more than a quarter (and up to almost 50%) of each measure took place during the PRPs of the ***DRL*** schedule. ***Jump at lid*** was not observed in either group during these sessions.

For the groups with objects absent during ***schedule*** sessions (DRLOE & VROE), the percentage of total frequency and duration occurring during the PRPs was noticeably higher in the ***DRL*** group for all behavioural categories. No ***pica***, ***digging/burying*** or ***jump at lid*** took place during the PRPs for the ***variable-ratio*** group, and for the other behavioural categories the amounts were almost negligible (<2%). More than 15% (<40%) of each measure occurred during the PRPs on the ***DRL*** schedule.

Thus, as with the ***variable-interval*** schedule in Experiment 1 (Hypothesis 1), the unpredictability of the ***variable-ratio*** schedule appeared to prevent a regular PRP from developing. In fact, if objects were absent (*i.e.*, no distraction or alternative sources of stimulation), a PRP was virtually non-existent. The range of behaviours that were engaged in during PRPs by the ***variable-ratio*** rats was also smaller. The ***DRL*** group rats engaged in ***behaviour directed at the bar and food-trough area***, ***exploratory behaviour directed at the stimulus objects*** (if objects were present), ***exploratory behaviour directed at the peripheral areas of the box***, ***displacement***, ***digging/burying***, ***rearing*** and ***pica***. The ***variable-ratio*** group rats engaged in no (or virtually no)

pica and ***digging/burying*** during the PRPs. Clearly, however, there were no PRPs to speak of for the VROE group.

If a PRP did exist (***DRL*** groups), rats were not passive. They engaged in the full range of behavioural categories possible (except ***jump at lid*** in some cases). If a PRP did not exist (***variable-ratio*** groups), then rats still engaged in all categories of behaviour (see Hypothesis 9), but they occurred outside the PRPs (during other periods of non-instrumental responding throughout the interval).

7.4.1.2 HYPOTHESIS EIGHT: EFFECT OF NOVEL STIMULUS OBJECTS ON PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF DRL15-s AND VR30 SCHEDULES

Some support was found for the prediction that the presence or absence of objects during ***schedule*** sessions would have an effect on the proportion of non object-related behaviours that took place during PRPs.

When objects were absent during ***DRL*** sessions (DRLOE group), the proportions were lower (by up to 17%) for the frequency and duration of ***rearing***, ***propping*** and ***bar-related behaviour*** and the duration of ***digging/burying*** (when compared to the DRLOS group). For this same group, the proportion was higher (by about 6.5%) for the duration of ***pica***. The proportions were very similar (<5% difference) irrespective of presence or absence of objects for the frequency of ***pica***, ***digging/burying***, ***displacement*** and the duration of ***displacement***. Thus, some behavioural measures during PRPs of ***DRL*** sessions were clearly not influenced by whether objects were present or not. ***Jump at lid*** only took place if objects were absent.

When objects were absent during ***variable-ratio*** sessions (VROE group), the proportions were slightly lower (than for the VROS group) for the frequency and duration of ***displacement*** (<5% difference) and ***bar-related behaviour*** (<7% difference). The proportions were very similar (<1.5% difference) irrespective of presence or absence of objects for the frequency and duration of ***pica***, ***rearing*** and ***propping*** (all measures were lower for the VROE group). Again, some behavioural measures during PRPs of ***variable-ratio*** sessions were not influenced by whether objects were present or not. With respect to ***digging/burying***, no instances occurred during the PRPs for either group. ***Jump at lid*** was only observed if objects were absent during schedule sessions, and all instances occurred outside the PRPs.

7.4.2 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE DURING THE PRPs, OVER SESSIONS, AND BETWEEN GROUPS

As with Experiment 1, the graphs were examined purely for descriptive purposes. A number of differences over sessions were not statistically significant (discussed in the next section). Nonetheless, descriptive examination of the graphs may indicate tendencies to change, which would perhaps become statistically significant if larger sample sizes were employed.

Visual inspection of Figures 7.1 - 7.4 (II) shows that the frequency and duration of all non object-directed behaviours were consistently lowest for the ***variable-ratio*** groups. That is, either no instances or only a few of these behaviours were observed during the PRPs. For the ***object-directed behaviours*** (Figure 7.2), the highest frequency and duration measures during the PRPs were found for the DRLOS group.

As expected, the frequency and duration of the three ***object-directed behaviours*** during PRPs decreased (albeit slightly) over the three sessions for the VROS group. However, for the DRLOS group, only the measures of ***sniff object*** decreased over the three sessions. For the other categories of behaviour, the patterns of change varied across the three sessions.

7.4.3 CHANGES IN BEHAVIOURS DURING PRPs OVER SCHEDULE SESSIONS, BETWEEN SCHEDULES AND BETWEEN OBJECT CONDITIONS

The behavioural categories of ***jump at lid*** and ***chew/bite object*** were not included in the statistical analysis, since these behaviours occurred too infrequently in the four groups. The remaining behaviours included in the statistical analysis were: ***bar-related behaviour***, ***sniff object***, ***sniff and touch object***, ***propping***, ***displacement***, ***digging/burying***, ***pica*** and ***rearing***.

(a) Changes over schedule sessions

Over the three ***schedule*** sessions only the duration of ***sniff object*** showed a statistically significant difference. The time spent ***sniffing objects*** during PRPs decreased over sessions. Thus, over time a greater proportion of this measure took place outside the PRPs (during other times of non-operant responding). Perhaps as a result of habituation, the objects were less likely to attract the rats' attention immediately after pellet consumption. Two measures yielded statistically significant ***object by session*** interactions (discussed subsequently).

(b) Differences between schedules

The differences between the ***DRL*** and ***variable-ratio*** schedules were statistically significant for the frequency and duration measures of all behavioural categories. Thus, the schedule that rats were run on affected the frequency and duration of behaviours during the PRPs. Rats run on the ***variable-ratio*** schedule engaged in less ***sniff object***, ***sniff and touch object***, ***propping***, ***displacement***, ***digging/burying***, ***rearing***, ***bar-related behaviour*** and ***pica*** during the PRPs (frequency & duration measures). These findings indicate that all the behaviours were less likely to take place during PRPs on ***variable-ratio*** schedules. This is to be expected, since the "unpredictable" ***variable-ratio*** schedule is characterised by the lack of PRPs, and behaviours occur at other periods of non-instrumental responding.

(c) Differences between object conditions

No measure of behaviour showed statistically significant differences between the object conditions (although there were a couple of ***object by session*** interactions, which will be discussed next). Thus, the presence or absence of stimulus objects alone had no apparent effect upon the frequency or duration of behaviours occurring during the PRPs.

(d) Interaction effects

Object by session interaction effect

An ***object by session*** effect was found for the frequency of ***displacement*** and the duration of ***bar-related behaviour***, indicating that both the object (present or absent) and the session conditions affected these two measures. There was a noticeable increase in frequency of ***displacement*** in the second sessions if objects were present, and there was also a noticeable change in the second session for most groups. As rats began to habituate to the objects, there may have been an increase in conflict, with respect to which areas of the box to explore next. Although there appeared to be little change in the duration of ***bar-related behaviour*** over sessions, this measure decreased for the groups with objects present, whereas the scores increased if objects were absent. That is, the presence of objects to explore as potential sources of food or stimulation, resulted in less time spent around the bar and food-trough area.

7.4.4 THE MOST FREQUENTLY OCCURRING BEHAVIOURS, AND ONES OF LONGEST DURATION IN SCHEDULE AND EXTINCTION SESSIONS

7.4.4.1 HYPOTHESIS NINE: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING DRL15-s AND VR30 SCHEDULES

Hypothesis nine predicted that higher frequency and duration scores of non-object behaviours would be observed in the DRLOE and VROE groups during schedule sessions (when compared to the DRLOS & VROS groups respectively). The absence of objects during these sessions allowed more time and effort to be devoted to other behaviours.

As expected, the measures of non object-directed behaviours (frequency & duration) were markedly higher in the DRLOE group than the DRLOS group during ***DRL*** sessions. The only exception was ***displacement***, which was higher in the group with objects present (DRLOS group). ***Jump at lid*** occurred a few times if objects were absent (but not at all in the DRLOS group). The frequency and duration of non object-directed behaviours were also markedly higher in the VROE group than the VROS group during ***variable-ratio*** sessions, especially frequency and duration of ***pica***, ***rearing***, ***propping*** and ***bar-related behaviour***, and frequency of ***displacement***. ***Jump at lid*** occurred a few times if objects were absent (but not at all in the VROS group).

Hypothesis nine also predicted that the frequency and duration of ***bar pressing*** would be higher in the DRLOE and VROE groups (compared to the DRLOS & VROS groups, respectively), since the absence of objects (a "distraction" or source of alternative stimulation) allowed the schedule to exert maximal control. Certainly, this was the finding for the ***DRL*** groups. However, for rats run on the ***variable-ratio*** schedule, the frequency and duration of ***bar pressing*** was much higher (>50%) in the group with objects present (VROS). That is, the presence of objects actually increased the bouts of ***bar pressing*** and the time spent engaged in this operant behaviour.

7.4.4.2 HYPOTHESIS TEN: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

Hypothesis ten predicted that more ***exploratory behaviour directed towards the stimulus objects*** would be observed in the DRLOE group during ***extinction***, since it was this group's first encounter with stimulus objects (compared to the DRLOS group). Whilst this was the case for the frequency and duration of ***sniff object***, the ***sniff and touch object*** and ***chew/bite object*** measures were actually lower (especially the latter). Prior exposure to objects increased ***exploratory manipulatory responses*** (i.e. ***sniffing & touching & chewing/biting***), but decreased responses that involved ***inspection***. That is, the topography of the response during ***extinction*** was affected by prior exposure to objects during ***DRL*** schedule running.

With respect to the other behaviours, the frequency of ***rearing*** and ***displacement*** and both measures of ***bar pressing*** were similar in the two ***DRL*** groups during ***extinction***. The frequency and duration of ***digging/burying***, ***propping*** and ***bar-related behaviour***, and duration of ***pica*** and

displacement were higher in the DRLOE group, whereas the frequency of ***pica*** and duration of ***rearing*** were lower. ***Jump at lid*** did not occur in the DRLOE group, and only a few times in the DRLOS group (the reverse of ***DRL*** sessions).

Hypothesis ten also predicted that less ***exploratory behaviour*** would be directed towards objects in the VROE group during ***extinction***, since this group was more likely to be under "control" of the previous schedule (with its high ***resistance to extinction***), despite it being this group's first encounter with stimulus objects. Whilst the frequency of ***sniff object*** was indeed lower, the duration was markedly higher in the VROE group. The frequency and duration of ***sniff and touch object*** were higher, whilst the frequency and duration of ***chew/bite object*** were markedly lower in the VROE group. That is, if objects were first encountered during ***extinction***, rats engaged in fewer bouts of ***object inspection*** (but of a longer duration) and ***chewing/biting of the objects***, but engaged in more bouts (of a longer duration) of ***sniffing and touching***. As with the ***DRL*** groups, the topography of the response observed in the ***variable-ratio*** groups during ***extinction*** was affected by prior exposure to objects during schedule running.

With respect to the other behaviours, the frequency and duration of ***pica***, ***digging/burying***, ***propping***, and frequency of ***displacement*** were higher in the VROE group during ***extinction***, whereas the frequency and duration of ***rearing***, ***bar-related behaviour***, ***jump at lid*** and ***bar pressing*** and duration of ***displacement*** were lower. Frequency and duration of ***bar pressing*** was far lower (>60%) in the VROE group during ***extinction***. Thus, rats that had no prior exposure to objects, engaged in far less ***bar pressing*** once objects were present during ***extinction***. Objects with maximal novelty appeared to facilitate the ***extinction*** of the operant response (after being run on a schedule known to have a high ***resistance to extinction***), presumably by providing potential sources of food or stimulation when the food source became depleted.

7.4.4.3 HYPOTHESIS ELEVEN: FREQUENCY AND DURATION OF BEHAVIOURS DURING DRL15-s AND VR30 SCHEDULES

Hypothesis eleven predicted that the frequency and duration of ***bar pressing*** would be lower for the ***DRL*** groups, since the ***DRL*** schedule typically evokes low rates of instrumental responding. This was indeed found to be the case. Hypothesis eleven also predicted that the frequency and duration scores of all other behaviours would be higher for the DRL groups, since more time was available to engage in other behaviours. As expected, the frequency and duration of ***digging/burying*** and ***rearing*** were higher for both ***DRL*** groups.

If objects were present (DRLOS & VROS groups), all frequency measures as well as the duration of ***propping***, ***displacement*** and the three ***object-directed behaviours*** of behaviour were higher for rats run on the ***DRL*** schedule. The more predictable ***DRL*** schedule, which also encouraged non-instrumental behaviours, since it required low rates of ***bar pressing***, did indeed result in higher frequencies of every behavioural category. This schedule also resulted in more time spent engaged in all forms of ***object exploration***, as well as ***escape-directed propping***. That is, the ***DRL*** schedule resulted in more time spent engaged in attempted ***exploration beyond the box***, and ***exploration of objects*** within the box. Clearly, however, this schedule also resulted in more ***conflict***, as shown by the higher levels of ***displacement*** activities. This is perhaps not surprising, since the whole period between reinforcers might be considered aversive, since all operant responding must be suppressed. ***Jump at lid*** was not observed if objects were present during ***schedule*** sessions, irrespective of type of schedule. Thus, the presence of objects to explore appears to suppress this behaviour, which may be an ***escape-directed behaviour*** or a form of stimulation.

Clearly, the presence or absence of objects (and not just predictability of the schedule) had an effect on some categories of behaviour. If objects were absent (DRLOE & VROE), the frequency of all behaviours apart from ***displacement*** and ***bar-related behaviour*** were higher for rats run on the ***DRL*** schedule. However, only the duration of ***pica*** and ***jump at lid*** were higher for the DRLOE group. Thus, if there were no objects to explore, then rats on the ***DRL*** schedule, with its requirement of non-operant responding, engaged in more bouts of behaviour centred at the food source and ***displacement*** activities, but these bouts were of a shorter duration. Rats run on the ***variable-ratio*** schedule spent more time engaged in these two behaviours (but few bouts). In the absence of objects, the ***DRL*** rats spent more time engaged in the ***jump at lid*** category (***escape-directed*** or a stimulatory behaviour), and in ***pica***, or eating an alternative source of food.

7.4.4.4 HYPOTHESIS TWELVE: FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION

Hypothesis twelve predicted that the frequency and duration of ***bar pressing*** for the ***DRL*** groups would be lower during ***extinction***, since ***DRL*** rats should more readily discriminate between ***extinction*** and the previous ***DRL*** schedule. As expected, the ***DRL*** measures of ***bar pressing*** were much lower. Thus, even the more naturalistic experimental chamber with objects to explore did not appear to affect the pattern of operant responding during ***extinction***. Therefore, the ***discrimination hypothesis*** (Church, 1963) was still applicable in this case, in the open-field style Skinner box. ***Resistance to extinction*** was, as expected, higher for rats previously run on the unpredictable ***variable-ratio*** schedule.

Hypothesis twelve also predicted that the ***DRL*** groups would demonstrate higher frequency and duration of behaviours other than ***bar-pressing***, since these rats should more readily discriminate between the previous ***DRL*** schedule and the new ***extinction*** sessions (thus allowing more time for other activities). The frequency scores of most of the behavioural categories were indeed higher for the ***DRL*** groups, but a number of the duration scores were lower. The frequency and duration scores of ***jump at lid*** were almost negligible in all groups (although slightly higher in the ***variable-ratio*** groups).

If objects were first encountered during ***schedule*** sessions (DRLOS & VROS groups), the frequency and duration of ***bar-related behaviour*** scores were lower for rats previously run on the ***DRL*** schedule. That is, the DRLOS rats spent less time (& bouts) around the now depleted food source, since ***extinction*** was more readily discriminated after the previous predictable ***DRL*** schedule.

If objects were first encountered during ***extinction*** sessions (DRLOE & VROE groups), the frequency scores of ***pica*** and ***chew/bite object*** were marginally lower and the duration of ***pica***, ***bar-related behaviour***, and all three ***object-directed behaviours*** were lower for rats previously run on the ***DRL*** schedule. Thus the DRLOE rats engaged in slightly fewer bouts of alternative feeding (***pica***) and also spent less time engaged in this activity. These rats also spent less time around the bar and food-trough area (***bar-related behaviour***) once the food source was depleted, since they more readily discriminated between the new ***extinction*** sessions and previous ***DRL*** conditions.

When objects were first encountered during ***extinction***, rats previously run on the ***DRL*** schedule engaged in more bouts of ***sniff object*** and ***sniff and touch object***, but devoted less time to these activities than the rats previously run on the ***variable-ratio*** schedule. There were also fewer bouts (but of longer duration) of ***aggression*** directed towards the objects (***chew/bite objects***) for the DRLOE rats. Thus, although there was a lower ***resistance to extinction*** for the DRLOE rats, and there were objects to explore, these rats did not spend more time exploring the objects. This seems somewhat counter-intuitive. However, the DRLOE rats did spend more time in ***aggressive behaviour*** directed towards the objects. Therefore, the topography of the exploratory responses must be taken into account.

7.4.5 PERCENTAGE OF TOTAL SESSION TIME SPENT ENGAGED IN EACH BEHAVIOURAL CATEGORY, OVER SESSIONS, AND BETWEEN GROUPS

(a) The schedule sessions

Not scored category

All groups spent more than 29% of ***schedule*** session time (<51%) engaged in behaviours that were ***not scored***. As with Experiment 1, it was not possible to score every category of behaviour, but most of the ***not scored*** category was ***general ambulatory behaviour***. The presence of objects resulted in lower amounts of the ***not scored*** category during both ***DRL*** and ***variable-ratio*** schedules. That is, ***general ambulatory activity*** was higher if there were no objects to explore. Instead of spending time investigating objects, the rats moved around the box, particularly if run on the predictable ***DRL*** schedule. This schedule was characterised by predictable periods of non-reinforcement and encouraged activities other than ***bar pressing*** (since it required low rates of operant responding). There was a slight between-session increase in the ***not scored*** category for all but the DRLOS group. Thus, for most of the groups, ***general ambulatory activity*** did not appear to decrease over sessions as a result of habituation to the experimental chamber (unlike the findings of Experiment 1).

Behaviours directed at the bar and food-trough area

The ***DRL*** groups spent less than 15% of time engaged in ***behaviours directed at the bar and food-trough area***, whilst the ***variable-ratio*** groups engaged in these behaviours for more than 15% of time (but <25%). Thus, the ***variable-ratio*** schedule evoked higher amounts of behaviours centered at the food source. Therefore, if reinforcement was very unpredictable (or the food source), more activity occurred around the food source, since the very next ***bar press*** might be rewarded. Not surprisingly, the ***DRL*** rats on the schedule that required low rates of operant responding spent noticeably less time around the food source. There was no clear pattern between sessions, and no clear effect of presence or absence of objects on time spent engaged in ***behaviours directed at the bar and food-trough area***.

Behaviours directed at the stimulus objects

During ***schedule*** sessions, the DRLOS and VROS groups spent more than 26% (<31%) and 22% (<28%), respectively, of total session time engaged in ***object-directed behaviours***. (The ***chew/bite object*** category took up less than 2% of total session time). In every session, the rats run on the ***DRL*** schedule spent more time ***exploring the objects***. Thus, the schedule that required low levels of operant responding resulted in higher levels of ***object exploration***. These objects provided possible alternative sources of food or stimulation. As with Experiment 1, a between-session decrease in time spent ***exploring objects*** was observed for both schedule types, reflecting a habituation effect. Very little time was spent in ***aggressive behaviour*** directed at the stimulus objects (***chew/bite object***).

Behaviours directed at the peripheral areas of the box

Less than 15% of total session time was spent engaged in ***behaviour directed at the peripheral areas of the box*** if objects were present during schedule sessions, and a between-session decrease was observed. More time was spent in these activities during the ***DRL*** sessions. If objects were absent, more than 15% of time (<20%) was spent engaged in these behaviours, and a between-session decrease was also observed. More time was spent in ***behaviour directed at the peripheral areas of the box*** during the ***DRL*** sessions. Since the ***jump at lid*** category took up <1% of total session time in all cases, most of the ***behaviour directed at the peripheral areas of the box*** was in the form of ***propping***. As in Experiment 1, the presence or absence of objects affected this category of behaviour. Rats spent more time engaged in ***escape-directed behaviours*** if there were no objects to ***explore***.

Other behavioural categories

If objects were absent, less than 13% of total session time (>7%) was spent ***rearing***, whereas for groups with objects present less than 8% of time was spent engaged in this behaviour (<5.5% for the VROS group). Again, as in Experiment 1, the presence of objects reduced the amount of time spent ***rearing***. Without objects to explore, the rats spent more time inspecting their immediate well-lit surroundings (which provided no shelter or hiding places) for predators or conspecifics. Unlike Experiment 1, there was an effect of object. If objects were present, there was an overall between-session increase in ***rearing***. As the rats became habituated to the objects, they began to ***visually inspect*** their surroundings more. Once explored, the objects provided no suitable shelter or alternative food, and the rats began to spend more time looking out for potential predators or competitors for food. If objects were absent, rats spent slightly less time over sessions visually inspecting their environment, which may reflect habituation to the experimental box and conditions, which provided no apparent threat.

All groups spent less than 10% of time engaged in ***displacement*** (a slight between-session increase for all groups) and ***pica*** (a between-session increase in all but the VROS group), and less than 1% engaged in ***digging/burying***. None of these behaviours appeared to be ***schedule-induced***. However, if objects were absent, the levels of ***pica*** were approaching the 10% of total session time point in the latter sessions. Given more sessions (***DRL*** or ***variable-ratio***), these hungry rats may have devoted higher amounts of time to eating inappropriate food (***pica***), thereby developing an "eating disorder". The conflict-related ***displacement*** activities were not excessive (although in one session they approached the 10% mark for the DRLOS group). ***Digging/burying***, which may have incorporated a variety of behaviours (***escape-directed behaviour***, ***foraging***, or flurries of ***sawdust pushing***), took up very little time in all groups.

(b) The extinction sessions

Not scored category

More than 15% (<33%) of ***extinction*** session time was spent engaged in behaviours that were ***not scored***. All groups devoted less time to these behaviours during ***extinction***. As in Experiment 1, ***extinction*** appeared to result in less ***general ambulatory behaviour***. The highest percentages in every ***extinction*** session were obtained by the VROS group. Again, in line with the findings oft Experiment 1, prior experience with objects during an "unpredictable" schedule (higher ***resistance to extinction***) resulted in higher levels of this category of behaviour. The lowest percentage in every session was found for the DRLOS group (prior experience with objects on a "predictable" schedule). The amount of total session time devoted to the ***not scored*** category showed a between-session decrease (as in Experiment 1). As rats habituated to the objects, and the ***bar pressing*** response was extinguished, less time was devoted to ***general ambulatory behaviour***.

Behaviour directed at the bar and food-trough area

The ***DRL*** groups spent less than 18.5% of total session time (>10%) engaged in ***behaviour directed at the bar and food-trough area***, whereas the ***variable-ratio*** groups engaged in these behaviours for less than 12.5% of total session time (>6.5%). For all groups there was very little decrease over sessions (& a slight overall increase for the VROE group). If objects were first encountered during ***extinction*** for rats previously run on the ***variable-ratio*** schedule, less time was devoted to activities centered at the depleted food source. Thus, prior exposure to objects that had not provided an alternative food source resulted in more time being spent at the only known food source. No such effect of object was apparent for the ***DRL*** groups. Although the amount of time spent engaged in ***behaviour directed at the bar and food-trough area*** was lower during extinction, the bar pressing response had not yet extinguished by the third extinction session, and rats were still spending time at the depleted food source (the only known food source).

Behaviour directed at the stimulus objects

During ***extinction*** sessions, between 24% and 37% of total session time, was spent engaged in ***object-directed behaviours*** by all groups. Therefore, all groups spent a large proportion of total session time devoted to ***object exploration***. There was a between-session increase in time spent engaged in these behaviours or little change (for the VROE group), indicating that the rats were not habituating to the objects. Depletion of the food source and extinction of ***bar pressing*** resulted in more time spent ***exploring objects***, since they represented a potential source of food or stimulation. The groups that first encountered objects during ***extinction*** (DRLOE & VROE) spent less than 2% of total session time engaged in ***chew/bite object***. That is, most ***exploration*** was in the form of ***sniffing and touching***. By contrast, groups with prior experience of objects (DRLOS & VROS) spent more than 8% of the third ***extinction*** session engaged in ***chew/bite object***. Thus, ***aggressive behaviour*** directed towards objects was higher in groups that had previously encountered objects, and found that they did not provide alternative sources of food.

Behaviours directed at the peripheral areas of the box

The ***DRL*** groups spent less than 19.5% of session time (>13%) engaged in ***behaviours directed at the peripheral areas of the box***, while the ***variable-ratio*** groups spent less than 16% of time (>7.5%) engaged in these behaviours. (The ***jump at lid*** category took up <1% of total session time in all cases). With the exception of the VROS group, rats devoted more time to ***escape-directed behaviours*** (mainly ***propping***) over ***extinction*** sessions. Rats previously run on the "unpredictable" ***variable-ratio*** schedule spent slightly less time engaged in ***behaviours directed at the peripheral areas of the box*** during ***extinction*** than previous schedule sessions. Rats previously run on the "predictable" ***DRL*** schedule spent more ***extinction*** session time (than the VROS & VROE groups) devoted to ***escape-directed behaviours***. Thus, lower ***resistance to extinction*** appeared to result in an increased attempt to leave the box and seek shelter or food. Depletion of the food source increased the "cost" of remaining in the exposed and well-lit environment (Russell, 1983). The levels of ***behaviours directed at the peripheral areas of the box*** (>10%) could be considered ***excessive*** for all but the VROS group.

Other behavioural categories

Prior experience with objects (VROS & DRLOS groups) resulted in a decline in ***rearing*** over ***extinction*** sessions, and little change between ***schedule*** and ***extinction*** sessions. If rats first encountered objects during ***extinction***, on the other hand, time spent ***rearing*** tended to increase over sessions, but the percentages were noticeably lower during ***extinction***. All groups spent less than 7% of total session time engaged in ***rearing***. Therefore, if depletion of the food source coincided with the appearance of objects to explore, then rats which had previously engaged in slightly ***excessive*** amounts of ***visual inspection*** at times (>10% in some sessions) spent their time engaged in other activities. The low levels of ***rearing*** found during ***extinction*** in this study (all groups) are different to the findings of Experiment 1. The current findings suggest that depletion of the food source does not result in increased ***vigilance*** for predators or conspecifics.

Although all groups spent less than 13% of total session time (>5%) engaged in ***displacement***, all groups spent more than 10% of the latter ***extinction*** sessions engaged in this ***conflict-related*** activity (between-session increase). That is, once the food source was depleted, as ***bar pressing*** was extinguished, and as the rats habituated to the objects, the conflict inherent in the situation increased. The rats were unable to leave the well-lit open environment to seek food or shelter. Thus, ***displacement*** activities were potentially ***extinction-induced***, and when ***excessive***, may be akin to the ***over-grooming*** observed in some other captive environments. All groups spent less than 9% engaged in ***pica***, but time spent eating alternative (inappropriate) food tended to increase over sessions, and the VROE group spent >14.5% of one session in ***pica***. Given more sessions, it is possible that this behaviour could develop into an "eating disorder" (a potentially ***extinction-induced*** activity). All groups devoted less than 0.5% of total session time to ***digging/burying***. This behaviour was clearly neither ***extinction-induced*** nor ***schedule-induced*** (& included ***escape-directed digging***, ***digging*** to ***forage*** & flurries of ***sawdust pushing***).

7.4.6 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE OVER SESSIONS, AND BETWEEN GROUPS

In summary, Figures 7.6 - 7.9 (inclusive) show that there was an overall decrease across the six sessions in all groups, for the frequency and duration of ***bar pressing*** and ***rearing*** (except duration in the VROS group), and frequency of ***bar-related behaviour*** and ***propping***. There was an overall increase across the six sessions in all groups for the frequency and duration of ***displacement*** (except frequency for the VROE group) and ***pica*** (except frequency for the DRLOE group & duration for the VROS group).

Across the six sessions, there was an overall decrease in duration of ***bar-related behaviour*** for the VROE and DRLOS groups. There was also an overall decrease in duration of ***propping*** for the VROE and VROS groups, frequency and duration of ***jump at lid*** for the VROE and DRLOE groups, and frequency and duration of ***digging/burying*** for the DRLOS and DRLOE groups. Thus, for some measures, the schedule (***DRL*** or ***variable-ratio***) or object (objects first present during ***schedule*** or ***extinction*** sessions) conditions had an effect on the pattern observed.

For groups with objects first present during ***schedule*** sessions, there was an overall increase across the six sessions in the frequency and duration of ***chew/bite object*** and duration of ***sniff and touch object***, whereas there was an overall decrease in the frequency and duration of ***sniff object***. Frequency of the ***sniff and touch object*** category increased across the six sessions for the VROS group but decreased for the DRLOS group. When objects were first encountered during ***extinction***, there was an overall decrease across sessions for the frequency and duration of ***sniff object***, and an overall increase for the frequency and duration of ***sniff and touch object***. There was a slight overall increase in frequency and duration of ***chew/bite object*** in the VROE group, whereas these scores decreased slightly across ***extinction*** for the DRLOE group.

Again, as mentioned for Experiment 1, these figures are presented as an adjunct to statistical analysis, pointing to general patterns that might exist if larger sample sizes were used.

7.4.7 CHANGES IN BEHAVIOURS OVER SESSIONS, BETWEEN SCHEDULES, AND BETWEEN OBJECT CONDITIONS

The previous section highlighted general patterns or trends apparent in the Figures (visual inspection). This section discusses the statistically significant differences that were found.

7.4.7.1 SCHEDULE SESSIONS

(a) Changes over schedule sessions

Over the three ***schedule*** sessions, only the ***bar pressing*** measures showed statistically significant differences. The frequency and duration of ***bar pressing*** increased over sessions. Although operant performance (***bar pressing***) appeared stable after 14 days of schedule sessions (prior to experimental sessions), these findings suggest that schedule performance may not have been stable yet. However, other factors (*e.g.*, presence of objects) may also have affected ***bar pressing*** over these three sessions. A number of measures showed statistically significant ***object by schedule by session*** interactions and ***object by session*** interactions, which will be discussed subsequently.

(b) Differences between schedules

The differences between the ***DRL*** and ***variable-ratio*** schedules were statistically significant for only one measure of behaviour. This indicates that the frequency and duration of most of the behavioural categories was similar in both ***DRL*** and ***variable-ratio*** groups. The schedule rats were run on did, however, affect the frequency of ***sniff and touch object***. The ***DRL*** rats (DRLOS group) engaged in more bouts of this behaviour, although the time spent engaged in ***sniff and***

touch object was similar. That is, ***DRL*** rats engaged in more bouts of a shorter duration. In addition, the frequency of this behaviour showed a more noticeable decrease over sessions for the ***variable-ratio*** groups. A few measures showed statistically significant ***object by schedule by session*** interactions, which will be discussed subsequently.

(c) Differences between object conditions

The presence or absence of objects during ***schedule*** sessions had an effect upon three measures of behaviour, namely the frequency and duration of ***rearing***, and the frequency of ***propping***. If objects were absent (DRLOE & VROE groups), the frequency and duration of ***rearing*** was higher during these sessions. These groups engaged in more bouts of ***rearing***, and spent more time engaged in this behaviour. Without objects to explore, rats spent more time and effort ***visually inspecting*** their surroundings (*e.g.*, for potential predators, conspecifics). In addition, if objects were present, there was a slight overall increase in time spent ***rearing*** over sessions, whereas there was an overall decrease in this measure if objects were absent. If objects were absent, rats also engaged in more bouts of ***propping*** (although there were no statistically significant differences for duration). These rats engaged in more bouts of this ***escape-directed behaviour,*** but of a shorter duration. That is, they did not spend more time trying to leave the experimental box, but they made far more attempts to do so.

(d) Interaction effects

Object by session interaction effect

An ***object by session*** interaction was found for the frequency of ***bar-related behaviour*** and duration of ***displacement***. The frequency of ***bar-related behaviour*** tended to increase over time (particularly if objects were absent), and the scores were lower if objects were present. That is, more bouts of ***bar-related behaviour*** occurred over sessions, and more bouts tended to occur in the absence of objects. Without objects to explore, rats engaged in more quick checks of the food source. All rats made more quick checks of the food source over sessions. Over time, they no longer spent long bouts checking the food-trough, but instead made quick checks more often throughout the session.

The duration of ***displacement*** also tended to increase over sessions, and a marked increase in session 2 was observed when objects were present. Thus, the bouts of ***displacement*** became longer over sessions, suggesting that the conflict inherent in the experimental session appeared to increase over time, particularly if objects were present in session 2. In session 2, rats were already habituating to the objects, and had discovered that the objects did not provide an alternative source of food. This may have increased the conflicting tendencies to explore (*i.e.*, explore objects or explore peripheral areas or explore around the food source). By session 3, the objects were no longer as arousing, and the bouts of ***displacement*** decreased in duration.

Object by schedule by session **interaction effect**

An ***object by schedule by session*** interaction was found for the frequency of ***digging/burying***, and the frequency and duration of ***sniff object***. These three measures were affected by all three grouping variables.

The grouping variable "object" has an obvious effect on ***sniff object*** (since objects were only present in two groups), but the frequency and duration of ***sniff object*** also decreased over time (more noticeable for the ***DRL*** groups), and the scores were higher in the ***DRL*** groups. The frequency and duration of ***sniff object*** decreased as a result of habituation towards the stimulus objects. That is, the number of ***orienting responses*** decreased and less time was spent ***visually inspecting*** the objects as they became more familiar. However, the ***DRL*** groups, run on the more "predictable" schedule, spent more time engaged in this form of ***exploration***.

The frequency of ***digging/burying*** tended to increase over sessions, scores were higher in the ***DRL*** rats overall, and scores tended to be higher if objects were absent. Over time, rats tended to engage in more quick flurries of ***digging/burying***, particularly if they were run on the "predictable" ***DRL*** schedule and there were no objects to explore.

7.4.7.2 EXTINCTION SESSIONS

(a) Changes over extinction sessions

Over the three ***extinction*** sessions, measures of four behavioural categories showed statistically significant differences. Thus, a number of behaviours did not show statistically significant declines or increases over ***extinction***.

The frequency and duration of ***bar pressing*** decreased over ***extinction***, as the instrumental response became extinguished. The frequency of ***bar-related behaviour*** also decreased over the three ***extinction*** sessions. Once the food source was depleted, the number of bouts centered at the food source decreased, but the time spent engaged in ***bar-related behaviour*** remained stable over sessions. That is, there were fewer bouts, but bouts were of a longer duration as the rats thoroughly investigated the only known source of food.

Over ***extinction*** the frequency of ***sniff and touch object*** tended to remain fairly stable. (Although not statistically significant, the duration of this behaviour also tended to increase). Thus, a habituation effect was not apparent. The objects did not appear to decrease in ***novelty*** or ability to arouse, which supports Forster's (1986) assertion that ***extinction*** produces ***exploration***. Rats engaged in similar numbers of bouts of ***manipulation and exploration*** of the objects with the forepaws and snout over time.

The duration of ***pica*** increased over ***extinction***, particularly in the second ***extinction*** session (session 5). Since no other source of food was available, and the rats were hungry, the rats may have spent more time eating other items (such as wood shavings).

(b) Differences between schedules

The differences between the ***DRL*** and ***variable-ratio*** rats were not statistically significant for any measure of behaviour. (However, a statistically significant ***schedule by session*** interaction, and ***object by schedule by session*** interaction was found, which will be discussed subsequently). This suggests that the number of bouts as well as the time spent engaged in the various behaviours was similar irrespective of whether rats had previously been run on ***DRL*** or ***variable-ratio*** schedules.

Based on the ***discrimination hypothesis*** (Church, 1963), it was predicted that ***DRL*** rats would engage in exploration and other non-instrumental behaviours to a greater extent. Extinction of ***bar pressing*** should have occurred more rapidly in the ***DRL*** groups, since these animals should have been able to discriminate more easily between the ***DRL*** and ***extinction*** conditions. Although the differences were not statistically significant, the ***bar pressing*** scores were indeed lower in every session for the ***DRL*** groups. However, the scores for the VROE group were similarly low. Only the VROS scores were markedly higher in every ***extinction*** session. Thus, a greater ***resistance to extinction*** in the ***variable-ratio*** groups was not apparent (although inspection of Figure 7.6 shows that the VROS group did show a greater ***resistance to extinction***).

(c) Differences between object conditions

Whether objects were first present during ***schedule*** or ***extinction*** sessions had an effect upon the frequency and duration of ***chew/bite object***. These measures showed little change over sessions for groups which first encountered objects during ***extinction***. Prior experience with objects ("OS" groups) resulted in scores that increased over sessions and were noticeably higher in every ***extinction*** session (than the "OE" groups). Prior experience may have shown these rats that objects did not provide an alternative source of food, and once the food source was depleted, frustration or ***aggression*** may have been directed towards stimulus objects.

(d) Interaction effects

Object by session **interaction effect**

An ***object by session*** interaction was found for the frequency and duration of ***sniff object***. These measures decreased over ***extinction*** (most noticeably in the "OE" groups), and the scores tended to be higher in the groups that first encountered objects during ***extinction***. This is not surprising, since the DRLOE and VROE groups were first exposed to objects during these sessions. As a result of ***novelty***, arousal was heightened in these rats, and more instances (and more time) of the orienting response of ***sniff object*** were directed towards the objects. Over sessions, as a result of habituation less ***exploration*** in the form of ***sniffing*** was directed towards the objects.

Schedule by session **interaction effect**

A ***schedule by session*** interaction was also found for the frequency of ***sniff object***. This measure decreased over sessions, and scores tended to be lower in the ***variable-ratio*** groups (except in session 5, when the ***DRL*** rats' scores dropped noticeably). Thus, the number of bouts of ***exploratory orienting responses*** decreased, reflecting a habituation effect, but the scores tended to be lower in rats previously run on the unpredictable ***variable-ratio*** schedule.

Object by schedule by session **interaction effect**

The duration of ***displacement*** yielded a statistically significant ***object by schedule by session*** interaction. This measure increased over sessions, the scores were lower in the ***variable-ratio*** groups, and scores were slightly lower if objects were first encountered during ***extinction*** sessions. During ***extinction***, there were objects present in every group. The amount of time spent in ***displacement*** increased over sessions. As the ***bar pressing*** response extinguished, and rats became habituated to the stimulus objects, the ***conflict*** may have increased. The food source was depleted, they were unable to leave the box, and the objects did not provide an alternative source of food. Slightly less time was spent in ***displacement*** if objects were at maximum ***novelty*** (never encountered before) and if rats were previously run on the unpredictable ***variable-ratio*** schedule (made up of some longer periods of "extinction" or lack of reinforcement).

7.4.7.3 ALL SIX SESSIONS

(a) Changes over all six sessions

Three measures of behaviour showed statistically significant differences over the six sessions. In addition, ***object by session***, ***schedule by session***, and ***object by schedule by session*** interactions were found for a number of behavioural measures (to be discussed subsequently).

The frequency and duration of ***bar pressing*** increased over ***schedule*** sessions and then decreased over ***extinction***. Perhaps the ***DRL*** and ***variable-ratio*** baselines (established before the commencement of observation) were less "stable" than realized, since these measures did not remain stable over ***schedule*** sessions. The increases over ***schedule*** sessions were more marked for the ***variable-ratio*** rats. The decrease in ***bar pressing*** measures over ***extinction*** was expected, as the instrumental response was extinguished.

There was an overall increase in the duration of ***pica*** across the six sessions. The time spent engaged in ***pica*** tended to increase over both ***schedule*** and ***extinction*** sessions, but more noticeably over the latter. Thus, the hungry rats ate other inappropriate foods (*e.g.*, wood shavings) in an attempt to assuage their hunger, particularly once the food source was depleted.

(b) Differences between schedules

The differences between the ***DRL*** and ***variable-ratio*** rats were not statistically significant for any behavioural measures. However, statistically significant interaction effects were found for a number of behavioural measures (to be discussed subsequently). Thus, the schedule condition alone (***DRL*** or ***variable-ratio***) did not affect the frequency or duration of the scored behaviours.

(c) Differences between object conditions

No measures of behaviour showed statistically significant differences between the object conditions. Whether objects were first present during ***schedule*** or ***extinction*** sessions had no effect upon the frequency or duration of the scored behaviours. However, a number of interaction effects were obtained, which will be discussed next.

(d) Interaction effects

Object by session interaction effect

A statistically significant ***object by session*** interaction was found for measures of six behavioural categories. The frequency of ***bar-related behaviour*** increased over ***schedule*** sessions, decreased in the first ***extinction*** session and continued to decrease over sessions. That is, rats engaged in more quick checks of the food source over time during ***schedule*** sessions, and then made fewer checks once the food source was depleted. The scores were higher during ***schedule*** sessions if objects were absent, and then lower during ***extinction*** for these same groups. Thus, if objects could be explored during ***schedule*** sessions, rats made fewer checks of the food source during those sessions. If objects were first encountered during ***extinction***, fewer checks were made of the food source during ***extinction***. Therefore, when objects were most ***novel*** or ***arousing***, the bar area was visited less often (although this may not result in less time spent there overall).

The interaction effects found for the measures of ***object-directed behaviours*** were only relevant for the ***extinction*** sessions (since object had an obvious effect during ***schedule*** sessions). The duration of ***sniff object*** decreased over ***extinction***, indicating that the rats were ***visually inspecting*** the objects less as a result of habituation to the objects. The scores were noticeably higher during the first two ***extinction*** sessions for the groups that first encountered objects during ***extinction***. As these rats had never encountered objects before, the objects were highly ***novel*** and ***arousing*** during the early sessions.

The frequency of ***sniff and touch object*** showed little overall change during ***extinction***, although there was a noticeable drop in the second ***extinction*** session (session 5). This suggests that there was little habituation to the objects in terms of number of bouts of ***exploratory sniffing and manipulation***. The scores tended to be slightly lower in the "OE" groups, which first encountered objects during these sessions. For these rats, the objects were most ***novel*** and ***arousing***. The duration of ***sniff and touch object*** tended to increase over ***extinction***. That is, rather than habituate to the objects, the rats spent more time engaged in ***exploratory sniffing and manipulation*** over time. This increase was most noticeable if objects were first encountered during ***extinction*** and the scores also tended to be higher in those groups ("OE" groups). Again, these rats had never encountered objects before, and as a result they were highly ***novel*** and ***arousing***.

The frequency and duration of ***chew/bite object*** increased over sessions for groups with prior exposure to objects ("OS" groups), whereas there was little change over sessions for the "OE" groups. These scores were much lower in every session if objects were first encountered during ***extinction***. Thus, prior experience with objects that did not provide an alternative source of food resulted in higher levels of ***aggressive behaviour*** towards the objects once the food source was depleted (or increased frustration).

In summary, with respect to the ***object-directed behaviours***, a habituation effect was only apparent in the time spent engaged in the ***inspective*** form of ***object exploration***. As the ***bar pressing*** response extinguished, since the food source was depleted, rats spent more time ***exploring objects*** (***sniffing & touching***), in accordance with Forster's (1986) findings. During ***extinction*** there was more time available for other responses (than ***bar pressing***), and the hungry rats were seeking alternative sources of food. Clearly, more than three ***extinction*** sessions were needed to observe a habituation effect. Prior experience with objects had an effect on all forms of ***exploratory behaviour***. During ***extinction***, the second set of objects had less impact in terms of ***novelty*** and ability to ***arouse***, which was reflected in less time spent in ***visual inspection*** and also ***sniffing and touching***. However, by contrast, the objects aroused more ***aggressive behaviour*** in these same groups. That is, they spent more time ***chewing and biting*** the objects. Clearly, the topography of the ***exploratory response*** must be taken into account.

The frequency of ***propping*** decreased over ***schedule*** sessions, decreased in the first ***extinction*** session and then decreased slightly over the remaining sessions. Thus, the rats engaged in fewer bouts of this ***escape-directed behaviour*** over time. The scores were much higher during ***schedule*** sessions if objects were absent. Without objects to explore, rats engaged in more attempts to escape the box. During ***extinction***, the number of bouts of ***propping*** actually increased over sessions, and scores were higher, if objects were first encountered during ***extinction***. Thus, the "OE" groups engaged in more bouts of ***propping*** during ***schedule*** and ***extinction*** sessions. Clearly, prior exposure to objects during times when food is available led to fewer bouts of ***escape-directed behaviour*** even when food was no longer available.

The duration of ***rearing*** decreased slightly overall during ***schedule*** sessions, decreased in the first ***extinction*** session and then continued to decrease. However, the scores were much lower and actually increased over ***schedule*** sessions if objects were present ("OS" groups). That is, with objects to explore, rats spent less time ***rearing*** and ***visually inspecting*** their surroundings (for predators etc). During ***extinction***, the opposite pattern was observed. That is, the scores were much lower and increased over sessions for the "OE" groups. The objects were highly ***novel*** for these groups (their first encounter with objects), and as a result, less time was spent ***rearing***. Therefore, when the rats first encountered objects (& ***novelty***) had an effect upon time spent ***visually inspecting*** their surroundings.

Schedule by session **interaction effect**

The frequency and duration of ***sniff object*** yielded a statistically significant ***schedule by session*** interaction. Both measures decreased over ***schedule*** sessions, increased in the first ***extinction*** session and decreased over the remaining sessions. The scores were higher and the decrease more marked over ***schedule*** sessions for rats run on the more predictable ***DRL*** schedule. The ***DRL*** schedule allowed rats to engage in more ***visual exploration*** of objects during predictable periods of non-reinforcement. During ***extinction***, rats previously run on the ***variable-ratio*** schedule tended to engage in slightly fewer bouts of ***sniff object***, but spent slightly more time ***visually inspecting*** the objects. This is somewhat counter-intuitive, since one might expect rats previously run on the ***DRL*** schedule to spend more time ***exploring objects***, since that schedule has a lower ***resistance to extinction*** (& should allow more time for non-operant responses). Perhaps rats run on a schedule with a higher ***resistance to extinction*** engaged in more ***visual inspection*** of objects (requiring less time & effort away from the food source), rather than physically touching them (i.e., topography of ***exploratory response*** is important).

Object by schedule **interaction effect**

A statistically significant ***object by schedule*** interaction was found for the frequency of ***sniff and touch object*** and the duration of ***sniff object***. If objects were present during ***schedule*** sessions, rats run on the ***DRL*** schedule engaged in far more bouts of ***sniff and touch object***. During ***extinction***, scores tended to be higher if rats had prior exposure to objects ("OS" groups), and scores were also higher for rats previously run on the ***DRL*** schedule. Thus, rats tended to engage in more bouts of ***sniffing and manipulating*** objects if they had been exposed to objects during ***schedule*** sessions and if they were run or had been run on the predictable ***DRL*** schedule.

If objects were present during ***schedule*** sessions, rats run on the more predictable ***DRL*** schedule spent more time ***visually inspecting*** the objects (***sniff object***). During ***extinction***, the scores were noticeably higher during the first two sessions for the "OE" groups. As a result of maximum ***novelty*** (their first encounter with objects), more time was spent engaged in the orienting response (***sniff object***). Slightly more time was spent engaged in ***sniff object*** if rats were previously run on the unpredictable ***variable-ratio*** schedule. Again, rats run on the schedule with a higher ***resistance to extinction*** may have engaged in more ***visual inspection*** of objects (requiring less time & effort away from the food source), rather than physically touching them.

Object by schedule by session **interaction effect**

Measures of six behavioural categories yielded statistically significant ***object by schedule by session*** interactions. These frequency and duration measures were affected by all three grouping variables. The measures were the frequency and duration of ***digging/burying***, frequency of ***pica***, ***rearing*** and ***sniff object***, and duration of ***displacement*** and ***bar-related behaviour***.

The duration of ***displacement*** increased gradually over ***schedule*** sessions. However, this increase was less marked overall for the ***DRL*** groups, who tended to have lower scores (although there was a noticeable increase in the second session). The predictability of reinforcement on the DRL schedule may have resulted in lower conflict, and less time spent in ***displacement***. The pattern in session 2 was different depending upon the object condition. If objects were present ("OS" groups) there was a massive increase in this session (before dropping in the next session), whereas there was a slight decrease in session 2 if objects were absent. For the "OS" groups, by session 2, the rats had discovered that the objects did not provide an alternative source of food, and this may have resulted in conflicting response tendencies (whether to explore objects, peripheral areas or the food source).

Although there was little change in duration of ***displacement*** in the first ***extinction*** session, the scores increased slightly for the ***DRL*** groups (predictable food source suddenly depleted) and "OS" groups (objects that did not provide food present), whereas the opposite effect was observed for the ***variable-ratio*** (first ***extinction*** session was not so different to the previous unpredictable schedule) and "OE" groups (novel stimulus objects to explore). Over ***extinction***, all rats spent more time engaged in ***displacement***. However, the scores were higher in every session for rats previously run on the ***DRL*** schedule, and also for the "OS" groups. Thus, depletion of the food source, for rats previously run on the predictable schedule or for rats that had prior experience with objects that did not provide an alternative source of food, led to more conflict and hence more ***displacement***.

An overall decrease in frequency of ***rearing*** over ***schedule*** sessions was observed in all groups. However, scores were noticeably higher for the ***DRL*** groups and if objects were absent ("OE" groups. Rats run on the more predictable schedule engaged in more bouts of ***visual inspection*** of their surroundings. Without objects to explore, rats also engaged in more bouts of ***rearing***. This behaviour allowed them to increase their height, and in natural surroundings would increase the area that could be inspected for predators or competitors for resources. Without objects to hold their attention, or provide possible shelter in the well-lit open environment, or a schedule that required higher levels of ***bar pressing***, rats were more focused on their immediate surroundings.

The frequency of ***rearing*** decreased in the first ***extinction*** session (except in the "OS" groups). Over ***extinction*** sessions, there was a slight decrease in this measure. However, the scores actually increased slightly for rats previously run on the ***DRL*** schedule (scores higher in every session) and the "OE" groups (although scores were lower in every session). That is, once the food source was depleted, after being run on a predictable schedule (low ***resistance to***

extinction), rats were again more focused on their well-lit unsheltered surroundings (high risk for predation in natural environments). Prior exposure to objects also resulted in more bouts of ***rearing***. Experience had shown that objects did not provide shelter or food and therefore rats engaged in more bouts of ***visual inspection*** of the surroundings.

If objects were present during ***schedule*** sessions, the frequency of ***sniff object*** decreased over sessions, as a result of habituation. However, scores were markedly higher in every session if rats were run on the ***DRL*** schedule. The more predictable schedule, which encouraged time away from the bar area, resulted in rats engaging in more bouts of ***visual exploration*** of objects. Over ***extinction***, there was a decrease in the number of bouts of ***sniff object***, again as a result of habituation. The scores were higher in every session in the "OE" groups. For these rats, this was the first encounter with objects. That is, the objects were particularly ***novel*** and ***arousing***. The scores also tended to be higher in groups previously run on the ***DRL*** schedule. These rats more easily discriminated between the previous predictable ***schedule*** and ***extinction***. Therefore, more attention was directed towards the objects (in the form of bouts of ***sniff object***).

The duration of ***bar-related behaviour*** decreased over ***schedule*** sessions (except for the ***DRL*** groups). Time devoted to this behaviour was much greater in every session for rats run on the ***variable-ratio*** schedule. The unpredictability of reinforcement resulted in greater time spent around the food source and bar area. If objects were absent, the duration of ***bar-related behaviour*** scores were also noticeably higher in every session. Without objects to explore as potential sources of food or stimulation, rats spent more time around the known food source. This measure then decreased in the first ***extinction*** session (except for the "OS" groups).

Over ***extinction***, the duration of ***bar-related behaviour*** increased slightly (except for the ***DRL*** groups). The scores were much lower in every session for rats previously run on the ***DRL*** schedule. These rats were able to discriminate between the predictable conditions of the ***DRL*** schedule and the new ***extinction*** conditions. As a result, they spent less time around the depleted food source, and more time engaged in other activities. The scores were also slightly lower if objects were most ***novel*** and ***arousing*** ("OE" groups).

7.5 CONCLUSIONS BASED ON THE FINDINGS OF EXPERIMENT 2

This section provides a summary of the general findings of this study. Some practical implications of these findings are discussed subsequently, particularly with respect to schedules of reinforcement in other captive environments.

7.5.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

During ***schedule*** sessions, the ***DRL*** groups spent at least 9% (& up to 13%) of total session time engaged in ***behaviour directed at the bar and food-trough area***, whereas for the ***variable-ratio*** groups these behaviours represented more than 17% (& up to 22%) of total session time. For the ***variable-ratio*** groups, the time spent in these behaviours may appear somewhat ***excessive***, but not necessarily maladaptive, since higher levels of ***bar pressing*** on such a schedule should result in more reinforcers (& time was needed to retrieve the pellets).

During ***extinction*** sessions, the ***DRL*** groups spent more than 10% (& up to 18%) of total session time engaged in ***behaviour directed at the bar and food-trough area***. The ***variable-ratio*** groups spent less than 12% (>6%) of ***extinction*** sessions engaged in these behaviours. In some sessions, the time spent engaged in these behaviours by the ***DRL*** groups may seem somewhat ***excessive***, but again, not necessarily maladaptive, since the depleted food source was nonetheless the only known source of food.

Most bouts of ***bar-related behaviours*** (>90%), as well as the time spent in this behaviour (>90%), took place outside the PRPs for the ***variable-ratio*** groups. Thus, the rats spent little time investigating around the food source just after reinforcement, but no doubt made brief checks for food at the source at other times. More than 20% (>30% for the DRLOS group) of the frequency and duration of ***bar-related behaviour*** took place during the PRPs in the ***DRL*** groups. Again, most bouts (& time spent in this behaviour) occurred outside the PRPs for these groups.

In summary, ***behaviour directed at the bar and food-trough area*** might be considered somewhat excessive during some sessions, but not maladaptive. Less than a third of frequency and duration of ***bar-related behaviour*** took place during the PRPs for all groups.

7.5.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

During ***schedule*** sessions, the DRLOS group spent more than a quarter of total session time (& up to 30%) engaged in ***behaviour directed at the stimulus objects***. For the VROS group, these behaviours represented at least 22% (& up to 27%) of total session time. These levels of

exploratory behaviour should be considered adaptive rather than ***excessive***. The stimulus objects represented a source of potential food and stimulation.

During ***extinction***, at least a quarter (& up to 37%) of total session time was spent engaged in ***behaviour directed at the stimulus objects*** by all groups. Rats would be expected to search for alternative sources of food, once the food source was depleted. Again, the levels of this ***exploratory behaviour*** should be considered adaptive. As mentioned previously, Forster (1986; 1992; 1995) found that higher levels of ***object exploration*** occurred during ***extinction***.

For the DRLOS group, at least 30% of bouts of ***object-directed behaviours*** occurred during PRPs, and at least 29% (up to 45% for ***chew/bite object***) of the total duration. That is, rats on the predictable ***DRL*** schedule ***explored objects*** immediately after consumption of the food pellet, but they tended to explore these objects more outside the PRPs. For the VROS group, less than 11% of frequency and duration of ***object-directed behaviours*** occurred during the PRPs. That is, rats run on the unpredictable schedule tended to explore objects outside the PRPs, which is not surprising, since a stable PRP was unlikely to develop.

In summary, levels of ***behaviour directed at the stimulus objects*** were not found to be excessive during ***DRL***, ***variable-ratio*** or ***extinction*** sessions. For the DRLOS group, more than 29% (frequency & duration) of ***object exploration*** took place during the PRPs. For the VROS group, less than 11% of these behaviours (frequency & duration) occurred during the PRPs.

7.5.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

During ***schedule*** sessions, the presence of objects resulted in less than 13% (>8%) of total session time devoted to ***behaviour directed at the peripheral areas of the box***. If objects were absent, these behaviours represented more than 15% (& up to 19%) of total session time. In the absence of objects, irrespective of schedule (***DRL*** or ***variable-ratio***), the time spent engaged in these ***escape-directed behaviours*** (mainly ***propping***) appears ***excessive***. The rats may have been attempting to explore outside the box (for food, water, shelter). Clearly, the presence of objects to explore reduced the amount of ***behaviour directed towards the peripheral areas of the box***, although the levels observed in the DRLOS group are also ***excessive*** (>10%). Therefore, the ***DRL*** schedule (which encourages time away from the bar area, since low levels of ***bar pressing*** are required) also appears to result in more time spent engaged in ***escape-directed behaviour***.

During ***extinction*** sessions, the VROS group spent less than 10% of total session time engaged in ***behaviour directed at the peripheral areas of the box***, whereas the other groups spent at least

12% (& up to 19%) of total session time devoted to these ***escape-directed behaviours***. Thus, for three of the groups, ***excessive*** levels of these behaviours took place when the food source was depleted (although not necessarily higher than previously, for some groups). These rats may have been attempting to seek food or shelter (to minimise susceptibility to predation) outside the box (Russell, 1983; Lucas, Timberlake & Gawley, 1988). As mentioned in the discussion for Experiment 1, it is unclear whether this behaviour is adaptive or not. Attempting to seek food and shelter elsewhere would be adaptive, but struggling in vain to leave the captive environment could be considered maladaptive (& perhaps akin to stereotypic behaviours observed in other captive environments).

The ***jump at lid*** category, found to occur during a ***fixed-ratio*** schedule (Litchfield, 1987) and during the ***fixed-interval*** and ***variable-interval*** schedules in Experiment 1, was also present in this study. However, less than 1% of total session time was spent engaged in this behaviour in all cases, and it was absent in some sessions. The levels were not ***excessive***, and this behaviour may represent an ***anti-predator*** or ***escape behaviour*** (Hole & Einon, 1984).

For the ***DRL*** groups, more than 22% (>38% for the DRLOS group) of frequency and duration of ***propping*** took place during the PRPs. Thus, ***propping*** tended to occur more outside the PRPs, particularly in the absence of objects. Therefore, the presence of objects resulted in more ***propping*** immediately after consumption of the food pellet. The objects may have increased ***general activity*** levels following reinforcement, when the likelihood of reinforcement was lowest. Most bouts of ***jump at lid*** (>80%) occurred outside the PRPs in the DRLOE group. Most bouts of ***propping*** (>88%) and all bouts of ***jump at lid*** (if it occurred) took place outside the PRPs for the ***variable-ratio*** groups. This is not surprising, since a stable PRP was unlikely to develop on this unpredictable schedule.

In summary, levels of ***behaviour directed at the peripheral areas of the box*** were ***excessive*** during ***DRL*** sessions (even when objects were present), ***variable-ratio*** sessions when objects were absent, and during ***extinction*** for most groups (except VROS group). For the ***DRL*** group, more than 22% of ***escape-directed propping*** occurred during the PRPs, whereas virtually no bouts (frequency & duration) took place during PRPs for the ***variable-ratio*** groups.

7.5.4 OTHER BEHAVIOURAL CATEGORIES

Less than 10% of total ***DRL*** and ***variable-ratio*** time was spent engaged in ***displacement***. All groups spent more than 10% of at least one ***extinction*** session (except the first ***extinction*** session) engaged in this activity. Thus, when the food source was depleted (and rats became habituated to the objects), the level of this ***conflict-related behaviour*** became ***excessive***.

More than 23% (<34%) of the frequency and duration of ***displacement*** took place during the PRPs for the ***DRL*** groups. If objects were absent (DRLOE group), a slightly greater proportion of each measure occurred during the PRPs. Most ***displacement*** activities (frequency & duration were < 6%) occurred outside the PRPs for the ***variable-ratio*** groups, particularly if objects were absent (VROE group). This suggests that a stable PRP did not develop during the ***variable-ratio*** schedule, and most time was devoted to this ***conflict-related behaviour*** at other periods of non-reinforcement. However, the ***DRL*** rats also engaged in more ***displacement*** activities outside the PRPs, indicating that the period immediately after food delivery was less ***conflict arousing*** than other periods of non-reinforcement throughout the interval.

All groups spent less than 1% of total session time (***DRL***, ***variable-ratio*** & ***extinction***) engaged in ***digging/burying***. In some cases, these behaviours may have been related to ***foraging***. In other instances, they may have been ***escape-directed***. Flurries of ***sawdust pushing*** may occur in the presence of aversive stimuli or as an ***anti-predator response*** (Litchfield, 1987). The levels of this behaviour were very low.

For the ***DRL*** groups, more than a quarter (<36%) of the frequency and duration of ***digging/burying*** took place during the PRPs. If objects were present, rats engaged in slightly higher amounts of this behaviour (frequency & duration) during ***DRL*** sessions. This behaviour, whether related to ***foraging***, ***escape*** or ***sawdust pushing*** during periods of aversive stimulation, was not exclusively associated with the stimuli present during PRPs. In fact, it was more likely to occur at other times of non-reinforcement. All bouts of ***digging/burying*** occurred outside the PRPs for both ***variable-ratio*** groups. Clearly, this activity did not occur immediately after food delivery on this unpredictable schedule.

If objects were present during ***DRL*** or ***variable-ratio*** sessions, rats spent less than 10% of total session time engaged in ***rearing***. Slightly higher proportions (<13%) were observed in the absence of objects. Thus, as with Experiment 1, rats did not engage in ***excessive*** amounts of ***rearing*** if objects were present. As mentioned in the discussion for Experiment 1, the absence of objects in the well-lit and open box resulted in higher levels of ***visual inspection*** (***rearing***), allowing early detection of predators or competitors. Thus, it may have been an adaptive response, but it may also reflect the aversive stimuli present during ***schedule*** sessions, if there were no objects to explore. Less than 10% of total ***extinction*** session time was spent engaged in

rearing by all groups. Thus, the levels were not ***excessive*** when the food source was depleted. This suggests that ***rearing*** was more likely to be ***schedule-induced*** than ***extinction-induced***. This finding is contrary to the findings of Experiment 1, where the opposite was true.

Almost no ***rearing*** (<1%) took place during the PRPs for the ***variable-ratio*** groups. For the ***DRL*** groups, more than a quarter (<43%) of the frequency and duration of this behaviour occurred during PRPs. These percentages were noticeably higher (>10% difference) if objects were present. Thus, rats engaged in more ***rearing***, or ***visual inspection*** of their environment during PRPs if objects were available to explore. For these rats, objects representing potential food sources were available, their arousal levels were high (objects still novel), and this may have heightened their awareness of potential predators or competitors.

Less than 10% (>4%) of total ***DRL*** or ***variable-ratio*** session time was spent in ***pica***, although in the absence of objects ("OE" groups), levels approached 10%. For the "OE" groups, ***pica*** may have been developing into an ***eating disorder***. Without objects to explore and "distract" them, the hungry rats spent more time eating wood shavings, which may have helped satiate them, but this food supplement may have been potentially harmful over the long-term. Over ***extinction***, the levels of ***pica*** still remained below 10% of total session time, except in one instance. For the VROE group, almost 15% of the second extinction session was devoted to this behaviour. That is, the level of ***pica*** was clearly ***excessive*** in at least one session. The food source was depleted, the objects did not provide an alternative food source, and wood shavings were the only source of food (although inappropriate).

Almost no instances of pica (<1%) were observed during PRPs for the ***variable-ratio*** groups (none at all in the VROE group), whereas more than a quarter (<40%) of both measures occurred immediately after reinforcement for the ***DRL*** groups. Thus, even after consuming a food pellet, rats on the predictable schedule ate other items of inappropriate food (wood shavings). Rats on the unpredictable schedule only engaged in ***pica*** at other times of non-reinforcement (*i.e.*, not just after consuming a food pellet).

In summary, ***displacement*** may have been ***extinction-induced*** (***excessive***) in a number of cases, and ***pica*** was clearly ***excessive*** for one group in one ***extinction*** session. If objects were not present to explore, then ***rearing*** was ***excessive*** in a number of cases and ***pica*** approached excessive (10%) levels, suggesting that these behaviours may have been ***schedule-induced***. Clearly, more stable PRPs occurred during the more predictable DRL sessions (higher proportions of total frequency & duration). Almost all, or indeed all, instances of these other behavioural categories took place outside the PRPs for the ***variable-ratio*** rats, indicating that stable PRPs were lacking.

7.5.5 PRACTICAL IMPLICATIONS OF THESE FINDINGS

Contrary to the findings of Experiment 1, this study found that the ***discrimination hypothesis*** (Church, 1963) was still relevant for rats run on a ***DRL 15-s*** or ***variable-ratio 30*** schedule of reinforcement in a larger and more naturalistic open-field environment. Extinction of ***bar pressing*** did indeed occur more rapidly in the ***DRL*** groups, with a ***greater resistance to extinction*** apparent for the ***variable-ratio*** groups.

The amount of session time (***DRL***, ***variable-ratio*** & ***extinction***) spent engaged in various behaviours was ***excessive*** in some cases, but not necessarily ***maladaptive***. For example, the high levels of the three ***object-directed behaviours*** (>20% or even 30%) observed in all sessions, and the somewhat excessive amounts of ***behaviour directed at the bar and food-trough area*** (>10% or even 20%) during some sessions, were unlikely to have been maladaptive. That is, ***exploration*** of stimulus objects is adaptive since it could have led to other sources of food & stimulation. ***Behaviour centered at the food source*** could also be adaptive, especially if the food source was unpredictable (***variable-ratio*** schedule). Some levels of ***escape-directed behaviour*** (***behaviour directed at the peripheral areas of the box***) and ***visual inspection of the surroundings*** (***rearing***) were also excessive, but were unlikely to have been maladaptive. Rather, they may have indicated how aversive the experimental conditions were in some cases. However, the excessive levels of ***displacement*** (in a number of cases) and ***pica*** (>10% or approaching 10% in a number of cases) could be considered potentially maladaptive, and akin to aberrant behaviours observed in other captive environments. As mentioned previously, Shepherdson (1989) suggests that if captive animals spend more than 10% of their day engaged in a particular activity, then it can be considered ***excessive*** or ***stereotypic***.

More stable PRPs occurred during the predictable ***DRL*** sessions (high proportions of total frequency & duration measures occurred during PRPs). By contrast, the unpredictable ***variable-ratio*** sessions lacked stable PRPs (low proportions of total frequency & duration measures occurred during PRPs). Therefore, as found in Experiment 1, the predictions concerning PRP development (or lack of it) for these two types of schedule were supported, even though the experimental apparatus was larger and more naturalistic (open-field) in nature. The development of PRPs and lower ***resistance to extinction*** on the more predictable DRL 15-s schedule appear to be robust phenomena. However, it must be noted, that a greater proportion of every behavioural measure did take place outside the PRPs, at other times of non-operant responding.

CHAPTER 8

EXPLORATORY AND OTHER BEHAVIOURS IN THE LABORATORY RAT DURING FIVE SIMPLE SCHEDULES (FR, FI, VI, VR & DRL)

8.1 SUMMARY OF FINDINGS OF EXPERIMENT 1 AND 2, AND LITCHFIELD'S (1987) STUDY

The previous two chapters presented the findings for Experiment 1 and 2. If the findings of Litchfield's 1987 study are also taken into account, then a series of five simple schedules of intermittent reinforcement has been investigated (FR, VR, FI, VI & DRL). It should be noted that the experiments were conducted at different times, and with different subjects. However, in every other aspect, the experimental conditions were kept as similar as possible, to allow some comparative analysis across experiments. That is, the same equipment was used in each experiment, the same stimulus objects, the same grouping variables, and subjects of similar age. This chapter will present and discuss patterns of behaviour observed during these five schedules of intermittent reinforcement (and subsequent ***extinction*** sessions), and provide possible explanations that take the ecology and evolutionary aspects of the rat into account.

Under natural conditions, a rat's food would be ***patchily*** distributed in both space and time. Food resources would be scattered around the animal's home range and some sources would be richer than others. The ***patch*** of food would have to be found, sampled, exploited, and then left when it was depleted. If a food source did not provide the minimum energy requirements of the rat, then continuing to utilise this food source would be ***risky***. The rat should reject this nutrient-poor resource and search for potentially richer sources (Davey, 1989). ***Optimal foraging strategies*** might account for the behavioural patterns observed during schedules of intermittent food reinforcement in a laboratory situation.

The more naturalistic open-field style Skinner box provides an opportunity to assess behaviour centered at a food source, as well as exploratory and other behaviours away from this source. Schedules of intermittent food reinforcement might be considered to mimic a ***patchy*** resource (in time). That is, food is only available under certain conditions, and one would expect the rat to explore the experimental box in search of alternate food sources. Initially, the stimulus objects would be investigated, as would the outer perimeters of the experimental box. The ***fixed*** schedules are perhaps the least ***patchy*** of the five schedules investigated (with food arrival being more predictable), whereas, the ***variable*** schedules are the most ***patchy*** (with food arrival being least predictable). ***DRL*** schedules might be considered to encourage leaving the food patch, since low rates of ***bar pressing*** are required. Whether the schedule is ***variable*** or ***fixed***, ***ratio*** or ***interval***, a rat would continue to return to the manipulandum and food-trough area, since this is the only known source of food available.

The ***extinction*** schedule, which follows each of the intermittent reinforcement schedules, may mimic the situation where a food patch has become depleted. It is now less ***risky*** for the rat to leave the food-trough area and engage in other behaviours. In fact, it could more ***risky*** to stay (especially, in a "real-life" situation). Exploratory behaviour directed towards stimulus objects and other areas of the experimental box might bring the rat into contact with other potential sources of food. Thus, ***patch-depletion*** may account for increases in exploratory behaviour, since a new food patch must be found to meet the rat's food/energy requirements.

8.2 PRESENCE OF EXPLORATORY AND OTHER BEHAVIOURS DURING THE POST-REINFORCEMENT PAUSES

The values presented in this section can be found for each group individually in the previous chapters and in Litchfield (1987). Here, they are all presented at the same time, to allow some comparison between the different schedules of reinforcement, and object conditions. In Table 8.1, the left-hand value in each cell is for the group that had objects present during schedule sessions ("OS" groups), whilst the right-hand value is for the group with objects absent during these schedule sessions ("OE" groups).

Two schedules stand out as being different, with percentages of total behaviours occurring during the PRPs falling at opposite extremes (Table 8.1). Very low percentages are observed for the ***variable-ratio*** groups (VROS & VROE). At the other end of the scale, the highest percentages of all are seen for the ***fixed-interval*** groups (FIOS & FIOE), with the exception of frequency of ***bar-related behaviour*** (duration is still the highest). A simple explanation for this difference might be that the period of non-reinforcement on a ***fixed-interval*** schedule is very predictable. Thus, a predictable PRP is likely to develop, with a number of behaviours other than ***bar pressing*** likely to occur during this period. On the other hand, non-reinforcement on a ***variable-ratio*** schedule is unpredictable. Thus, a predictable PRP is unlikely to develop, and behaviours other than ***bar pressing*** would be likely to occur at any time during the inter-reinforcement interval.

Table 8.1
The mean frequency and duration of behaviours occurring during the PRPs summed over the three schedule sessions, presented as a percentage of the total mean frequency or duration of each behaviour summed over the same three sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study).

BEHAVIOURAL MEASURE	**% OF TOTAL * FROS & FROE GROUPS** (Litchfield,1987)	**% OF TOTAL * FIOS & FIOE GROUPS** (Experiment 1)	**% OF TOTAL * VIOS & VIOE GROUPS** (Experiment 1)	**% OF TOTAL * VROS & VROE GROUPS** (Experiment 2)	**% OF TOTAL * DRLOS & DRLOE GROUPS** (Experiment 2)
FREQUENCIES					
Pica	Not measured	79.25 & 66.67	30.77 & -	0.87 & 0	27.78 & 31.93
Digging/Burying	Not measured	83.2 0 & 75.39	31.48 & 14.29	0 & 0	31.42 & 28.73
Rearing	Not measured	53.18 & 55.03	23.82 & 12.80	0.89 & 0.75	42.58 & 26.15
Propping	35.70 & 36.08	51.04 & 40.33	19.69 & 10.54	1.79 & 0.71	38.35 & 22.98
Displacement	39.04 & 49.36	48.67 & 51.93	22.25 & 7.8	4.10 & 0.82	28.51 & 33.33
Bar-related behaviour	36.30 & 50.16	23.85 & 16.82	13.59 & 10.82	7.65 & 2.50	32.82 & 23.90
Sniff Object	33.72 & n/a	59.86 & n/a	25.36 & n/a	4.79 & n/a	31.74 & n/a
Sniff and Touch Object	33.58 & n/a	58.52 & n/a	21.25 & n/a	5.62 & n/a	33.07 & n/a
Chew/Bite Object	included above	52.30 & n/a	66.67 & n/a	8.93 & n/a	32.96 & n/a
Jump at Lid	62.50 & 18.47	- & 73.43	13.49 & 10.13	- & 0	- & 17.65
DURATIONS (in seconds)					
Pica	Not measured	78.79 & 77.06	34.88 & -	0.46 & 0	33.01 & 39.40
Digging/Burying	Not measured	90.63 & 78.95	30.04 & 13.67	0 & 0	35.84 & 28.65
Rearing	Not measured	55.49 & 61.58	23.61 & 14.66	0.51 & 0.24	39.98 & 28.24
Propping	36.09 & 39.07	60.9 & 53.36	23.70 & 12.54	1.53 & 0.38	39.07 & 24.56
Displacement	36.04 & 51.73	60.49 & 63.20	21.33 & 7.7	5.29 & 0.26	23.45 & 24.02
Bar-related behaviour	33.70 & 52.22	54.71 & 55.97	20.32 & 23.02	8.46 & 1.74	32.23 & 22.90
Sniff Object	31.51 & n/a	63.10 & n/a	29.11 & n/a	6.30 & n/a	29.93 & n/a
Sniff and Touch Object	32.38 & n/a	60.22 & n/a	20.33 & n/a	6.0 & n/a	33.74 & n/a
Chew/Bite Object	included above	46.61 & n/a	21.18 & n/a	10.29 & n/a	45.57 & n/a
Jump at Lid	51.02 & 16.29	- & 72.49	12.79 & 10.44	- & 0	- & 15.79

Note. A dash (-) indicates that no instances of the behaviour were observed, whereas a zero (0) indicates that the behaviour did occur but all instances took place outside the PRPs

8.2.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

Groups with objects present during schedule sessions ("OS" groups)
With respect to ***bar-related behaviour***, the frequency and duration occurring during the PRPs varied quite markedly between the five groups (Table 8.1). The percentages ranged between 7.65% and 36.3% for the frequency and between 8.46% and 54.71% for the duration. From lowest to highest frequency the groups were as follows: VROS, VIOS, FIOS, DRLOS and FROS. However, the duration order was not the same. From lowest to highest duration the groups were as follows: VROS, VIOS, DRLOS, FROS and FIOS.

For the FIOS and VIOS groups, the duration scores are higher than the frequency scores, with this behaviour engaged in for longer amounts of time per instance (Table 8.1). For the other three groups the frequency and duration scores are similar, indicating that each case of ***bar-related behaviour*** was brief.

Both the frequency and duration of ***bar-related behaviour*** during the PRPs is noticeably lower for the VROS group, and then the VIOS group (Table 8.1). These two groups were run on the least predictable schedules, with predictable PRP's unlikely to develop. For the VROS group, only ***chew/bite object*** has a higher frequency or duration than ***bar-related behaviour***. For the VIOS group the frequency scores of ***bar-related behaviour*** and ***jump at lid*** are similar.

For the FROS group, the frequency and duration measures of ***bar-related behaviour*** are similar to the scores of all behaviours except ***jump at lid***, which is much higher (> 25% higher for frequency). For the FIOS group, the frequency of ***bar-related behaviour*** is much lower than for any other behaviour, whereas the duration value is similar to ***rearing***, and higher than ***chew/bite object***. For the DRLOS group, the frequency of ***bar-related behaviour*** is similar to those of the other behaviours (***rearing & propping*** are somewhat higher), whilst the duration score lies in the middle and is similar to ***pica*** and ***sniff and touch object*** (Table 8.1).

In summary, the lowest percentages for frequency and duration of ***bar-related behaviour*** occurring during the PRPs are found for the ***variable-ratio*** and then ***variable-interval*** schedules (Table 8.1). These are the least predictable schedules with respect to periods of non-reinforcement, and are thus least likely to develop PRPs. The highest percentages were found for the more predictable ***fixed-ratio*** (frequency) or ***fixed-interval*** (duration) groups.

Groups with objects absent during schedule sessions ("OE" groups)

The frequency and duration of ***bar-related behaviour*** occurring during the PRPs varied substantially between the five groups (Table 8.1). For the frequency, the percentages ranged from 2.5% to 50.16%. The percentages ranged from 1.74% to 55.97% for the duration. From lowest to highest frequency the groups were VROE, VIOE, FIOE, DRLOE and FROE. The order from lowest to highest duration differed: VROE, DRLOE, VIOE, FROE, and FIOE. For the FIOE and VIOE groups, the duration scores are higher than the frequency scores (approximately triple or double respectively), indicating that fewer instances of ***bar-related behaviour*** occurred, but the behaviour was engaged in for longer amounts of time per instance. For the other three groups the frequency and duration scores are similar, indicating that each case of ***bar-related behaviour*** was brief.

As with the groups that had objects present during schedule sessions, both the frequency and duration of ***bar-related behaviour*** during the PRPs is noticeably lower for the VROE group (but still the highest value for any behaviour), and then the VIOE group (Table 8.1). These two groups were run on the least predictable schedules, with predictable PRPs unlikely to develop. For the VIOE group the frequency scores of ***bar-related behaviour***, ***propping*** and ***jump at lid*** are similar. For the FROE group, the frequency and duration scores of ***bar-related behaviour*** are similar to those obtained for ***displacement***. For the FIOE group, the frequency value is by far the lowest of any behaviour, whereas the duration score is similar to ***propping*** and less noticeably lower than for the other behaviours. Thus, there are fewer instances of ***bar-related behaviour*** but of longer duration. For the DRLOE group, only ***jump at lid*** has a lower duration than ***bar-related behaviour***, whilst the frequency is similar but also slightly higher than for ***propping***.

In summary, the lowest percentages for frequency and duration of ***bar-related behaviour*** occurring during the PRPs are found for the ***variable-ratio*** schedule, with its unpredictable periods of non-reinforcement. The highest percentages were found for the more predictable ***fixed-ratio*** (frequency) or ***fixed-interval*** (duration) groups (Table 8.1).

8.2.2 BEHAVIOURS DIRECTED AT THE STIMULUS OBJECTS

Only half the groups had objects present during schedule sessions, so this section is only relevant to the "OS" groups.

Groups with objects present during schedule sessions ("OS" groups)

For these groups, the frequency and duration of ***object-directed behaviours*** (***sniff object***, ***sniff and touch object***, & ***chew/bite object***) occurring during the PRPs varied quite substantially

(Table 8.1). Less than 11% of the frequency and duration measures occurred during the PRPs for the VROS group. The next lowest percentages were seen in the VIOS group, with a notable exception. The percentages ranged between 20% and 30%, except for the frequency of ***chew/bite object*** (>66%). Almost a third of the frequency and duration of these behaviours occurred during the PRPs for the FROS group (ranging between 31.5% & 34%). It should be noted that ***chew/bite object*** was included in the ***sniff and touch object*** category for this group. For the DRLOS group, approximately a third of the frequency of object-directed behaviours also occurred during the PRPs, whereas the duration measures ranged from 29.93% to 45.57%. The measures for the FIOS group were highest, with over 50% of the frequency values and as high as 63.1% of the duration scores occurring during the PRPs.

In summary, the lowest percentages for frequency and duration of ***object-directed behaviours*** occurring during the PRPs are found for the ***variable-ratio*** schedule, with its unpredictable periods of non-reinforcement. The highest percentages were found for the more predictable ***fixed-ratio*** group (Table 8.1).

8.2.3 BEHAVIOURS DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

Groups with objects present during schedule sessions ("OS" groups)
Less than 2% of the frequency and duration of ***propping*** occurred during the PRPs for the VROS group (Table 8.1). At the other extreme, these scores were higher than 50% for the FIOS group. The frequency and duration scores were close to 20% for the VIOS group, and over 30% for the FROS and DRLOS groups.

For the ***jump at lid*** category, there were no instances during schedule sessions for three of the groups (FIOS, VROS & DRLOS). For the VIOS group, the frequency and duration scores were lower than for any other behaviour. However, the frequency of ***bar-related behaviour*** was strikingly similar. For the FROS group, the frequency and duration scores for ***jump at lid*** were markedly higher than for any other behaviour (Table 8.1).

In summary, the lowest percentages for frequency and duration of ***behaviours directed at the peripheral areas of the box*** occurring during the PRPs are found for the ***variable-ratio*** schedule, with its unpredictable periods of non-reinforcement (Table 8.1). The highest percentage of ***jump at lid*** was found for the more predictable ***fixed-ratio*** schedule. It is interesting to note that ***jump at lid*** only occurred during ***fixed-ratio*** and ***variable-interval*** schedules (both very different with respect to predictability of non-reinforcement). The highest percentages of ***propping*** frequency and duration during the PRPs were obtained for the ***DRL*** schedule. This schedule is likely to encourage activity away from the bar area, since low rates of operant responding are required. Thus, ***escape-directed behaviours*** are likely to occur.

Groups with objects absent during schedule sessions ("OE" groups)

The percentages of frequency and duration scores for ***propping*** during the PRPs for the VROE group were almost negligible (Table 8.1). These values were also quite low (<13%) for the VIOE group. For the DRLOE group, almost a quarter of the frequency and duration of ***propping*** occurred during the PRPs, and for the FROE group the values were greater (>35%). The highest percentages were obtained for the FIOE group, with over 40% of frequency and over 50% of duration of ***propping*** occurring during the PRPs.

If objects were absent during schedule sessions, ***jump at lid*** occurred on all 5 schedules of reinforcement (Table 8.1). However, in the VROE group no instances of this behaviour occurred during the PRPs. For the VIOE, DRLOE and FROE groups, the percentage of frequency and duration of ***jump at lid*** during the PRPs was less than 20%. For the FIOE group on the other hand, more than 70% of the frequency and duration of this behaviour occurred during the PRPs.

For the DRLOE group over a quarter of the frequency and duration of ***propping*** occurred during the PRPs (Table 8.1). More than half of this behaviour (frequency and duration) took place during PRPs for the FIOE group.

In summary, the lowest percentages (almost negligible) for frequency and duration of ***behaviours directed at the peripheral areas of the box*** occurring during the PRPs are found for the ***variable-ratio*** schedule, with its unpredictable periods of non-reinforcement. In fact, no instances of ***jump at lid*** occurred during the PRPs for this group. The highest percentages (>50% & as high as 73.43%) were found for the more predictable ***fixed-interval*** schedule (Table 8.1).

8.2.4 OTHER BEHAVIOURAL CATEGORIES

Groups with objects present during schedule sessions ("OS" groups)

For the VROS group, less than 6% of the frequency and duration of ***displacement*** occurred during the PRPs (Table 8.1). These percentages were between 21.33% and 28.51% for the VIOS and DRLOS groups. Just less than 40% of the frequency and duration of ***displacement*** occurred during the PRPs in the FROS group. The highest percentage of frequency (48.67%) and duration (60.49%) of this behaviour during the PRPs was obtained in the FIOS group.

Digging/burying was not scored for the FROS group. This behaviour was observed in the VROS group, but no instances occurred during the PRPs. Strikingly similar percentages of frequency (>30%) and duration (>30%) of ***digging/burying*** occurring during the PRPs were observed for the DRLOS and VIOS groups. Most instances of this behaviour took place during the PRPs for the FIOS group, and these were the highest percentages obtained for any behaviour (Table 8.1).

It should be noted that ***rearing*** was not measured for the FROS group. Almost negligible frequency and duration scores were obtained for percentage of ***rearing*** occurring during PRPs for the VROS group. For the VIOS group, almost a quarter of the frequency and duration of ***rearing*** occurred during the PRPs. These values increased to about 40% for the DRLOS group, and to over 50% in the FIOS group (Table 8.1). The highest percentage of ***rearing*** was found for the more predictable ***fixed-interval*** schedule.

Pica was not scored for the FROS group. The percentage of frequency and duration occurring during PRPs was almost negligible for the VROS group. By contrast, these values were greater than 75% for the FIOS group. As with ***digging/burying***, similar percentages (about one third) of frequency and duration of ***pica*** occurring during the PRPs were observed for the DRLOS and VIOS groups (Table 8.1).

In summary, the lowest percentages for frequency and duration of ***displacement***, ***digging/burying***, ***rearing*** and ***pica*** occurring during the PRPs are found for the ***variable-ratio*** schedule, with its unpredictable periods of non-reinforcement. In fact, no instances of ***digging/burying*** occurred during the PRPs for this group. The highest percentages (ranging between 48.67% & 90.63%) were found for the more predictable ***fixed-interval*** group.

Groups with objects absent during schedule sessions (“OE” groups)

For the VROE group, almost negligible amounts of ***displacement*** (frequency & duration) took place during the PRPs, and for the VIOE group these values were less than 8% (Table 8.1). Approximately, a third of the frequency and a quarter of the duration of ***displacement*** occurred during PRPs in the DRLOE group. For the FROE and FIOE groups, about half the instances of ***displacement*** (frequency & duration) occurred during PRPs.

For the VROE group all instances of ***digging/burying*** occurred outside the PRPs (Table 8.1). Less than 15% of the frequency and duration of this behaviour was observed during PRPs in the VIOE group. For the DRLOE group, more than a quarter of ***digging/burying*** (frequency &

duration) took place during the PRPs. The highest percentage of frequency and duration (both >75%) of this behaviour during the PRPs was obtained in the FIOS group.

Rearing was not scored for the FROE group. For the VROE group, almost negligible frequency and duration scores were obtained for percentage of ***rearing*** occurring during PRPs. Less than 15% of the frequency and duration of this behaviour took place during PRPs in the VIOE group (Table 8.1). More than a quarter of ***rearing*** took place during the PRPs for the DRLOE group, and over 60% of this behaviour occurred during PRPs in the FIOE group.

With respect to the ***pica*** category, no instances were observed during schedule sessions for the VIOE group. For the VROE group all instances of ***pica*** occurred outside the PRPs. The highest percentage of frequency (66.67%) and duration (77.06%) of this behaviour during the PRPs was obtained in the FIOS group. About a third of this behaviour (frequency & duration) occurred during the PRPs for the DRLOE group (Table 8.1).

In summary, the lowest percentages for frequency and duration of ***displacement***, ***digging/burying***, ***rearing*** and ***pica*** occurring during the PRPs are found for the ***variable-ratio*** schedule, with its unpredictable periods of non-reinforcement. In fact, no instances of ***digging/burying*** or ***pica*** occurred during the PRPs for this group. The highest percentages (ranging between 51.93% & 78.95%) were found for the more predictable ***fixed-interval*** group.

8.3 GROUPS WITH HIGHEST OR LOWEST TOTAL MEAN FREQUENCY AND DURATION SCORES FOR BEHAVIOURS OCCURRING DURING PRP'S

Some interesting patterns emerge when the highest and lowest total (mean) frequency and duration values, for behaviours occurring during the PRPs, are investigated (Table 8.2). In 13 of the 14 cells for highest frequency and duration, a ***fixed-interval*** group was represented (FIOE or FIOS). Thus, many or most instances of the behaviours scored took place during the PRPs on this predictable schedule. In all 14 cells for lowest frequency and duration, a ***variable-ratio*** group was represented (VROE or VROS). Thus, few or no cases of the behaviours observed occurred during the PRPs on this unpredictable schedule.

Table 8.2
The groups with the highest or lowest percentage of total mean frequency or duration scores for behaviours occurring during the PRPs (for all groups from Experiment 1 & 2, & Litchfield's 1987 study).

BEHAVIOURAL CATEGORY	**HIGHEST TOTAL MEAN FREQUENCY**	**HIGHEST TOTAL MEAN DURATION**	**LOWEST TOTAL MEAN FREQUENCY**	**LOWEST TOTAL MEAN DURATION**
Behaviours directed at the bar and food-trough area (***bar-related behaviour***)	FROE	FIOE	VROE	VROE
Behaviour directed at the stimulus objects (***sniff object***; ***sniff and touch object***; ***chew/bite object***)	FIOS	FIOS	VROS	VROS
Behaviour directed at the peripheral areas of the box (***propping***; ***jump at lid***; ***rearing****) Note. No cases of ***jump at lid*** were observed in the FIOS, VROS or DRLOS groups	FIOE	FIOE	VROE	VROE
Displacement	FIOE	FIOE	VROE	VROE
Digging/Burying*	FIOS	FIOS	VROS/ VROE Both = 0	VROS/ VROE Both = 0
Rearing*	FIOE	FIOE	VROE	VROE
Pica* Note. No cases were observed in the VIOE group	FIOS	FIOS	VROE	VROE

Note. The * indicates that this behaviour was not measured in the 1987 study

8.3.1 OBJECTS PRESENT DURING SCHEDULE SESSIONS ("OS" GROUPS)

Rats on the ***fixed-interval*** schedule (FIOS) showed the highest frequency and duration scores during PRPs for ***behaviours directed at the stimulus objects***, ***digging/burying***, and ***pica***. That is, of all groups, the highest percentages of these behaviours took place during the PRPs (Table 8.2).

The lowest frequency and duration scores during PRPs were observed for rats run on the ***variable-ratio*** schedule (VROS) for ***behaviours directed at the stimulus objects***. All cases of ***digging/burying*** occurred outside the PRPs for this group (Table 8.2).

8.3.2 OBJECTS ABSENT DURING SCHEDULE SESSIONS ("OE" GROUPS)

If objects were absent during schedule sessions, rats on the ***fixed-interval*** schedule (FIOE) showed the highest frequency and duration scores during PRPs for ***behaviours directed at the peripheral areas of the box***, ***rearing*** and ***displacement***. The highest frequency of ***bar-related behaviour*** occurring during the PRPs was for the FROE group, and the highest duration for the FIOE group.

The lowest frequency and duration scores during PRPs were observed for rats run on the ***variable-ratio*** schedule (VROE) for ***bar-related behaviour***, ***behaviours directed at the peripheral areas of the box***, ***rearing*** and ***displacement***. All instances of ***digging/burying*** and ***pica*** occurred outside the PRPs for this group.

8.3.3 SUMMARY

The most stable or lengthy PRPs occurred during ***fixed-interval*** schedules. If objects were absent for rats run on this schedule, ***escape-directed behaviours*** (***propping***, ***jump at lid***), ***rearing*** or ***conflict-related behaviours*** (***displacement***) were most prevalent during PRPs.

The least stable or shortest PRPs typically occurred during ***variable-ratio*** schedules. If objects were absent for rats run on this schedule, ***bar-related behaviour***, ***escape-directed behaviours*** (***propping***, ***jump at lid***), ***rearing*** or ***conflict-related behaviours*** (***displacement***) were least prevalent during PRPs. No instances of ***digging/burying*** occurred during the PRPs in either ***variable-ratio*** group (VROS & VROE), and no ***pica*** occurred during the PRPs in the VROE group.

8.4 TOTAL TIME SPENT ENGAGED IN EXPLORATORY AND OTHER BEHAVIOURS DURING SCHEDULE AND EXTINCTION SESSIONS

Presenting the results in this way is simply intended to provide an opportunity to make some very general comparisons between the five schedules investigated. The frequency data will be discussed in section 8.8. The tables in this section show how much (mean) time rats spent (in each group) engaged in the various behaviours during the three ***schedule*** and three ***extinction*** sessions.

8.4.1 BEHAVIOURS DIRECTED AT THE BAR AND FOOD-TROUGH AREA

During schedule sessions

Not surprisingly, the ***DRL*** groups spent the least amount of time engaged in these behaviours (<640 seconds). This schedule, by definition, encourages a low rate of operant responding. Thus one would expect less time to be spent in the vicinity of the manipulandum. In order of ascending time spent engaged in ***behaviours directed at the bar and food-trough area*** are FROS, VIOS, VROS, VIOE, VROE, FIOS, FROE, and FIOE (Table 8.3). In each case, the group with objects present during schedule sessions ("OS" groups) spent less time at the bar area than its same schedule counterpart ("OE" groups). The time spent in the bar area was highest for the FIOE group (1361.51 seconds), and the FIOS group value was also high. Irrespective of whether objects were present or not, it appears that the ***fixed-interval*** schedule results in a relatively large amount of time being spent engaged in ***behaviours directed at the bar and food-trough area***.

Table 8.3
The total mean time (duration) spent by rats in each group engaged in behaviours directed at the bar and food-trough area (***bar-pressing + bar-related behaviour***) during the three schedule and three extinction sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Duration (in seconds) FROS & FROE (Litchfield,1987)	**Total Mean Duration (in seconds) FIOS & FIOE (Experiment 1)**	**Total Mean Duration (in seconds) VIOS & VIOE (Experiment 1)**	**Total Mean Duration (in seconds) VROS & VROE (Experiment 2)**	**Total Mean Duration (in seconds) DRLOS & DRLOE (Experiment 2)**
- Schedule 748.8 & 1193.99 (562.25+186.55 / 961.41+232.58)	- Schedule 1178.7 & 1361.51 (459.79+718.91 / 517.78+843.73)	- Schedule 894.97 & 1086.64 (543.18+351.79/ 592.88+493.76)	- Schedule 1032.89 & 1087.39 (513.13+519.76/ 212.26+875.13)	- Schedule 481.92 & 636.84 (119.91+362.01/ 159.23+477.61)
- Extinction 731.25 & 910.32 (199.21+532.04 / 360.71+549.61)	- Extinction 920.77 & 806.55 (315.06+605.71 / 368.46+438.09)	- Extinction 844.46 & 612.29 (308.35+536.11/ 260.46+351.83)	- Extinction 887.09 & 638.09 (244.43+642.66/ 86.06+552.03)	- Extinction 427.22 & 509.34 (54.54+372.68/ 50.88+458.46)

During extinction sessions

The ***DRL*** groups again spent the least amount of time engaged in ***behaviours directed at the bar and food-trough area*** (<510 seconds). Time spent in the bar area in ascending order for the other groups is VIOE, VROE, FROS, FIOE, VIOS, VROS, FROE, and FIOS. For all the "OE" groups, which have objects present for the first time in these ***extinction*** sessions, the drop in time spent in the bar area in schedule compared to ***extinction*** sessions is more dramatic than in their "OS" group counterparts (Table 8.3). Even during ***extinction***, time is spent around the food-trough area, since it was a previous source of food.

8.4.2 BEHAVIOURS DIRECTED AT THE STIMULUS OBJECTS

During schedule sessions

Objects were absent for the "OE" groups, so these categories of behaviour are only relevant for half the groups. The least amount of time spent engaged in these behaviours was for the VIOS group (446.37 seconds), followed by the FROS and FIOS groups. Noticeably higher values were observed for the VROS and DRLOS groups (Table 8.4).

Table 8.4
The total mean time (duration) spent by rats in each group engaged in behaviours directed at the stimulus objects (***sniff object*** + ***sniff and touch object*** + ***chew/bite object***) during the three schedule and three extinction sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Duration (in seconds) FROS & FROE (Litchfield,1987)	**Total Mean Duration (in seconds) FIOS & FIOE (Experiment 1)**	**Total Mean Duration (in seconds) VIOS & VIOE (Experiment 1)**	**Total Mean Duration (in seconds) VROS & VROE (Experiment 2)**	**Total Mean Duration (in seconds) DRLOS & DRLOE (Experiment 2)**
- Schedule 530.65 & N/A (91.26+439.39/ n/a)	- Schedule 725.66 & N/A (168.78+523.28+33.6/ n/a)	- Schedule 446.37 & N/A (147.98+296.36+2.03/ n/a)	- Schedule 1312.06 & N/A 159.21+1132.34+20.51/ n/a)	- Schedule 1540.97 & N/A (234.93+1254.58+51.46/ n/a)
- Extinction 552.38 & 514.46 (135.95+416.43 / 172.83+341.63)	- Extinction 602.83 & 806.52 (144.06+408.41+50.36 / 138.43+652.73+15.36)	- Extinction 805.62 & 777.07 (146.38+598.25+60.99/ 120.65+634.26+22.16)	- Extinction 1574.2 & 1753.68 (146.83+1107.19+320.18 /257.26+1425.26+71.16)	- Extinction 1917.03 & 1540.31 (160.23+1377.26+379.54 /212.25+1269.43+58.63)

Note. ***Chew/Bite Object*** was included in the ***Sniff-and-Touch Object*** category in the 1987 study

The DRLOS group spent most time exploring the stimulus objects (1540.97 seconds). This group spent less time in the vicinity of the manipulandum. On this ***DRL*** schedule, the less time that is spent at the food source, the more likely the rat is to be reinforced upon its return. Thus, there is little ***risk*** involved if it leaves the area. This may provide a good example of ***central area foraging***. That is, the rat takes time to explore other areas around the central food source (food-trough), and then returns to this area. The ***variable-interval*** schedule, on the other hand, is very unpredictable. Thus, it may be more ***risky*** for the rat to leave this area of food, especially if the rat explores surrounding areas for food and discovers no other source of food. However, the ***variable-ratio*** schedule is also unpredictable, but apart from the ***DRL*** schedule, rats on this schedule showed the highest amount of time (1312.06 seconds) spent ***exploring the stimulus objects*** (Table 8.4).

During extinction sessions

The ***fixed-ratio*** groups spent the least amount of time ***exploring the stimulus objects*** (<560 seconds). The ***variable-ratio*** and ***DRL*** groups spent the most time engaged in these behaviours (>1540 seconds). Interestingly, the "OE" groups, which had objects present for the first time, did not necessarily spend more time exploring the objects than their "OS" counterparts. Less time was spent in ***exploration of the objects*** in the FROE, VIOE, and DRLOE groups than in their "OS" counterparts. More time was spent in FIOE and VROE than in their "OS" counterparts. Compared to the "OS" groups when they first encountered objects during schedule sessions, more time was spent exploring objects if they were first encountered in ***extinction*** sessions for the FIOE, VIOE, and VROE groups. With the exception of the FIOS group, more time was spent exploring objects for the "OS" groups than in the schedule sessions. Thus, ***extinction*** produces more ***exploration of stimulus objects*** than schedule sessions for four of the five schedules investigated (Table 8.4).

8.4.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

During schedule sessions

In order of ascending time spent engaged in ***behaviours directed at the peripheral areas of the box*** the groups are VIOS, VROS, FROE, FIOS, DRLOS, FROS, FIOE, DRLOE, VROE and VIOE (Table 8.5). The total mean duration values ranged from 373.39 seconds to 1051.62 seconds. Of the two behaviours that were included in this category, the most time was spent engaged in ***propping*** by all groups. Only low (or zero) amounts of time were spent engaged in ***jump at lid*** for all groups (highest value was 71.78 seconds for the FROE group).

The rats run on the ***variable*** schedules, without stimulus objects present (VIOE & VROE), spent the most time engaged in ***behaviours that were directed at the outer perimeters of the box*** (particularly ***propping***). Thus, if the schedule was unpredictable, and there were no possible alternative sources of food or stimulation (objects) then the rats spent more time in these ***escape-directed behaviours***. If objects were present during the unpredictable ***variable-ratio*** and ***variable-interval*** schedules (VIOS & VROS), the rats spent the least amount of time of all the groups engaged in ***escape-directed behaviours*** (Table 8.5).

Table 8.5
The total mean time (duration) spent by rats in each directed at the peripheral areas of the box (***propping + jump at lid***) during the three group engaged in behaviours schedule and three extinction sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Duration (in seconds) FROS & FROE (Litchfield,1987)	**Total Mean Duration (in seconds) FIOS & FIOE (Experiment 1)**	**Total Mean Duration (in seconds) VIOS & VIOE (Experiment 1)**	**Total Mean Duration (in seconds) VROS & VROE (Experiment 2)**	**Total Mean Duration (in seconds) DRLOS & DRLOE (Experiment 2)**
- Schedule 684.56 & 511.61 (683.58+0.98/ 439.83+71.78)	- Schedule 543.03 & 762.72 (543.03+0/ 751.16+11.56)	- Schedule 373.39 & 1051.62 (353.76+19.63/ 1006.69+44.93)	- Schedule 472.73 & 993.04 (472.73+0/ 992.23+0.81)	- Schedule 665.21 & 921 (665.21+0/ 919.86+1.14)
- Extinction 639.02 & 358.32 (637.14+1.88 / 339.94+18.38)	- Extinction 745.69 & 659.72 (744.81+0.88/ 656.86+2.86)	- Extinction 535.2 & 1311.34 (518.44+16.76/ 1290.48+20.86)	- Extinction 453.83 & 749.06 (452.88+0.95/ 748.88+0.18)	- Extinction 851.73 & 894.73 (851.58+0.15/ 894.73+0)

During extinction sessions

Less amounts of time were spent engaged in ***behaviours directed at the peripheral areas of the box*** during ***extinction***, than in schedule sessions for the FROS, FROE, FIOE, VROS, VROE and DRLOE groups (Table 8.5). For the other four groups, the time spent in these behaviours increased during ***extinction*** sessions. One might expect these to increase in ***extinction***, since the main food source is now ***depleted*** and it is less ***risky*** to leave and seek new sources - not just in the immediate area (no food found around the stimulus objects), but beyond. Very little time was spent engaged in ***jump at lid*** during ***extinction***.

Even with objects now present, the rats run on the least predictable schedules (VROE & VIOE) still spent large amounts of time in ***escape-directed behaviours*** (table 8.5). Their same schedule counterparts also spent markedly less time engaged in these behaviours. Rats previously run on the ***fixed-interval*** schedule, without objects present, now directed the least amount of time towards the ***peripheral areas of the box*** in the presence of objects.

8.4.4 OTHER BEHAVIOURAL CATEGORIES

Digging/burying, rearing and ***pica*** were not scored for the ***fixed-ratio*** groups in Litchfield's (1987) study.

During schedule sessions

The VIOS group was the only group that spent less than 100 seconds engaged in ***displacement*** activities over the three sessions (Table 8.6). This group spent noticeably less time engaged in this behaviour than any other group. Only the ***fixed-ratio*** and ***DRL*** groups with objects present during schedule sessions spent more time engaged in ***displacement*** than their "OE" (objects absent) counterparts. That is, in most case the presence of objects resulted in less ***displacement*** activities. Overall, the ***variable-ratio*** and ***DRL*** rats spent the most time engaged in ***displacement*** activities.

All groups spent relatively small amounts of time engaged in ***digging/burying*** during schedule sessions (Table 8.6). The ***variable-ratio*** groups spent the least time, and the FIOE group spent the most time ***digging/burying***. If objects were absent ("OE" groups), the ***fixed-interval*** and ***DRL*** rats spent noticeably more time ***digging/burying*** than their same schedule counterparts ("OS" groups). By contrast, the presence of objects during the ***variable-interval*** schedule resulted in more of this behaviour.

If objects were absent during schedule sessions ("OE" groups), rats spent far more time ***rearing*** than their same schedule counterparts (Table 8.6). The FIOE group spent the most time engaged in this behaviour. The VIOS group spent the least time ***rearing***.

The VIOE group stands out as the only group that did not engage in ***pica*** during schedule sessions (Table 8.6). With the exception of the ***variable-interval*** rats, the absence of objects during schedule sessions ("OE" groups), resulted in far greater time spent engaged in ***pica*** (than for the same schedule counterparts). Overall, the ***fixed-interval*** and ***variable-interval*** rats spent little time engaged in ***pica***, whilst the ***variable-ratio*** and ***DRL*** rats spent noticeably more time engaged in this behaviour.

During extinction sessions

The ***DRL*** groups spent the most time engaged in ***displacement*** activities during ***extinction*** followed by the ***variable-ratio*** groups (Table 8.6). The VIOS group spent the least time engaged in this behaviour. If objects were first encountered during ***extinction*** ("OE" groups), then more time was spent in ***displacement*** activities (with the exception of the ***variable-ratio*** groups).

Relatively little time was spent ***digging/burying*** during ***extinction*** (Table 8.6). The ***fixed-interval*** groups spent the most time engaged in this behaviour. The least amount of time spent

digging/burying was for the VROS group, although the VIOE and DRLOS groups also spent less than 10 seconds engaged in this behaviour during ***extinction***.

Table 8.6
The total mean time (duration) spent by rats in each group engaged in other behavioural categories (***displacement***, ***digging/burying***, ***rearing*** and ***pica***) during the three schedule and three extinction sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Duration (in seconds) FROS & FROE (Litchfield,1987)	**Total Mean Duration (in seconds) FIOS & FIOE (Experiment 1)**	**Total Mean Duration (in seconds) VIOS & VIOE (Experiment 1)**	**Total Mean Duration (in seconds) VROS & VROE (Experiment 2)**	**Total Mean Duration (in seconds) DRLOS & DRLOE (Experiment 2)**
displacement - Schedule 251.08 & 218.23 - Extinction 286.26 & 316.96	***displacement*** - Schedule 186.78 & 200.1 - Extinction 224.1 & 327.43	***displacement*** - Schedule 78.03 & 156.43 - Extinction 150.13 & 237.73	***displacement*** - Schedule 327.36 & 341.03 - Extinction 490.71 & 405.38	***displacement*** - Schedule 368.71 & 282.03 - Extinction 504.84 & 559.03
digging/burying *Not measured in 1987 study	***digging/burying*** - Schedule 18.68 & 45.03 - Extinction 42.16 & 41.41	***digging/burying*** - Schedule 26.83 & 10.46 - Extinction 20.88 & 8.36	***digging/burying*** - Schedule 6.79 & 8.83 - Extinction 6.91 & 11.38	***digging/burying*** - Schedule 23.1 & 34.31 - Extinction 9.38 & 19.71
rearing *Not measured in 1987 study	***rearing*** - Schedule 335.88 & 599.31 - Extinction 779.38 & 812.73	***rearing*** - Schedule 175.2 & 555.46 - Extinction 445.83 & 674.04	***rearing*** - Schedule 217.76 & 528.48 - Extinction 239.03 & 122.23	***rearing*** - Schedule 353.81 & 574.89 - Extinction 301.43 & 246.69
pica *Not measured in 1987 study	***pica*** - Schedule 55.71 & 80.73 - Extinction 344.11 & 116.91	***pica*** - Schedule 90.03 & 0 - Extinction 265.86 & 86.7	***pica*** - Schedule 281.7 & 400.61 - Extinction 259.71 & 547.31	***pica*** - Schedule 235.46 & 443.56 - Extinction 393.83 & 424.88

The ***fixed-interval*** groups spent the most time ***rearing***, whilst the ***variable-ratio*** rats spent the least time engaged in this behaviour during ***extinction*** (Table 8.6). The ***fixed-interval*** and ***variable interval*** groups spent noticeably more time ***rearing*** during ***extinction*** than schedule sessions. For these groups, if objects were first encountered during ***extinction***, more time was spent ***rearing*** during those sessions than for the same schedule counterparts. For the ***variable-ratio*** and ***DRL*** groups, the opposite was true. That is, if objects were first encountered during ***extinction*** less time was spent ***rearing*** than for the same schedule counterparts. Overall, most groups spent noticeably more time ***rearing*** during ***extinction*** than schedule sessions. The exceptions were the ***DRL*** groups and the VROE group.

The VROE group engaged in substantially more ***pica*** than any other group. Similarly, the VIOE group engaged in very little ***pica*** during ***extinction*** (Table 8.6). With the exception of the VROS and DRLOE groups, noticeably more time was spent engaged in ***pica*** during ***extinction*** than during schedule sessions.

8.5 GROUPS WITH THE HIGHEST OR LOWEST TOTAL MEAN SCORES FOR TIME SPENT ENGAGED IN THE VARIOUS BEHAVIOURS

Some interesting patterns emerge when the highest and lowest total mean values for total session time spent engaged in various behaviours are investigated (Table 8.7). In seven of the 14 cells for highest and lowest duration, the same group had an extreme score in the schedule sessions, as well as the ***extinction*** sessions (*i.e.*, highest score for both, or lowest score for both).

8.5.1 OBJECTS PRESENT DURING SCHEDULE AND EXTINCTION SESSIONS ("OS GROUPS)

The FROS group was the only group, which did not record a highest or lowest value for any duration measure of behaviour. However, second lowest values were recorded for ***behaviours directed at stimulus objects*** in both schedule and ***extinction*** sessions. (It should be noted that the 1987 study did not measure ***rearing***, ***digging/burying*** or ***pica*** for the ***fixed-ratio*** groups). This exploratory activity is second lowest during ***extinction***, after the FROE group, despite the fact that ***resistance to extinction*** following the predictable ***fixed-ratio*** schedule should be low, and thus encourage exploratory behaviour.

Rats in the FIOS group spent the highest amount of time engaged in ***behaviours directed at the bar and food-trough area*** and ***digging/burying*** during ***extinction*** sessions. ***Extinction*** should be readily discriminated (low ***resistance to extinction***) by rats that have been run on the very predictable ***fixed-interval*** schedule, but the rats that had stimulus objects present during schedule sessions have already had the opportunity to investigate other potential sources of reinforcement. ***Digging/burying*** may be either an ***escape-directed behaviour*** or related to ***foraging behaviour***.

The least amount of time spent engaged in ***displacement*** activities in both the schedule and ***extinction*** sessions, was recorded for the VIOS group. The least amount of time spent engaged in ***behaviours directed at the stimulus objects*** and ***rearing*** during schedule sessions was also recorded for this group. Despite the ***variable-interval*** schedule being unpredictable, with respect to the delivery of reinforcement, the rats spend less time than other "OS" groups exploring stimulus objects (which could be alternative sources of food). One might expect the ***variable-interval*** schedule to create considerable ***conflict*** in the rats (with its unpredictability of reinforcement), but instead these rats engage in less ***displacement*** activities than any other group.

Table 8.7
The groups with the highest or lowest total mean duration scores for time spent engaged in the various behavioural categories (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

BEHAVIOURAL CATEGORY	**HIGHEST TOTAL MEAN DURATION**	**LOWEST TOTAL MEAN DURATION**
Behaviours directed at the bar and food-trough area (***bar-pressing***; ***bar-related behaviour***)		
- schedule	FIOE	DRLOS
- extinction	FIOS	DRLOS
Behaviour directed at the stimulus objects (***sniff object***; ***sniff and touch object***; ***chew/bite object***)		
- schedule	DRLOS	VIOS
- extinction	DRLOS	FROE
Behaviour directed at the peripheral areas of the box (***propping***; ***jump at lid)***		
- schedule	VIOE	VIOS
- extinction	VIOE	FROE
Displacement		
- schedule	DRLOS	VIOS
- extinction	DRLOE	VIOS
Digging/Burying*		
- schedule	FIOE	VROS
- extinction	FIOS	VROS
Rearing*		
- schedule	FIOE	VIOS
- extinction	FIOE	VROE
Pica*		
- schedule	DRLOE	VIOE
- extinction	VROE	VIOE

Note. The * indicates that the behaviour was not scored in the 1987 study.

The VROS group spent the least amount of time engaged in ***digging/burying*** in both schedule and ***extinction*** sessions. No other highest or lowest values were recorded. It is unclear why only this behaviour should be lowest on this unpredictable schedule, which should show a high ***resistance to extinction***. That is, rats should still spend high amounts of time near the bar area and therefore spend less time engaged in any other activities.

The DRLOS rats spent the least amount of time engaged in ***behaviours directed at the bar and food-trough area*** during both schedule and ***extinction*** sessions. However, this group also spent the most time engaged in ***behaviours directed at the stimulus objects*** for both schedule and ***extinction*** sessions. The DRLOS group also spent the most time engaged in ***displacement*** activities during schedule sessions. It should be noted that these were the sessions in which the DRLOS rats first encountered stimulus objects, as well as, having to learn to ***bar press*** at a low rate. Thus, it is unclear which factor (or a combination of both) could account for this ***conflict*** behaviour. ***General exploratory activity*** is not highest in this group, since only ***stimulus object exploration***, not ***peripheral area exploration*** is highest (although the latter may be ***escape-directed behaviour***). The inter-reinforcement time on this ***DRL*** schedule is only 15 seconds. This may not allow enough time to explore areas further away from the only food source, since ***optimal foraging*** on this schedule might only encourage short forays away from the bar, and the objects would be more thoroughly investigated as nearby potential food sources.

8.5.2 OBJECTS ONLY PRESENT DURING EXTINCTION SESSIONS ("OE" GROUPS)

Rats in the FROE group spent the least amount of time engaged in ***behaviours directed at the peripheral areas of the box*** during both schedule and ***extinction*** sessions. They also spent the least amount of time engaged in ***behaviours directed at the stimulus objects*** during ***extinction*** sessions. Thus, ***exploratory activity*** is lowest in this group (both ***stimulus object exploration***, and ***peripheral area exploration***- although the latter may be ***escape-directed behaviour***). This group had the second highest score for time spent at the ***bar and food-trough area*** (during schedule and ***extinction*** sessions). Thus, rats in this group spent higher amounts of time at the bar and food-trough and very little time exploring the stimulus objects or peripheral areas of the box. (It should be noted that the 1987 study did not measure ***rearing***, ***digging/burying*** or ***pica*** in the ***fixed-ratio*** groups).

The FIOE group spent the highest amount of time engaged in ***behaviours directed at the bar and food-trough area*** during schedule sessions. This group also spent the highest amount of time engaged in ***digging/burying*** during schedule sessions. For this group there were no stimulus objects to explore during schedule sessions, and reinforcement arrived at regular intervals, so one would expect high amounts of behaviour directed at the food source to occur. Although the highest values for the duration of ***digging/burying*** were recorded for this group, the value was too low to be considered a ***schedule-induced*** or ***adjunctive behaviour***. It could be either ***escape-directed*** or related to some aspect of ***foraging behaviour***.

The VIOE group spent the highest amount of time engaged in ***behaviours directed at the peripheral areas of the box*** in both schedule and ***extinction*** sessions. This group also spent the least amount of time engaged in ***pica*** in both schedule and ***extinction*** sessions. Unlike the ***DRL*** groups with their short inter-reinforcement times of 15 seconds, the inter-reinforcement time for the ***variable-interval*** group is on average 60 seconds. It is a quite unpredictable schedule with randomly distributed, and at times quite long inter-reinforcement times. This schedule, in this instance, elicits higher amounts of ***exploratory behaviour directed towards peripheral areas*** (or ***escape-directed behaviour***), rather than towards the stimulus objects. ***Optimal foraging*** on this schedule may encourage the rats to move further afield from the only food source, since food is only available at unpredictable times. Once ***extinction*** occurs, it takes time for the rat to discover that the food source or ***patch is depleted***. However, the time spent engaged in ***behaviours directed at peripheral areas of the box*** is longer than during schedule sessions, suggesting that the rats are treating it as a ***depleted food patch***. Since the rats are unable to actually leave the box, they still continue to return to the only food source known. It is unclear why the ***pica*** value is lowest for this group.

The highest amount of time spent engaged in ***pica*** during ***extinction*** sessions was recorded in the VROE group. ***Pica*** could be considered to provide the rats with an alternative source or type of food. However, the actual time spent engaged in this behaviour could be high enough to suggest that this activity is an ***adjunctive*** or ***extinction-induced behaviour*** (which will be discussed in the next section).

The DRLOE group recorded the highest amounts of time spent engaged in ***displacement*** activities during ***extinction*** sessions and in ***pica*** during schedule sessions. ***Pica*** might be considered an alternative food source, on a schedule that might be considered to encourage foraging away from the known food source. ***Extinction*** following a ***DRL*** schedule may create ***conflict***, as reflected by high amounts of time spent engaged in ***displacement*** activities, since the food source is now ***depleted***, but the rats were previously reinforced for spending time away from the bar area. Stimulus objects are present, but provide no alternative source of food. However, the actual time spent engaged in ***displacement*** could be high enough to suggest that this activity is an ***adjunctive*** or ***extinction-induced behaviour*** (which will be discussed in the next section).

8.6 BEHAVIOURAL CATEGORIES ENGAGED IN FOR MORE THAN 10% OF TOTAL SESSION TIME

The total mean time spent engaged in some behaviours was possibly high enough to suggest that these behaviours might have been ***adjunctive*** or ***schedule/extinction-induced behaviours***. The "10% of total time" (usually of a whole day) criterion is sometimes used as a means of defining ***stereotypic behaviour*** (Shepherdson, 1989), which an ***adjunctive behaviour*** could be considered to be. The mean total of each duration measure for the three schedule and three ***extinction*** sessions (from Tables 8.3 – 8.6) has been divided by the total duration for the three schedule sessions (5400 seconds) or three ***extinction*** sessions (5400 seconds). This percentage of total session time spent engaged in each behaviour (mean for the group) is provided in Table 8.8. It is then possible to determine which behavioural categories were engaged in for more than 10% of the total session time.

8.6.1 BEHAVIOURS DIRECTED AT THE BAR AND FOOD-TROUGH

Bar pressing was engaged in for more than 10% of the total time during schedule sessions in both ***fixed-ratio*** and ***variable-interval*** groups. During ***extinction***, this behaviour took up less than 10% of the total session time for all groups.

Both ***fixed-interval*** groups, and the VROE group spent more than 10% of total session time engaged in ***bar-related behaviour*** during schedule sessions. In ***extinction***, both ***variable-ratio*** groups, and the FROE and FIOS groups spent more than 10% of total session time engaged in this behaviour.

As a combined score, ***behaviours directed at the bar and food-trough area***, these behaviours took up more than 10% of the total time during schedule sessions in all, except the DRLOS group (Table 8.8). In fact, the FROE, both ***fixed-interval*** groups, VIOE and VROE groups spent more than 20% of total schedule time engaged in these behaviours. All groups (except the two ***DRL*** groups) spent more than 10% of total session time during ***extinction*** engaged in these behaviours.

Table 8.8

The percentage (> 10%) of total session time spent engaged in the various behavioural categories (for all groups from Experiment 1 & 2, & Litchfield's 1987 study). A dash (-) indicates that the percentage was less than 10%.

GROUP	**Behaviours directed at the bar & food-trough area** (***bar-pressing; bar-related behaviour***)	**Behaviours directed at the stimulus objects** (***sniff object; sniff-&-touch object; chew/bite object***)	**Behaviours directed at the peripheral areas of the box** (***propping; jump at lid***)	***Rearing***	***Displace-ment***	***Pica***	***Dig / Bury***
FROS -schedule	13.9%	-	12.7%	Not scored	-	-	-
-extinction	13.5%	10.2%	11.8%		-	-	-
FROE -schedule	22.1%	No objects present	-	Not scored	-	-	-
-extinction	16.9%	-	-		-	-	-
FIOS -schedule	21.8%	13.4%	10.1%	-	-	-	-
-extinction	17.1%	11.2%	13.8%	14.4%	-	-	-
FIOE -schedule	25.2%	No objects present	14.1%	11.1%	-	-	-
-extinction	14.9%	14.9%	12.2%	15.1%	-	-	-
VIOS -schedule	16.6%	-	-	-	-	-	-
-extinction	15.6%	14.9%	-	-	-	-	-
VIOE -schedule	20.1%	No objects present	19.5%	10.3%	-	-	-
-extinction	11.3%	14.4%	24.3%	12.5%	-	-	-
VROS -schedule	19.1%	24.3%	-	-	-	-	-
-extinction	16.4%	29.2%	-	-	-	-	-
VROE -schedule	20.1%	No objects present	18.4%	-	-	-	-
-extinction	11.8%	32.5%	13.9%	-	-	10.1%	-
DRLOS -schedule	-	28.5%	12.3%	-	-	-	-
-extinction	-	35.5%	15.8%	-	-	-	-
DRLOE -schedule	11.8%	No objects present	17%	10.7%	-	-	-
-extinction	-	28.5%	16.6%	-	10.4%	-	-

8.6.2 BEHAVIOURS DIRECTED AT THE STIMULUS OBJECTS

All groups spent less than 10% of total session time during schedule and ***extinction*** sessions engaged in ***sniff object*** and ***chew/bite object***. With respect to ***sniff and touch object***, the VROS and DRLOS groups spent more than 20% of total schedule session time engaged in this behaviour. For the other groups with objects present during schedule sessions (half the groups had no objects present until ***extinction***), less than 10% of total schedule time was spent engaged in this behaviour. During ***extinction***, more than 10% of total session time was spent engaged in ***sniff and touch object*** by the FIOE and both ***variable-interval*** groups, and more than 20% by both ***variable-ratio***, and ***DRL*** groups.

As a combined score, ***behaviours directed at the stimulus objects***, two groups with objects present during schedule sessions (VROS & DRLOS) spent more than 20% of the total schedule time engaged in these behaviours, and one group more than 10% (FIOS). However, during ***extinction*** only one group (FROE) spent less than 10% of total session time engaged in ***behaviours directed at the stimulus objects*** (Table 8.8). More than 30% of total time during ***extinction*** was spent engaged in these behaviours by the VROE and DRLOS groups, more than 20% of total time by the VROS and DRLOE groups, and more than 10% by the remaining groups (FROS, both ***fixed-interval***, & both ***variable-interval*** groups).

8.6.3 BEHAVIOURS DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

More than 10% of total schedule and total ***extinction*** time was spent engaged in ***propping*** by all groups, except FROE, VIOS and VROS. For the VIOE group more than 20% of total ***extinction*** time was spent engaged in this behaviour. Less than 10% of total session time (schedule & ***extinction***) was taken up by ***jump at lid*** in all groups of rats.

As a combined score, ***behaviours directed at peripheral areas of the box***, it accounted for more than 10% of total schedule session time in most groups (except FROE, VIOS & FIOS groups). Since there were no objects present in the "OE" groups, a different type of exploratory behaviour is observed, namely, ***exploration directed at the outer perimeters*** of the box (Table 8.8). This could also represent an attempt to leave the box (***escape-directed behaviour***), perhaps to explore other areas. During ***extinction*** sessions, ***behaviours directed at peripheral areas of the box*** accounted for more than 10% of total session time in all groups (except FROE, VIOS & FIOS groups).

8.6.4 OTHER BEHAVIOURAL CATEGORIES

All groups spent less than 10% of total schedule session time engaged in ***displacement*** (Table 8.8). During ***extinction***, only the DRLOE group engaged in this behaviour for more than 10% of the total session time. Similarly, less than 10% of total schedule session time was spent engaged in ***pica*** by all groups of rats (Table 8.8). During ***extinction***, only the VROE group engaged in this behaviour for more than 10% of the total session time. All groups spent less than 10% of total session time (schedule & ***extinction***) engaged in ***digging/burying*** (Table 8.8). More than

10% of total schedule session time was spent ***rearing*** by the FIOE, VIOE and DRLOE groups (Table 8.8). These groups did not have stimulus objects present during these sessions. The FIOS, FIOE and VIOE groups spent more than 10% of total ***extinction*** session time engaged in this behaviour.

8.6.5 SUMMARY

As already mentioned, Table 8.8 shows what behavioural categories took up more than 10% of the total schedule or ***extinction*** session time for each group of rats. ***Pica*** and ***displacement*** were both only engaged in for more than 10% by one group during ***extinction***. These behaviours might be considered ***extinction-induced*** in these two groups (VROE, and DRLOE). For the FIOE and VIOE groups, ***rearing*** could be considered both ***schedule-induced*** and ***extinction-induced***, since it occurred for more than 10% of session time during schedule and ***extinction*** sessions. ***Rearing*** was also ***schedule-induced*** for the DRLOE group (>10% of schedule session time), and ***extinction-induced*** for the FIOS group (>10% of ***extinction*** time).

There are a number of instances in which the mean total session time spent engaged in behaviours (***behaviours directed at the bar and food-trough area***, ***behaviours directed at the stimulus objects***, and ***behaviours directed at the peripheral areas of the box***) is greater than 20% (ranging from 20.1% to 35.5%). For these "combined" behavioural categories the 10% criterion may be too low when determining whether the behaviour is being engaged in to an ***excessive*** degree. The following section presents mean behavioural duration values that account for greater than 20% of total session time.

8.6.6 CONCLUSIONS

If more than 10% of total session time is devoted to ***rearing***, ***displacement*** or ***pica***, can these behaviours be considered to be ***stereotypic*** in nature? Certainly in the wild the expression of these behaviours may enhance a rat's chance of survival. ***Rearing*** allows the rat to see further (increases the rat's height) and continually monitor the immediate surroundings, which may help detect potential predators or conspecific rivals for resources. ***Displacement*** activities allow the rat, which is in a ***conflict*** situation (*e.g.*, approach or avoid) to delay its immediate response, while it assesses the situation more closely. Finally, ***pica*** may provide the rat with alternative sources of food, if the usual preferred or more nutritious foods are not available (although Erwin & Deni, 1979, suggest that this behaviour does not occur in natural environments). However, if these behaviours are excessive in a captive environment, they may indeed qualify as ***stereotypic*** or aberrant in nature.

The lack of objects to explore as potential sources of food or stimulation during ***fixed-interval***, ***variable-interval*** and ***DRL*** schedules ("OE" groups) resulted in more than 10% of schedule session time being devoted to ***rearing***. Despite the availability of stimulus objects during ***extinction***, the FIOE and VIOE groups still engaged in ***rearing*** for more than 10% of session time, as did the FIOS group. ***Rearing*** might have become a ***stereotypic behaviour*** for these groups, particularly for the two groups that showed even higher percentages in ***extinction*** (FIOE & VIOE groups). Excessive ***rearing*** may simply reflect increased vigilance or it may be the start of a qualitatively aberrant behaviour (such as ***head tossing***) or a quantitatively aberrant behaviour (such as ***pacing***) observed in some captive animals (Erwin & Deni, 1979).

During ***extinction***, the DRLOE group spent more than 10% of session time engaged in ***displacement*** activities. For this group, these behaviours may be akin to the excessive ***over-grooming*** that is sometimes observed in captive settings (Bloomsmith, 1989).

The VROE group engaged in ***pica*** for more than 10% of ***extinction*** time. ***Pica*** may provide an alternative source of food during periods of non-reinforcement. However, when it comprises such a large proportion of total session time, it may have truly become an ***appetitive disorder***. Indeed, Erwin and Deni (1979) label ***pica*** as a qualitatively abnormal behaviour, which is only observed in captive settings.

8.7 BEHAVIOURAL CATEGORIES ENGAGED IN FOR MORE THAN 20% OF TOTAL SESSION TIME

Table 8.9 presents the percentage of total session time spent engaged in each combined behavioural category (mean for the group), if it took up more than 20% of the total session time.

8.7.1 BEHAVIOURS DIRECTED AT THE BAR AND FOOD-TROUGH AREA

Neither ***bar pressing*** nor ***bar-related behaviour*** was engaged in for more than 20% of the total time for any group during schedule or ***extinction*** sessions. However, as a combined score (***behaviours directed at the bar and food-trough area***) the FROE, FIOS, FIOE, VIOE and VROE group spent more than 20% of the total time during schedule sessions engaged in these behaviours (Table 8.9). Of these five groups, only the FIOS group had objects present during the schedule sessions. Thus, without objects to explore during schedule sessions, rats run on a ***fixed-interval***, ***variable-interval***, ***fixed-ratio*** or ***variable-ratio*** schedule devote more time to ***behaviours directed at the bar and food-trough area***.

Table 8.9
The percentage (> 20%) of total session time spent engaged in the various behavioural categories (for all groups from Experiment 1 & 2, & Litchfield's 1987 study). A dash (-) indicates that the percentage was less than 20%.

GROUP	**Behaviours directed at the bar & food-trough area (*bar-pressing*; *bar-related behaviour*)**	**Behaviours directed at the stimulus objects (*sniff object*; *sniff-&-touch object; chew/bite object*)**	**Behaviours directed at the peripheral areas of the box (*propping*; *jump at lid*)**
FROS -schedule	-	-	-
-extinction	-	-	-
FROE -schedule	22.1%	No objects present	-
-extinction	-	-	-
FIOS -schedule	21.8%	-	-
-extinction	-	-	-
FIOE -schedule	25.2%	No objects present	-
-extinction	-	-	-
VIOS -schedule	-	-	-
-extinction	-	-	-
VIOE -schedule	20.1%	No objects present	-
-extinction	-	-	24.3%
VROS -schedule	-	24.3%	-
-extinction	-	29.2%	-
VROE -schedule	20.1%	No objects present	-
-extinction	-	32.5%	-
DRLOS-schedule	-	28.5%	-
-extinction	-	35.5%	-
DRLOE-schedule	-	No objects present	-
-extinction	-	28.5%	-

8.7.2 BEHAVIOURS DIRECTED AT THE STIMULUS OBJECTS

With respect to ***sniff and touch object***, the VROS and DRLOS groups spent more than 20% of total schedule session time engaged in this behaviour (Table 8.9). More than 20% of total ***extinction*** session time was spent engaged in ***sniff and touch object*** by the VROS, VROE, DRLOS and DRLOE groups. It should be noted that the VROE and DRLOE groups did not have objects present during schedule sessions. As a combined score, ***behaviours directed at the stimulus objects***, no other groups spent more than 20% of total session (schedule or ***extinction***) time engaged in these behaviours. Thus if stimulus objects are present, rats on the unpredictable ***variable-ratio*** schedule, or the ***DRL*** schedule (which results in low rates of operant responding) spend large amounts of time ***exploring the stimulus objects***. In particular, these schedules elicit exploratory behaviours that involve both ***sniffing and touching***. That is, a specific topography of response is elicited.

8.7.3 BEHAVIOURS DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

Only the VIOE group spent more than 20% of total ***extinction*** time engaged in ***behaviours directed at the peripheral areas of the box***, mainly in the form of ***propping***. All of the other groups spent less than 20% of the total schedule or ***extinction*** time engaged in ***propping*** or ***jump at lid*** (Table 8.9).

8.7.4 OTHER BEHAVIOURAL CATEGORIES

No group engaged in ***displacement***, ***digging/burying***, ***rearing*** or ***pica*** for more than 20% of total schedule or ***extinction*** session time (Table 8.9).

8.7.5 SUMMARY

Groups with objects present during schedule sessions ("OS" groups)

During schedule sessions, the ***fixed-ratio*** (FROS) and ***variable-interval*** (VIOS) schedules do not result in any behavioural category being engaged in for more than 20% of the total session time (including "combined" categories). That is, no behaviour is engaged in to an ***excessive*** degree.

The ***fixed-interval*** (FIOS) schedule results in the highest proportion of total time spent engaged in ***behaviours directed at the bar and food-trough area***. Thus the highly predictable ***fixed-interval*** schedule maintains the highest amount of time spent around the known food source (bar area), even though stimulus objects (potential alternative sources of food) are present.

Rats in the ***variable-ratio*** (VROS) and ***DRL*** (DRLOS) groups spent more than a quarter of total session time engaged in ***behaviours directed at stimulus objects*** (> 20% of time being spent engaged in ***sniff and touch object***). Thus, with respect to exploratory behaviours, schedules that ***induced*** the highest amounts of total time spent in ***exploration directed towards the stimulus objects*** were the ***variable-ratio*** (VROS) and ***DRL*** (DRLOS) schedules.

No "OS" group engaged in ***behaviour directed at the peripheral areas of the box*** for more than 20% of schedule or ***extinction*** session time. Thus with stimulus objects available to explore, these groups of rats did not engage in excessive ***escape-directed behaviours***.

During ***extinction*** sessions, the ***fixed-ratio*** (FROS) and ***variable-interval*** (VIOS) schedules do not result in any behavioural category being engaged in for more than 20% of total session time.

Rats in the ***variable-ratio*** (VROS) and ***DRL*** (DRLOS) groups spent more than a quarter (or even a third in the case of the latter group) of the total schedule or ***extinction*** session time engaged in ***behaviours directed at the stimulus objects***. In addition, rats spent over 20% of session time ***sniffing and touching objects***. Thus, ***extinction induced*** high amounts of total session time spent in ***exploration directed at the stimulus objects***, following ***variable-ratio*** and ***DRL*** schedules.

Finally, for the VROS and DRLOS groups, ***behaviours directed at the stimulus objects*** might be considered both ***schedule-induced*** and ***extinction-induced***. In both cases the value is higher in ***extinction***, despite previous exposure to stimulus objects (and possible habituation to novel objects).

Groups with objects first present during extinction sessions ("OE" groups)

During schedule sessions, only the ***DRL*** schedule results in less than 20% of total session time being spent engaged in ***behaviours directed at the bar and food-trough area***. This is not surprising, since this schedule evokes low rates of operant responding, and thus less time would be spent around the bar area. Rats in the FIOE group spent the highest percentage of total session time (25.2%) engaged in these behaviours. Without stimulus objects to explore, rats are able to devote more time to behaviour centred at the only known food source.

Almost a quarter of total session time during ***extinction*** was spent engaged in ***behaviours directed at peripheral areas of the box*** in the VIOE group (>20% of total session time spent ***propping***). Thus, ***extinction*** following an unpredictable ***variable-interval*** schedule ***induced*** the highest amounts of total time spent engaged in ***behaviours directed at peripheral areas of the***

box. This value was higher in ***extinction***, despite stimulus objects being present for the first time (*i.e.*, the objects did not "hold their attention", as the ***escape-directed behaviours*** only increased).

During ***extinction*** sessions, the ***fixed-ratio*** (FROE) schedule did not result in any combined behavioural category being engaged in for more than 20% of total session time. This is despite the fact that it would have a ***low resistance to extinction***, which would allow more time to be spent engaged in behaviours away from the bar area.

Rats in the VROE and DRLOE groups spent more than a quarter of the total session time in ***exploration directed towards the stimulus objects*** (over 20% of this time spent in ***sniff and touch object***). This was their first encounter with stimulus objects. Thus, ***extinction*** following ***variable-ratio*** and ***DRL*** schedules ***induced*** high amounts of time spent in ***exploration of stimulus objects***.

8.7.6 CONCLUSIONS

If more than 20% of total session time is devoted to ***behaviours directed at the bar and food-trough area***, ***behaviours directed at the stimulus objects*** or ***behaviours directed at the peripheral areas of the box***, can these behaviours be considered to be ***stereotypic*** or aberrant in nature? In the wild, the expression of similar behaviours may enhance a rat's chance of survival. A rat would be expected to return to a predictable or reliable food source or indeed return to a less predictable or depleting food source if it were the only source available to the rat (***behaviours directed at the bar and food-trough area***). ***Exploration of stimulus objects*** could provide a rat with alternative sources of food or other resources. ***Behaviours directed at the peripheral areas*** of a rat's "home-range" would allow a rat to explore or monitor other areas for resources, as well as allowing a rat to physically remove itself from a depleting food patch.

Half of the groups spent more than 20% of total schedule session time engaged in ***behaviours directed at the bar and food-trough areas*** (FROE, FIOS, FIOE, VIOE & VROE groups). With the exception of the FIOS group, the other groups did not have stimulus objects to explore as potential alternative sources of food. Thus it is difficult to determine whether these levels of ***bar pressing*** and ***bar-related behaviour*** could be considered to be ***excessive***. (Section 8.10 compares the time and "effort" spent obtaining reinforcements by each group). The predictable ***fixed-interval*** schedule appears to encourage rats to remain around the only known source of food.

If stimulus objects are present, only rats in the ***variable-ratio*** and ***DRL*** groups (during both schedule & ***extinction*** sessions) spend more than 20% of total session time ***exploring the stimulus objects***. In particular, these schedules elicit high levels of object exploration in the form of ***sniffing and touching***.

The ***variable-ratio*** schedule is unpredictable, and thus rats would undoubtedly investigate objects that might provide alternative sources of food. However, time away from ***bar pressing*** merely postpones the next reinforcer (since it is based on number of ***bar presses***). Thus this level of object exploration may be ***excessive*** and detrimental to survival of food-deprived rats, and perhaps ***non-adaptive*** if it interferes with reinforcement (schedule sessions only). In fact, the ***variable-ratio*** groups obtained the least mean number of reinforcements during schedule sessions of all groups (Table 8.10). During ***extinction***, such levels of exploration could not be considered ***excessive***, since the formerly predictable source of food is now depleted.

For the ***DRL*** groups, which obtained the highest mean number of reinforcements during schedule sessions (Table 8.10), such high levels of ***object-directed exploration*** did not prevent high levels of food reinforcement occurring. Perhaps the presence of objects to explore allowed the rats to more accurately time their absence from the bar area. Thus this level of object exploration may be ***adaptive***. During ***extinction***, such levels of exploration could not be considered ***excessive***, since the only known source of food is now depleted.

Only the VIOE group engaged in ***behaviours directed at the peripheral areas of the box*** for more than 20% of session time during ***extinction*** sessions. Most of this activity was in the form of ***propping***. Although ***resistance to extinction*** should be high for this group (since the ***variable-interval*** schedule itself is made up of periods of ***extinction***), and objects are available for exploration, these rats nevertheless engage in high levels of this behaviour. ***Escape-directed behaviour*** or exploration beyond the confines of the box could be considered ***adaptive***. That is, the source of food is depleted, and activity is directed towards the perimeters of the box. It is, however possible that this level of ***propping*** is ***excessive***. Rats perhaps should not attempt to escape a situation that is “inescapable” just as it would be pointless for a zoo animal to continually attempt to escape its enclosure. At this level (>20%), ***propping*** may be akin to a ***stereotypic behaviour*** such as ***pacing*** (Tudge, 1991).

8.8 TOTAL FREQUENCY OF EXPLORATORY AND OTHER BEHAVIOURS DURING SCHEDULE AND EXTINCTION SESSIONS

Section 8.4 presented the total time spent engaged in each behavioural category by each group. This section presents the frequency data in a similar way, so that some very general comparisons between the five schedules of reinforcement can be made. Tables 8.10 – 8.13 show the mean frequency for each behavioural category, for each group of rats, during the three ***schedule*** and three ***extinction*** sessions.

8.8.1 BEHAVIOURS DIRECTED AT THE BAR AND FOOD-TROUGH AND NUMBER OF REINFORCEMENTS RECEIVED

During schedule sessions

The FIOE group engaged in the most bouts of ***behaviour directed at the bar and food-trough areas***, whilst the DRLOS group engaged in the least bouts (Table 8.10). Overall, the ***fixed-interval*** and ***variable-interval*** schedules generated particularly high scores, and the ***DRL*** schedule generated noticeably lower scores. The presence of objects resulted in lower scores for the "OS" groups, when compared with the same schedule "OE" counterparts (with the exception of the ***DRL*** schedule).

A number of differences in the ratio of ***bar presses*** to ***bar-related behaviours*** appeared to exist. The ***fixed-ratio*** groups engaged in very few bouts of ***bar-related behaviour*** compared to number of ***bar presses***. For these rats, the activities engaged in around the bar area tended to be ***bar pressing***. For the ***DRL*** and VROE rats, it was quite different. The DRLOS rats engaged in more bouts of ***bar-related behaviours*** than actual ***bar pressing***, whilst the DRLOE and VROE rats engaged in similar amounts of ***bar pressing*** and ***bar-related behaviours***. That is, behaviour around the bar area was just as likely to take the form of ***bar-related activities*** (such as sniffing or scratching around & in the food-trough) as ***bar pressing***. For the other groups, there were at least twice as many ***bar presses*** as ***bar-related behaviours*** (Table 8.10).

Overall, rats run on the ***DRL*** and ***variable-interval*** schedules received the highest number of reinforcements, whereas the ***variable-ratio*** schedule resulted in far lower numbers of reinforcements (Table 8.10). Presence or absence of objects had little affect upon the number of reinforcements received by the ***fixed-interval***, ***variable-interval*** and ***DRL*** groups (marginally higher if objects were present). For the ***fixed-ratio*** groups, far fewer reinforcements were received if objects were present (FROS group). The opposite was true for the ***variable-ratio*** groups. For these rats almost twice as many reinforcements were received if objects were present (VROS group).

Table 8.10
The total mean frequency of behaviours directed at the bar and food-trough area (***bar-pressing* + *bar-related behaviour***) during the three schedule and three extinction sessions and the total mean frequency of ***reinforcements received*** (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Frequency FROS & FROE (Litchfield, 1987)	**Total Mean Frequency FIOS & FIOE (Experiment 1)**	**Total Mean Frequency VIOS & VIOE (Experiment 1)**	**Total Mean Frequency VROS & VROE (Experiment 2)**	**Total Mean Frequency DRLOS & DRLOE (Experiment 2)**
- Schedule 1796 & 2863.5 (1661+135 / 2702+161.5)	- Schedule 3690.5 & 4978.75 (2494.25+1196.25 / 3427.25+1551.5)	- Schedule 3868.25 & 4388 (2894.75+973.5/ 3184+1204)	- Schedule 3496.75 & 2020.25 (2850+646.75/ 1028.25+992)	- Schedule 1271.75 & 1723.5 (563.25+708.5/ 891+832.5)
- Extinction 782.25 & 1292 (529.25+253 / 972.5+319.5)	- Extinction 3111 & 4015.25 (1990.75+1120.25 / 2969+1046.25)	- Extinction 2891.25 & 2264.75 (1850.25+1041/ 1631.25+633.5)	- Extinction 1971.25 & 812 (1380.5+590.75/ 404.25+407.75)	- Extinction 603.25 & 670.25 (262.75+340.5/ 257.75+412.5)
Reinforcements received - Schedule 55 & 89.5	***Reinforcements received*** - Schedule 89 & 88.5	***Reinforcements received*** - Schedule 127 & 125.25	***Reinforcements received*** - Schedule 45 & 23.5	***Reinforcements received*** - Schedule 138.25 & 127.25

During extinction sessions

The ***fixed-interval*** groups made the most number of ***bar presses*** during ***extinction***. The ***variable-interval*** groups and VROS group also made well over a thousand ***bar presses*** during the three sessions (Table 8.10). The ***DRL*** groups made the lowest number of ***bar presses***. For all groups the number of ***bar presses*** during ***extinction*** were lower than those made during schedule sessions, indicating that the operant response was extinguishing. However, the decrease was not as dramatic for the ***fixed-interval*** groups.

The total mean number of bouts of ***bar-related behaviours*** increased in ***extinction*** for the ***fixed-interval*** groups, and VIOS group (Table 8.10). Thus although the number of ***bar presses*** were decreasing, more bouts of other behaviours directed around the now depleted food source were taking place. The FIOS rats were still engaging in similar amounts of ***bar-related behaviour*** during ***extinction***. For the other groups, the ***bar pressing*** response was extinguishing, and as a result less activities centered at the depleted food-source were taking place.

As a combined category (***behaviours directed at the bar and food-trough area***), the ***fixed-interval*** groups stand out, since the total mean scores over ***extinction*** were not markedly lower than those obtained during schedule sessions (Table 8.10). Less ***bar presses*** were made, but surprisingly, it appears as though this predictable schedule was somewhat ***resistant to extinction***.

8.8.2 BEHAVIOURS DIRECTED AT THE STIMULUS OBJECTS

During schedule sessions

Again, it should be noted that objects were only present during ***schedule*** sessions for half the rats ("OS" groups). All groups engaged in more bouts of ***sniff object*** than ***sniff and touch object*** (Table 8.11). Thus, overall, more orienting responses were made than manipulatory responses. The ***variable-interval*** group engaged in virtually no ***chew/bite object***, whereas the ***DRL*** group engaged in the most bouts, although this number was still very low (<25).

As a combined score, the ***fixed-ratio*** rats engaged in far fewer bouts of ***object-directed behaviour*** than any other group (Table 8.11). Rats run on this predictable schedule would be expected to spend less time away from the bar area, since the rate of reinforcement is dependent upon the number of ***bar presses*** made. The ***DRL*** rats engaged in the most number of bouts. This schedule should encourage time away from the bar, since low rates of operant responding are critical. This is reflected in the high number of bouts of ***object-directed exploration***. The predictable ***fixed-interval*** and unpredictable ***variable-ratio*** schedules elicited similar amounts (frequency) of ***behaviour directed at the stimulus objects***.

During extinction sessions

As a combined score, the "OE" groups engaged in more bouts of ***object-directed behaviours*** during ***extinction*** following the ***fixed-ratio***, ***fixed-interval*** and ***variable-ratio*** schedules (Table 8.11). That is, for these groups, rats engaged in more exploratory bouts if it was their first encounter with objects. However, rats previously run on the ***variable-interval*** and ***DRL*** schedules engaged in fewer bouts of object exploration if it was their first encounter with stimulus objects ("OE" groups).

For the VIOS and VROS groups, more bouts of ***behaviour directed at the stimulus objects*** occurred during ***extinction*** than schedule sessions (Table 8.11). Thus ***extinction*** elicits even higher frequencies of object exploration in rats that have been previously run on unpredictable or ***variable*** schedules. For the "OS" group rats previously run on the predictable ***fixed-ratio***, ***fixed-interval*** and ***DRL*** schedules, less bouts of object exploration took place during ***extinction*** than schedule sessions.

Table 8.11
The total mean frequency of behaviours directed at the stimulus objects (***sniff object*** + ***sniff and touch object*** + ***chew/bite object***) during the three schedule and three extinction sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Frequency **FROS & FROE** **(Litchfield, 1987)**	**Total Mean Frequency** **FIOS & FIOE** **(Experiment 1)**	**Total Mean Frequency** **VIOS & VIOE** **(Experiment 1)**	**Total Mean Frequency** **VROS & VROE** **(Experiment 2)**	**Total Mean Frequency** **DRLOS & DRLOE** **(Experiment 2)**
- Schedule 377.25 & N/A (239.5+137.75/ n/a)	- Schedule 635.75 & N/A (368.75+250.75+16.25/n/a)	- Schedule 568.5 & N/A (367.75+200+0.75/n/a)	- Schedule 627.5 & N/A (329+284.5+14/n/a)	- Schedule 1080.75 & N/A (591.5+467.25+22/n/a)
- Extinction 312.25 & 380.5 (196.25+116 / 254+126.5)	- Extinction 532.75 & 555.5 (308.5+207.5+16.75 / 320.25+229.75+15.5)	- Extinction 683.75 & 604 (382.75+282+19/ 332.5+262.5+9)	- Extinction 717.25 & 791.5 (320.5+325.5+71.25/ 417+341.5+33)	- Extinction 881 & 845 (378.25+400+102.75/ 448+367+30)

Note. ***Chew/Bite Object*** was included in the ***Sniff-and-Touch Object*** category in the 1987 study

Overall, the ***DRL*** groups engaged in the most bouts of ***exploratory behaviour directed at the stimulus objects*** during ***extinction*** (Table 8.11). The ***fixed-ratio*** groups engaged in the least number of bouts, followed by the ***fixed-interval*** groups. This is perhaps somewhat surprising, since the ***fixed-ratio*** and ***fixed-interval*** groups should have a ***low resistance to extinction,*** which could be reflected in higher bouts of other behaviours during ***extinction***, including exploration of stimulus objects.

Most groups engaged in more bouts of ***sniff object*** than ***sniff and touch object*** (Table 8.11). Thus, overall, more orienting responses were made than manipulatory responses during ***extinction***. The exceptions were the VROS and DRLOS groups, who engaged in slightly more bouts of ***sniff and touch object*** than ***sniff object***. The "OS" groups all engaged in more ***chew/bite object*** during ***extinction*** than schedule sessions. Overall, the ***fixed-interval*** and ***variable-interval*** groups engaged in very few bouts of ***chew/bite object***, whilst the VROE and DRLOE groups engaged in slightly more bouts (<35). Much higher frequencies of ***chew/bite object*** were observed during extinction in the VROS and DRLOS groups (especially the latter).

8.8.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

During schedule sessions

For all groups, the frequency of ***propping*** was far greater than the frequency of ***jump at lid*** (Table 8.12). Thus the combined score is largely comprised of ***propping***. No bouts of ***jump at lid*** or negligible amounts (<5) were observed in the FROS, FIOS, ***variable-ratio*** and ***DRL*** groups. Moderate amounts of ***jump at lid*** (<55) took place in the FIOE and VIOS groups. Equally high amounts of this behaviour (>150) were recorded in the FROE and VIOE groups. However, the ratio of ***propping*** to ***jump at lid*** was very different for these two groups. Twice as many bouts of ***propping*** took place in the FROE group, whereas more than seven times as many bouts of ***propping*** compared to ***jump at lid*** occurred in the VIOE group. Thus, the rather bizarre ***jump at lid*** behaviour represented a higher proportion of the overall ***escape-directed behaviour*** combined score for rats run on the ***fixed-ratio*** schedule, if objects were absent. However, the VIOE group rats engaged in far more ***behaviour directed at the peripheral areas*** in the absence of objects.

Overall, the VIOE group engaged in markedly high rates of ***behaviour directed at the peripheral areas***, more than double the amount recorded in the next highest group (FIOE). The lowest number of bouts took place in the VROS group, followed by the DRLOS group (Table 8.12). For each schedule, the frequency of ***behaviour directed at the peripheral areas*** was noticeably lower if stimulus objects were present. This difference was particularly striking in the ***variable-interval*** groups. Thus if stimulus objects were present, as a potential source of alternative food or stimulation, then rats were less likely to direct ***behaviour towards the peripheral areas*** (to escape or explore beyond the box). Without objects, rats on the unpredictable ***variable-interval*** schedule directed far more behaviours towards the outer perimeters of the box than any other group.

During extinction sessions

The high number of bouts of ***jump at lid*** observed in the FROE and VIOE groups during schedule sessions decreased by at least half during ***extinction***. The frequency of this behaviour also decreased noticeably in the FIOE group. However, there was virtually no change in frequency of ***jump at lid*** for the VIOS group (Table 8.12).

Overall, the frequency of ***behaviour directed at the peripheral areas of the box*** decreased for most groups in ***extinction***. The exceptions were the FROS, FIOS and VIOS groups (Table 8.12). For most of the groups, which recorded a decrease in this category during ***extinction***, it was the first encounter with objects. Thus despite the depletion of the food source, the presence of objects may have resulted in less bouts of ***escape-directed behaviour***.

Table 8.12
The total mean frequency of behaviours directed at the peripheral areas of the box (***propping + jump at lid***) during the three schedule and three extinction sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Frequency **FROS & FROE** **(Litchfield, 1987)**	**Total Mean Frequency** **FIOS & FIOE** **(Experiment 1)**	**Total Mean Frequency** **VIOS & VIOE** **(Experiment 1)**	**Total Mean Frequency** **VROS & VROE** **(Experiment 2)**	**Total Mean Frequency** **DRLOS & DRLOE** **(Experiment 2)**
- Schedule 336.75 & 483.5 (334.75 + 2 / 333.25+150.25) - Extinction 421.5 & 351.5 (416.5 + 5/ 303.5 + 48)	- Schedule 433.5 & 648.25 (433.5+0/ 612.5+35.75) - Extinction 487.5 & 540 (484.5+3/ 530.25+9.75)	- Schedule 387.75 & 1346.5 (334+53.75/ 1196+150.5) - Extinction 505.5 & 1199.25 (452.25+53.25/ 1125+74.25)	- Schedule 223.75 & 388 (223.75+0/ 385+3) - Extinction 213.5 & 228 (212.75+0.75/ 227.5+0.5)	- Schedule 270.5 & 464.5 (270.5+0/ 460.25+4.25) - Extinction 254.75 & 283.75 (254.25+0.5/ 283.75+0)

The highest frequency of ***behaviour directed at the peripheral areas of the box*** was recorded for the VIOE group (as during schedule sessions). It was more than double the score obtained by the next highest scoring groups (FIOE & VIOS). The VROS group obtained the lowest frequency. Overall, the ***variable-ratio*** and ***DRL*** groups engaged in few bouts of ***behaviour directed at the peripheral areas of the box*** during ***extinction***.

8.8.4 OTHER BEHAVIOURAL CATEGORIES

During schedule sessions

If objects were present, fewer bouts of ***displacement*** were found for rats run on the ***variable-interval*** and ***variable-ratio*** schedules than for their same schedule counterparts ("OE" groups). That is, the presence of objects on the least predictable schedules appeared to reduce the number of ***conflict-induced displacement*** activities (Table 8.13). For the more predictable schedules, the presence of objects increased the number of ***displacement*** activities, when compared with their same schedule counterparts. The rats may have been experiencing an ***approach-avoidance conflict***. This could reflect a slight ***neophobic*** reaction (the objects could present a threat). However, the objects might have provided alternative food or stimulation. Overall, the VROS, DRLOE and VIOS groups engaged in the lowest number of bouts of ***displacement*** (<100), whilst the FIOS group frequency was the highest.

With the exception of the ***variable-interval*** schedule, the presence of objects appeared to result in lower frequencies of ***digging/burying*** (compared to the same schedule "OE" counterparts). The VIOE group recorded the lowest number of bouts of this behaviour (Table 8.13). The highest frequency of ***digging/burying*** took place in the DRLOE group. This score was markedly higher than for any other group.

If objects were present during schedule sessions ("OS" groups), the frequency of ***rearing*** was much lower for these groups when compared with their same schedule counterparts ("OE" groups). Thus, with objects to explore, rats were less likely to engage in bouts of ***rearing***. The VIOE group recorded the lowest frequency of this behaviour, whilst the VROS group scored the highest frequency of ***rearing*** (Table 8.13).

Only the VIOE rats did not engage in any bouts of ***pica*** (Table 8.13). If objects were absent during the ***fixed-interval***, ***variable-interval*** and ***DRL*** schedules ("OE" groups) then rats engaged in far greater bouts of ***pica***. Thus the mere presence of objects, which did not result in greater feeding opportunities, resulted in less eating of "inappropriate" foods. The DRLOE and VROE groups scored the highest mean frequency of this behaviour (>400), whilst the ***fixed-interval*** and VIOS groups scored much lower frequencies of ***pica*** (<100).

During extinction sessions

Overall, the ***variable-ratio*** and ***DRL*** groups obtained the lowest frequency of ***displacement*** scores (<100), whilst the ***fixed-ratio*** groups obtained the highest mean scores (>170). With the exception of the ***fixed-interval*** groups, the "OE" groups obtained higher scores than their "OS" (same) schedule counterparts (Table 8.13). That is, rats were more likely to engage in bouts of ***displacement*** activities if it was their first encounter with objects. The food source was now depleted, so the rats should have investigated alternative sources of food. However, the new objects might also have posed a potential threat (*e.g.*, a trap), resulting in slight ***neophobia***. For the ***fixed-ratio*** groups, more bouts of ***displacement*** occurred in ***extinction*** than schedule sessions.

For the ***fixed-interval***, ***variable-interval*** and ***variable-ratio*** groups, the frequency of ***digging/burying*** increased in ***extinction*** (Table 8.13). Thus the depletion of the food source resulted in more bouts of this behaviour, which could be another form of ***escape-directed behaviour*** or a ***foraging behaviour***. For the ***DRL*** groups, the opposite effect was seen. That is, ***extinction*** resulted in fewer bouts of ***digging/burying***. The VIOE group engaged in the least number of bouts of this behaviour, whilst its same schedule counterpart (VIOS group) engaged in the most bouts of ***digging/burying***. Thus the first encounter with objects seems to have a noticeable effect (far lower) on this behaviour for rats that have previously been run on the ***variable-interval*** schedule. By contrast, for the other groups, the first encounter with objects appears to increase the frequency of ***digging/burying*** (when compared to the same schedule "OS" counterparts).

Table 8.13
The total mean frequency of other behavioural categories (***displacement***, ***digging/burying***, ***rearing***, ***pica*** and ***reinforcements received***) during the three schedule and three extinction sessions (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

Total Mean Frequency FROS & FROE (Litchfield, 1987)	**Total Mean Frequency FIOS & FIOE (Experiment 1)**	**Total Mean Frequency VIOS & VIOE (Experiment 1)**	**Total Mean Frequency VROS & VROE (Experiment 2)**	**Total Mean Frequency DRLOS & DRLOE (Experiment 2)**
displacement - Schedule 150.5 & 136.25 - Extinction 171.75 & 190.25	***displacement*** - Schedule 178.75 & 129.5 - Extinction 161.25 & 133	***displacement*** - Schedule 95.5 & 160.25 - Extinction 118.25 & 141.75	***displacement*** - Schedule 73.25 & 121.5 - Extinction 84.25 & 93	***displacement*** - Schedule 124.5 & 90 - Extinction 94 & 98.75
digging/burying Not measured in 1987 study	***digging/burying*** - Schedule 31.25 & 64 - Extinction 41.25 & 61.5	***digging/burying*** - Schedule 54 & 14 - Extinction 71.25 & 17.75	***digging/burying*** - Schedule 21.5 & 30.75 - Extinction 31.25 & 38.5	***digging/burying*** - Schedule 65.25 & 114 - Extinction 41 & 61.5
rearing Not measured in 1987 study	***rearing*** - Schedule 259.5 & 439.75 - Extinction 497 & 491	***rearing*** - Schedule 175.25 & 607.25 - Extinction 328.25 & 582	***rearing*** - Schedule 141 & 333.5 - Extinction 186 & 106.75	***rearing*** - Schedule 259.5 & 461.75 - Extinction 191.25 & 193.75
pica Not measured in 1987 study	***pica*** - Schedule 55.71 & 80.73 - Extinction 344.11 & 116.91	***pica*** - Schedule 90.03 & 0 - Extinction 265.86 & 86.7	***pica*** - Schedule 281.7 & 400.61 - Extinction 259.71 & 547.31	***pica*** - Schedule 235.46 & 443.56 - Extinction 393.83 & 424.88

The VIOE, ***DRL*** and VROE groups engaged in ***rearing*** less frequently during ***extinction*** (Table 8.13). For the other groups the opposite was true. The ***fixed-interval*** and ***DRL*** groups engaged in very similar amounts of ***rearing*** (frequency) irrespective of when objects were first encountered. When objects were encountered did appear to affect the ***variable-interval*** and ***variable-ratio*** groups. The VIOE group engaged in more than 250 more bouts of ***rearing*** (the first encounter with objects) than the VIOS group. The opposite effect was recorded for the ***variable-ratio*** groups. After the VIOE group, the ***fixed-interval*** groups engaged in the highest frequency of ***rearing***. The VROE group engaged in the fewest number of bouts of this behaviour.

For all but the ***variable-ratio*** and DRLOE groups, the number of bouts of ***pica*** increased substantially during ***extinction*** (Table 8.13). That is, the absence of any food during ***extinction*** may have resulted in hungry rats consuming items of "inappropriate" food more frequently. Even the VIOE rats that had never indulged in this activity during ***variable-interval*** sessions engaged in pica on more than 80 occasions during ***extinction***. If stimulus objects were encountered for the first time during ***extinction*** following ***fixed-interval*** or ***variable-interval*** schedules, then far fewer bouts of ***pica*** were likely to occur. For the ***variable-ratio*** and ***DRL*** groups, the opposite was the case. The VROE group engaged in far more bouts of ***pica*** than any other group. The VIOE group frequency of ***pica*** was lowest.

8.9 GROUPS WITH THE HIGHEST OR LOWEST TOTAL MEAN SCORES FOR FREQUENCY OF BEHAVIOURS

Some interesting patterns emerge when the highest and lowest total mean values for frequency of behaviours are investigated (Table 8.14). In ten of the 14 cells (excluding the ones for reinforcements received) for highest and lowest duration, the same group that had an extreme score during ***schedule*** sessions also had an extreme score during ***extinction*** sessions (*i.e.*, highest score for both, or lowest score for both).

8.9.1 OBJECTS PRESENT DURING SCHEDULE AND EXTINCTION SESSIONS ("OS" GROUPS)

The FROS group showed the lowest frequency of ***behaviours directed at the stimulus objects*** during both ***schedule*** and ***extinction*** sessions. Thus this predictable schedule, where maximum reinforcement required steady ***bar pressing***, resulted in fewer bouts of activity directed towards the stimulus objects. This pattern was still observed once reinforcement had stopped altogether.

The highest frequency of ***displacement*** was seen in the FIOS group during ***schedule*** sessions. Thus the presence of objects on this predictable schedule results in a high level of ***conflict-related behaviour***. The predictable nature of the schedule required rats to be near the food source at specific times. However, the presence of objects to investigate may have at times conflicted with this requirement to remain near the food source.

Table 8.14
The groups with the highest or lowest total mean frequency scores for the various behavioural categories (for all groups from Experiment 1 & 2, & Litchfield's 1987 study)

BEHAVIOURAL CATEGORY	**HIGHEST TOTAL MEAN FREQUENCY**	**LOWEST TOTAL MEAN FREQUENCY**
Behaviours directed at the bar and food-trough area (***bar-pressing***; ***bar-related behaviour***) **- schedule**	FIOE	DRLOS
- extinction	FIOE	DRLOS
Behaviour directed at the stimulus objects (***sniff object***; ***sniff and touch object***; ***chew/bite object***) **- schedule**	DRLOS	FROS
- extinction	DRLOS	FROS
Behaviour directed at the peripheral areas of the box (***propping***; ***jump at lid***) **- schedule**	VIOE	VROS
- extinction	VIOE	VROS
Displacement **- schedule**	FIOS	VROS
- extinction	FROE	VROS
Rearing **- schedule**	VIOE	VROS
- extinction	VIOE	VROE
Digging/Burying* **- schedule**	DRLOE	VIOE
- extinction	VIOS	VIOE
Pica* **- schedule**	DRLOE	VIOE
- extinction	VROE	VIOE
Reinforcements received **- schedule**	DRLOS	VROE

Note. A * indicates that the behaviour was not scored in the 1987 study.

The VIOS group engaged in the highest frequency of ***digging/burying*** during ***extinction*** sessions. Despite the presence of objects during both ***schedule*** and ***extinction*** sessions, bouts of this behaviour were greatest once reinforcement ceased. This activity may have represented an ***escape-directed*** behaviour or a ***foraging-related*** behaviour.

The VROS group showed the lowest frequency of ***displacement*** and ***behaviours directed at the peripheral areas of the box*** during both ***schedule*** and ***extinction*** sessions. Thus bouts of ***conflict-related*** activities and ***escape-related*** behaviours were greatest during this unpredictable schedule, and once the food source was depleted. This group also engaged in the few bouts of ***general inspection***, in the form of ***rearing***, during ***schedule*** sessions.

The DRLOS group showed the lowest frequency of ***behaviours directed at the bar and food-trough area*** during ***schedule*** and ***extinction*** sessions. This schedule encouraged time away from the bar area. The pattern then continued once the food source was depleted. This group also showed the highest frequency of ***behaviours directed at the stimulus objects*** during ***schedule*** and ***extinction*** sessions. Thus the time away from the bar area was obviously spent investigating stimulus objects. Again, this pattern continued once the food source was depleted. This group also recorded the highest ***reinforcements received*** (during ***schedule*** sessions). Thus time away from the bar area and object exploration actually improved the rats' success at receiving reinforcements.

8.9.2 OBJECTS ONLY PRESENT DURING EXTINCTION SESSIONS ("OE" GROUPS)

The FROE group showed the highest frequency of ***displacement*** during ***extinction*** sessions. Thus the absence of any reinforcement following the previous predictable schedule, coupled with the presence of new stimulus objects resulted in numerous bouts of ***conflict-related*** activities.

The highest frequency of ***behaviours directed at the bar and food-trough area*** was seen in the FIOE group during ***schedule*** and ***extinction*** sessions. Without objects to "distract" them, these rats on the very predictable ***fixed-interval*** schedule engaged in the most bouts of behaviour centred at the food source. This continued to be the case even after the food source was depleted, and stimulus objects were available to investigate.

The highest frequency of ***behaviours directed at the peripheral areas of the box*** and ***rearing*** during ***schedule*** and ***extinction*** sessions was recorded for the VIOE group. In the absence of objects, this unpredictable schedule resulted in the highest levels of ***escape-directed*** behaviour and ***general inspection*** in the form of ***rearing***. This continued to be the case when objects were present during ***extinction***. This group also showed the lowest frequency of ***digging/burying*** and ***pica*** during ***schedule*** and ***extinction*** sessions. Whilst ***general inspection*** and ***escape-directed*** behaviours were high in frequency, the alternative feeding (***pica***) and foraging (or also ***escape-related***) in the form of ***digging/burying*** was low.

The highest frequency of ***pica*** and lowest frequency of ***rearing*** during ***extinction*** sessions was seen in the VROE group. That is, despite the presence of objects, once the food source was depleted, these rats engaged in high levels of alternative feeding and low levels of ***general inspection***. This group also received the lowest number of ***reinforcements*** (during ***schedule*** sessions). That is, despite the absence of "distracting" objects, this unpredictable schedule resulted in few reinforcements.

The DRLOE group showed the highest frequency of ***digging/burying*** and ***pica*** during ***schedule*** sessions. Thus without objects to explore on a schedule that encouraged time away from the bar area, these rats engaged in high levels of alternative feeding and ***foraging-related*** or ***escape-directed behaviour***.

8.9.3 CONCLUSIONS

It should be noted that groups, which recorded the highest mean frequency scores, may not have spent the highest amount of time (duration) engaged in a particular category (see section 8.5). They may have engaged in many short bouts, whilst another group may have engaged in a few long bouts. However, a number of groups recorded both the highest frequency and duration or the lowest frequency and duration.

The FIOE group engaged in the most bouts of ***behaviours directed at the bar and food-trough area***, and they also spent the most time engaged in these behaviours during ***schedule*** sessions. Thus clearly, in the absence of "distracting" stimulus objects, this predictable schedule resulted in the highest levels of ***behaviours directed at the bar and food-trough area***.

The DRLOS group engaged in the most bouts of ***behaviour directed at the stimulus objects*** and also spent the most time devoted to these activities in both ***schedule*** and ***extinction*** sessions. The DRLOS group also engaged in the fewest bouts and spent the least time engaged in ***behaviours directed at the bar and food-trough area*** during both ***schedule*** and ***extinction*** sessions. Thus if objects are available to explore on a schedule that by its very nature minimises number of ***bar presses***, then a large amount of time is directed towards the objects and minimal time is spent in the vicinity of the food source. These patterns continued during ***extinction***, despite the fact that objects had already been present for three sessions (even though they were different objects), and one might have expected the impact of objects not to be as great.

The DRLOE group spent the most time engaged in ***pica*** and had the most bouts of this behaviour during ***schedule*** sessions. Thus, in the absence of objects, the schedule that minimises time spent at the bar area also results in the highest levels of alternative feeding. That is, hungry rats that are encouraged to spend time away from the only known food source (but do not have objects to explore), engage in high levels of ***pica***.

The VIOE group had the highest frequency and duration scores for ***behaviours directed at the peripheral areas of the box*** during both ***schedule*** and ***extinction*** sessions. This group also engaged in the least number of bouts of ***pica*** and spent the least amount of time devoted to this activity during both ***schedule*** and ***extinction*** sessions. Thus without objects to explore during ***schedule*** sessions, rats run on the unpredictable ***variable-interval*** schedule directed the most activities towards escaping or exploring beyond the confines of the box and also engaged in less ***pica*** than other groups. Interestingly, the addition of objects during extinction had no apparent effect. That is, of all the groups the VIOE group still engaged in the most ***escape-related behaviours*** and least ***pica***.

The VROE group engaged in the lowest number of bouts of ***rearing*** and also spent the least amount of time engaged in this behaviour during ***extinction*** sessions. The VROE group also engaged in the most bouts of ***pica*** and spent the most time in this behaviour during ***extinction*** sessions. Thus despite their first encounter with objects taking place during ***extinction***, this group still engaged in the least ***rearing*** and most ***pica*** of all groups during those sessions. The absence of any food for these hungry rats, even though food had appeared unpredictably during schedule sessions, resulted in the highest levels of eating "inappropriate" foods.

8.10 TIME AND "EFFORT" SPENT OBTAINING REINFORCEMENTS

There is no "right" or "wrong" amount of time that should be spent by each rat at the bar and food-trough area of the box. Similarly, the actual number of ***bar presses*** or times that the rat investigates the food-trough cannot be held to be "right" or "wrong". However, one would expect that an ***optimal foraging strategy*** would be one in which the least amount of energy is exerted, for the maximum amount of food. That is, many pellets or reinforcers for few ***bar presses*** or other activities centered at the manipulandum. The ***fixed-ratio*** schedule is not included in this analysis, since 30 ***bar presses*** were required in order to receive reinforcement (no element of ***choice***).

With the available data for the groups discussed in this chapter, it is possible to ascertain which schedules generate behaviour that is most energy ***efficient*** for obtaining a food pellet. That is, which groups spend the least amount of time around the manipulandum and food-trough area, and exert the least physical energy (lowest number of mean ***bar presses*** and lowest frequency of ***bar-related behaviours***) per reinforcement. Table 8.16 presents the total mean frequency of ***reinforcements received*** during schedule sessions, the total mean frequency of ***bar pressing*** and the combined value for ***behaviours directed at the bar and food-trough area***. Finally, the mean duration and frequency per reinforcement is presented. Table 8.15 presents the total mean total mean duration of ***bar pressing*** and the combined value for ***behaviours directed at the bar and food-trough area***. The percent of total session time spent engaged in these behaviours by each group is also given. Finally, the mean duration of ***bar pressing*** and ***behaviours directed at the bar and food-trough area*** per reinforcement is presented.

Although it may be somewhat inappropriate to compare schedules that are very different, it is nevertheless interesting to see which schedule provides the most food pellets for the least ***effort*** in these half-hour sessions. Clearly, rats run on the ***DRL*** schedule expend the least energy ***bar pressing*** per reinforcement obtained. On average, less than seven ***bar-presses*** are made per reinforcer (Table 8.16). In addition, these rats engage in ***bar pressing*** for less than 1.5 seconds per reinforcer (Table 8.15). Even with ***bar-related behaviours*** included (combined score), ***DRL*** rats spent minimal amounts of time (<6 seconds) or effort (<14 for frequency) engaged in ***behaviours directed at the bar and food trough area.***

Very little time was spent ***bar pressing*** per reinforcement on the ***variable-interval*** (<5 seconds) and ***fixed-interval*** (<6 seconds) schedules as well (Table 8.15). However, as shown in Table 8.16, the actual number of ***bar presses*** per reinforcement is much higher (between 22 & 39). On all but the ***variable-ratio*** schedule, slightly less time is spent engaged in ***bar pressing*** per reinforcement if stimulus objects are present (Table 8.15). Similarly, less ***bar presses*** are made per reinforcement if objects are present, except for the ***variable-ratio*** schedule (& the ***fixed-ratio*** scores are almost identical, as shown in Table 8.16).

The ***variable-ratio*** schedule is perhaps the least ***energy efficient*** schedule. That is, it provided the least food pellets for the most ***effort*** in these half-hour sessions. The presence of objects (VROS group) on this schedule resulted in rats pressing the bar even more often per reinforcement. On average, the VROS group made more than 60 ***bar presses*** per reinforcer, which was 20 more ***bar presses*** than for the FROE group (Table 8.16). If the frequency of ***bar-directed behaviours*** was also taken into account (combined score), then as many as 85 ***behaviours directed at the bar and food trough area*** were made per reinforcer (VROE group).

Table 8.15
The total mean time spent ***bar pressing***, total mean time spent engaged in ***behaviours directed at the bar and food-trough area*** and total mean frequency of reinforcements received during schedule sessions (all groups from Experiment 1 & 2, & Litchfield's 1987 study). The last two columns provide the mean time spent ***bar pressing*** and mean time spent engaged in ***behaviours directed at the bar and food-trough area*** per reinforcement.

SCHEDULE	**Total mean duration of *bar-pressing* during schedule sessions (% total session)**	**Total mean duration of "behaviours directed at bar & food-trough area" during schedule sessions (% total session)**	**Total mean frequency of reinforcements received during schedule sessions**	**Mean time spent *bar pressing* per reinforcement**	**Mean time spent in "behaviours directed at the bar & food-trough area" per reinforcement**
FROS	562.25secs (10.4%)	748.8secs (13.9%)	55	10.22 secs	13.61 secs
FROE	961.41secs (17.8%)	1193.99secs (22.1%)	89.5	10.74 secs	13.34 secs
FIOS	459.79secs (8.5%)	1178.7secs (21.8%)	89	5.17 secs	13.24 secs
FIOE	517.78secs (9.59%)	1361.51secs (25.2%)	88.5	5.85 secs	15.38 secs
VIOS	543.18secs (10.1%)	894.97secs (16.6%)	127	4.28 secs	7.05 secs
VIOE	592.88secs (11.0%)	1086.64secs (20.1%)	125.25	4.73 secs	8.68 secs
VROS	513.13secs (9.50%)	1032.89secs (19.1%)	45	11.4 secs	22.95 secs
VROE	212.26secs (3.93%)	1087.39secs (20.1%)	23.5	9.03 secs	46.27 secs
DRLOS	119.91secs (2.22%)	481.92secs (8.92%)	138.25	0.87 secs	3.49 secs
DRLOE	159.23secs (2.95%)	636.84secs (11.8%)	127.25	1.25 secs	5.0 secs

The mean time spent ***bar pressing*** per reinforcement (Table 8.15) was also high for the ***variable-ratio*** rats (>9 seconds). Again, if the frequency of ***bar-directed behaviours*** was also taken into account (combined score), then more than 46 seconds was spent engaged in ***behaviours directed at the bar and food trough area*** by the VROE group per reinforcer. The ***fixed-ratio*** rats also expended a high amount of energy (>30 ***bar presses***) and time (>10 seconds spent ***bar pressing***) per reinforcement (Tables 8.15 & 8.16). However, compared to most groups, they did not spend more time or effort engaged in ***behaviours directed at the bar and food trough area*** per reinforcement.

In conclusion, the schedules varied quite substantially with respect to the time and effort made per reinforcement. As little as one second or more than ten seconds was spent ***bar pressing*** per reinforcer (Table 8.15). Less than ten ***bar presses*** were made per reinforcement in some cases, or more than 60 in one case (Table 8.16).

Taking both time and effort (***bar presses***) into account, by far the most ***energy-efficient*** or ***optimal*** schedule was the ***DRL*** schedule, irrespective of presence or absence of objects. By contrast, the least ***energy-efficient*** or ***optimal*** schedule was the ***variable-ratio*** schedule, especially if objects were present. Importantly, the actual number of ***reinforcements received*** is vastly different on these two schedules. Whilst the ***DRL*** rats on average received more than 125 reinforcers during schedule sessions, the ***variable-ratio*** rats received less than 50 (<25 if objects were present). Apart from possibly indicating some genuine differences, this analysis may indicate that the ***DRL15-s*** schedule resulted in rates of operant responding that were too low or the ratio chosen for the ***variable-ratio*** schedule (30) was too high to be able to make comparisons between the various schedules.

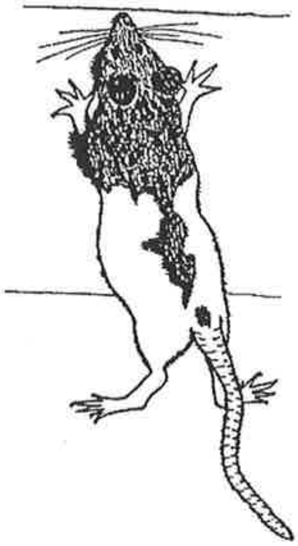
Table 8.16
The total mean frequency of ***bar presses***, total mean frequency of ***behaviours directed at the bar and food-trough area*** and total mean frequency of reinforcements received during schedule sessions (all groups from Experiment 1 & 2, & Litchfield's 1987 study). The last two columns provide the mean frequency of ***bar presses*** and mean frequency of ***behaviours directed at the bar and food-trough area*** per reinforcement.

SCHEDULE	Total mean frequency of *bar-presses* during schedule sessions	Total mean frequency of "behaviours directed at bar & food-trough area" during schedule sessions	Total mean frequency of reinforcements received during schedule sessions	Mean frequency of *bar presses* per reinforcement	Mean frequency of "behaviours directed at the bar & food-trough area" per reinforcement
FROS	1661	1796	55	30.2	32.66
FROE	2702	2863.5	89.5	30.19	31.99
FIOS	2494.25	3690.5	89	28.03	41.47
FIOE	3427.25	4978.75	88.5	38.73	56.26
VIOS	2894.75	3868.25	127	22.79	30.46
VIOE	3184	4388	125.25	25.42	35.03
VROS	2850	3496.75	45	63.33	77.71
VROE	1028.25	2020.25	23.5	43.76	85.97
DRLOS	563.25	1271.75	138.25	4.07	9.20
DRLOE	891	1723.5	127.25	7.0	13.54

CHAPTER 9

POLYDIPSIA, AGGRESSION AND EXPLORATORY BEHAVIOUR IN THE LABORATORY RAT:

EXPERIMENT 3



9.1 INTRODUCTION TO EXPERIMENT 3

The results for Experiment 1 demonstrate that rats engage in a number of behaviours, apart from ***bar pressing***, on a FI60-s schedule. The "open field" style Skinner box and the presence of stimulus objects provided an opportunity for exploratory behaviour to be investigated, and to determine whether the behaviours scored occurred during or outside the PRPs.

Falk (1971) found that a FI60-s schedule readily and reliably elicited ***polydipsia*** (***excessive drinking***) in rats, if a water source was available during schedule running. Typically such ***drinking*** took place immediately after the food reinforcement was delivered, namely, during the PRP. Whereas, the schedule sessions investigated in Experiments 1 and 2 were thirty minutes in length, Falk's (1971) sessions were 3.5-hours long.

This experiment seeks to discover whether excessive (or indeed any) ***drinking*** takes place in an "open field" style Skinner box, with the water source present in the same box. If ***drinking*** does occur, does it also tend to occur during the PRPs? If the rats do drink, is it ***excessive***? Once the rats have demonstrated ***drinking*** (excessive or not), does this ***drinking*** diminish or disappear altogether, if the opportunity to ***explore novel objects*** is provided. By providing alternate stimulation in the form of novel objects, it may be possible to reduce or eliminate ***polydipsia***. That is, the opportunity to engage in an ***adaptive*** behaviour may inhibit the rats from engaging in a potentially ***maladaptive*** or aberrant behaviour.

9.1.1 HYPOTHESES PERTAINING TO THE PRPs

Hypothesis Thirteen: **Proportion of behaviours occurring during PRPs of FI60-s schedules (when a water source is concurrently available**

*Since **fixed-interval** schedules are characterised by the existence of regular PRPs, it is expected that a large proportion of **drinking** (Falk, 1971) and each of the other scored behaviours (hypothesis one) will occur during the PRPs.*

Hypothesis Fourteen: **Effect of novel stimulus objects on proportion of behaviours occurring during PRPs of FI60-s schedules (when a water source is concurrently available**

*It is predicted that the presence or absence of novel stimulus objects during **fixed-interval** running may have an effect on the proportions of behaviours (including **drinking**) occurring during the PRPs. Thus, it is expected that there will be a difference between the FIOS group (objects present) and the FIOE group (objects absent) during **fixed-interval** sessions.*

Hypothesis Fifteen: **Within-session changes in proportion of behaviours occurring during PRPs (when a water source is concurrently available**

*There may be within-session changes in the proportions of behaviours occurring during the PRPs. That is, the proportions may differ depending on the part of session (first, middle or last 30 minutes). Higher percentages of total frequency and duration may occur during the PRPs as the session continues, since PRPs may stabilise over the 3.5-hour session. Thus, it is expected that percentage of frequency and duration occurring during PRPs will be higher in the **last 30 minutes** than in the **first 30 minutes**.*

9.1.2 HYPOTHESES PERTAINING TO CHANGES IN BEHAVIOUR OVER SCHEDULE AND EXTINCTION SESSIONS

Hypothesis Sixteen: Effect of novel stimulus objects on frequency and duration of behaviours during FI60-s schedules (when a water source is concurrently available)

*If objects are absent during **fixed-interval** sessions, more time and effort can be devoted to behaviours that are not object-directed. Thus, it is expected that higher frequencies and durations of non-object behaviours will be observed in the FIOE group during **fixed-interval** sessions. In addition, without objects present to "distract" them during **fixed-interval** sessions, the frequency and duration of **bar pressing** and **drinking** scores is expected to be higher in the FIOE group.*

Hypothesis Seventeen: Effect of novel stimulus objects on frequency and duration of behaviours during extinction (when a water source is concurrently available)

*When objects are first encountered during **extinction**, it is expected that higher frequencies and durations of object-directed behaviours will be observed. That is, the **FIOE** group will direct more behaviour towards novel stimulus objects during **extinction** sessions than the **FIOS** group. No firm expectations are held for the other behavioural categories.*

Hypothesis Eighteen: Within-session changes in behaviour during FI60-s schedules (when a water source is concurrently available)

*Within-session changes in behaviour may be observed during **fixed-interval** sessions. That is, the frequency and duration scores may differ depending on the part of session (**first**, **middle** or **last 30 minutes**).*

- *It is expected that late session decreases in **bar pressing** may occur (and fewer reinforcers may be obtained) as a result of satiation or habituation to the reinforcer (McSweeney and Roll, 1998).*

- *Late session decreases in exploratory behaviour directed at the stimulus objects (**sniff object**, **sniff and touch object** and **chew/bite object**) may be observed as a result of habituation to the objects.*
- *Other behaviours may peak at different times throughout the session (**first**, **middle**, **last 30 minutes**).*

Hypothesis Nineteen: **Within-session changes in behaviour during extinction (when a water source is concurrently available)**

*Within-session changes in behaviour may also be observed during **extinction** sessions. That is, the frequency and duration scores may differ depending on the part of session (**first**, **middle** or **last 30 minutes**).*

- *It is predicted that late session decreases in **bar pressing** may occur as the response extinguishes.*
- *Late session decreases in exploratory behaviour directed at the stimulus objects (**sniff object**, **sniff and touch object** and **chew/bite object**) may be observed as a result of habituation to the objects.*
- *Other behaviours may peak at different times throughout the session (**first**, **middle**, **last 30 minutes**).*

9.2 METHOD FOR EXPERIMENT 3

9.2.1 SUBJECTS

Ten experimentally naive male Hooded Wistar rats, bred at the Waite Institute Central Animal House, served as subjects. They were obtained at approximately 73 days of age, and subsequently, housed in separate cages (28cm x 19cm x 18cm) in the Psychology Department's animal holding room, at the University of Adelaide.

Eight of these rats were randomly divided into two groups of four animals. These two groups were designated as (1) Fixed-Interval/ Objects during Schedule running group (FIOS) and (2) Fixed-Interval/ Objects during Extinction group (FIOE). The two remaining rats were used in a pilot study to test the apparatus.

The rats were housed under controlled temperature and illumination conditions (12/12-hour light-dark cycle). All animals received *ad libitum* water, with *ad libitum* food received during the handling sessions. Prior to the start of testing, each rat was individually handled once daily for seven days. Testing commenced at approximately 80 days of age.

9.2.2 APPARATUS FOR EXPERIMENT 3

9.2.2.1 EXPERIMENTAL APPARATUS

The experimental apparatus consisted of two exploration boxes, which were identical in appearance and function. Each of these boxes was fitted with a bar manipulandum, food-trough and light on one wall (as in a Skinner box). A buzzer, pellet dispenser and pellet counter were situated on the other side of this wall in each box. The exploration boxes were made of stainless steel, with a perspex lid (raised slightly for ventilation). The dimensions of each box were 50cm x 49cm x 25cm. The floor of each exploration box was covered by sawdust, to a depth of approximately 1cm.

The exploration boxes were similar to the one used in Experiment 1 and 2, with one notable difference. A water bottle fixture above a metal grid was located between the bar manipulandum and one of the walls. This allowed a water bottle to be clipped to the wall. On the other side of this wall was a lick counter. Every time the rat took a drink from the water bottle, each ***lick*** was recorded. The metal grid provided the necessary surface for the electric current to be conducted. Each perspex water bottle, connected by two wires to the lick counter, was encased within a protective plastic bottle, with the bottom cut out to allow the inner bottle to be placed inside it (Figure 9.1).

A Gerbrands cumulative recorder, and hand-operated pellet dispenser were connected to each box. A second Gerbrands cumulative recorder was also connected to each box, in order to record the number of licks made by each rat at the water bottle. The whole system was controlled by an IBM-compatible personal computer, one for each box. All program commands were entered into the computer via a standard "QWERTY" keyboard.

Two groups of three removable objects were clipped onto the floor of the exploration boxes when required (Figure 9.2). Each box had its own set of objects. These stimulus objects were the same as those used in Experiments 1 and 2, previously described in section 6.2.2.1. Testing took place in two adjacent rooms, with one exploration box and accompanying equipment per room.

9.2.2.2 OBSERVATIONAL EQUIPMENT

Experimental sessions were recorded onto VHS videotapes, using two National WVP 100N video cameras with in-built timers, and two National NV 730A videocassette recorders (VCR), one per experimental room. The video camera on a tripod was situated on the edge of a table, directly above the exploration box in each room. The two Gerbrands cumulative recorders were set up against one of the walls in each of the testing rooms. The VCR and Sony CVM-111E video monitors were located behind a partition, thus separating them from the exploration box and camera in each room (see section 6.2.2.2 for photos). The video tapes of all sessions were viewed on a National TC-2633 video monitor and transcribed to behavioural records, via an event recorder, as described previously in section 6.2.3.

9.2.3 PROCEDURE

9.2.3.1 EXPERIMENTAL DESIGN

The experimental design used two different ***fixed-interval*** groups, depending on whether stimulus objects were present during <u>schedule</u> running, or during ***extinction***. The rats were allocated to a group at random. As there were only two exploration boxes and accompanying equipment available, and only two 3.5-hour sessions could be run daily for each box.

Initially, two rats (pilot study) were run through all the experimental phases (to test the equipment). Data from these sessions were not analysed. However, it was found that the rats ***attacked*** the water bottles during all sessions, by chewing the plastic housing around the glass bottle (Figure 9.3). The first housings were made of green plastic, but once destroyed, could only be replaced by ones made of brown plastic. Once these had been destroyed, the only ones that could be obtained were white plastic housings (Figure 9.4). This unexpected finding provided quite a challenge, since 180 plastic bottles (housings) had to be obtained on short notice. Only white plastic housings were used for the actual experiment.

Once the pilot rats had completed testing, the remaining animals were subjected to the same testing procedures. Table 9.1 illustrates the experimental design in more detail. Only videotapes of the last three <u>schedule</u> sessions (FI60-s) and first three ***extinction*** sessions were scored (sessions 8 – 13 inclusive).

Figure 9.1. The water bottle (encased within the plastic housing) clipped into place

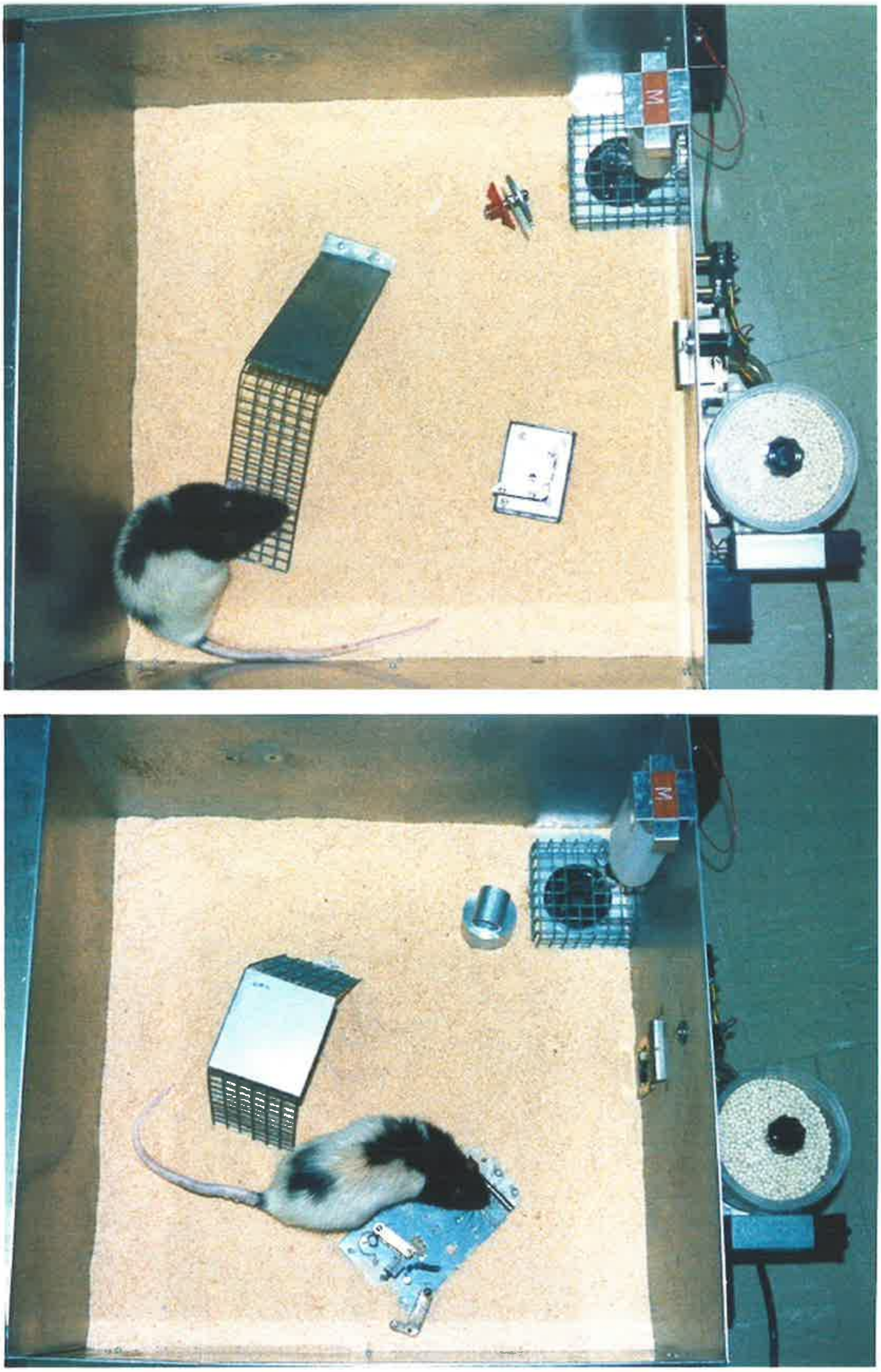


Figure 9.2. The exploration box with water bottle and stimulus objects present (top- Group A objects, and bottom- Group B objects)

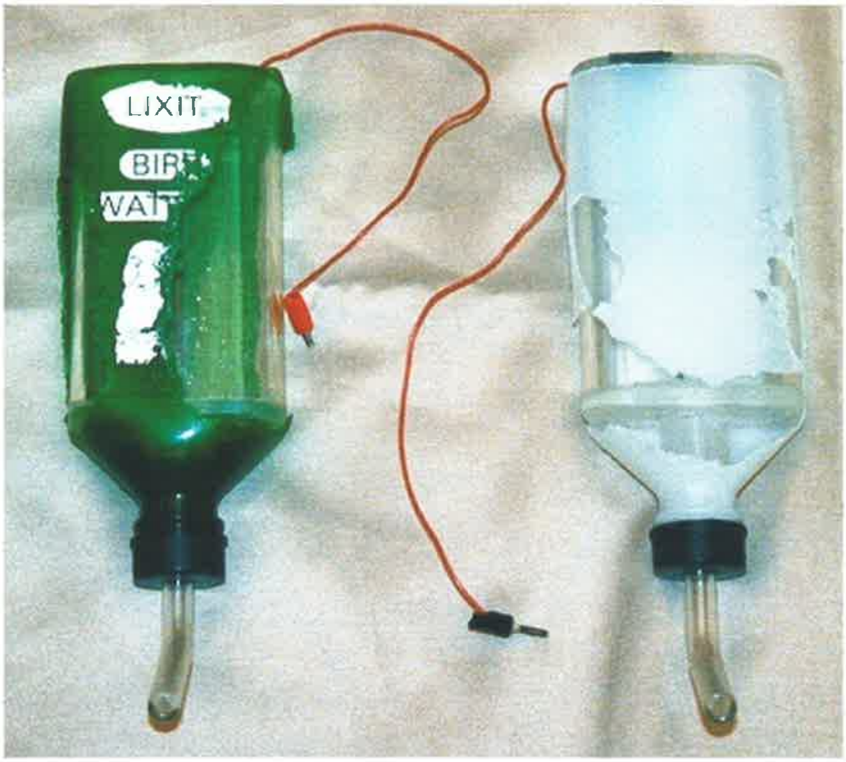


Figure 9.3. Examples of the damaged water bottle plastic housings

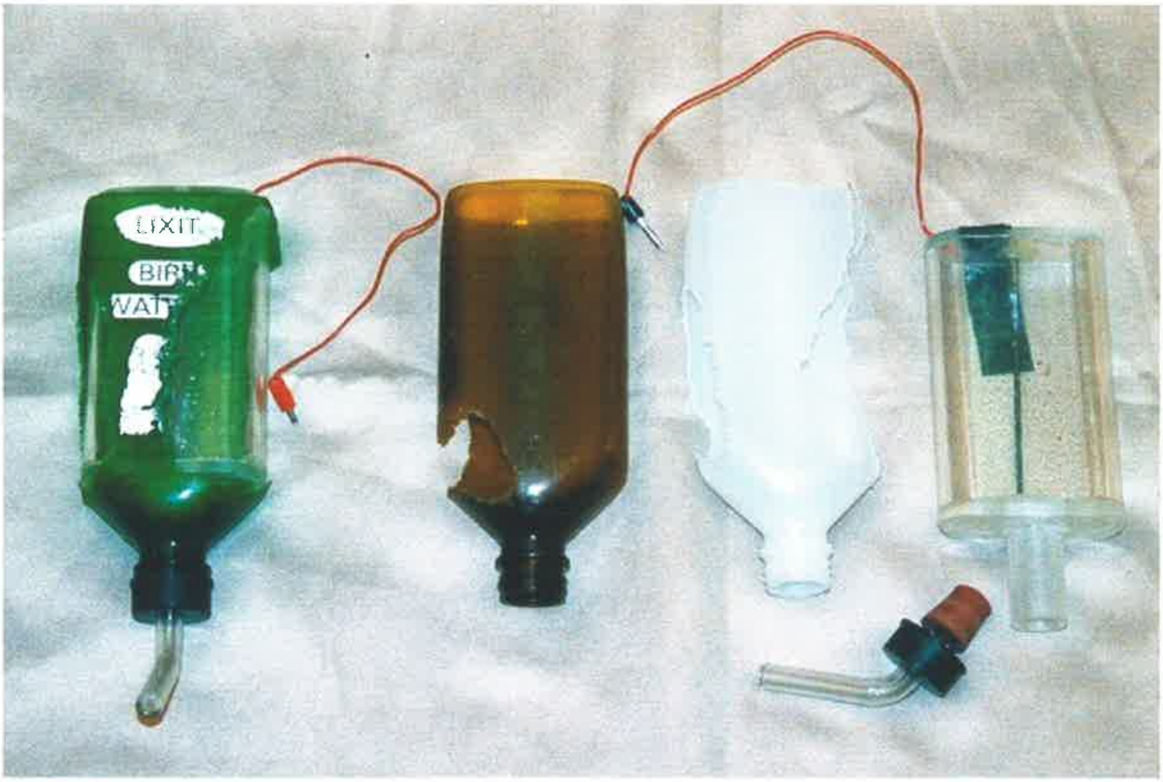


Figure 9.4. The three types of plastic housing used (and the inner glass water bottle)

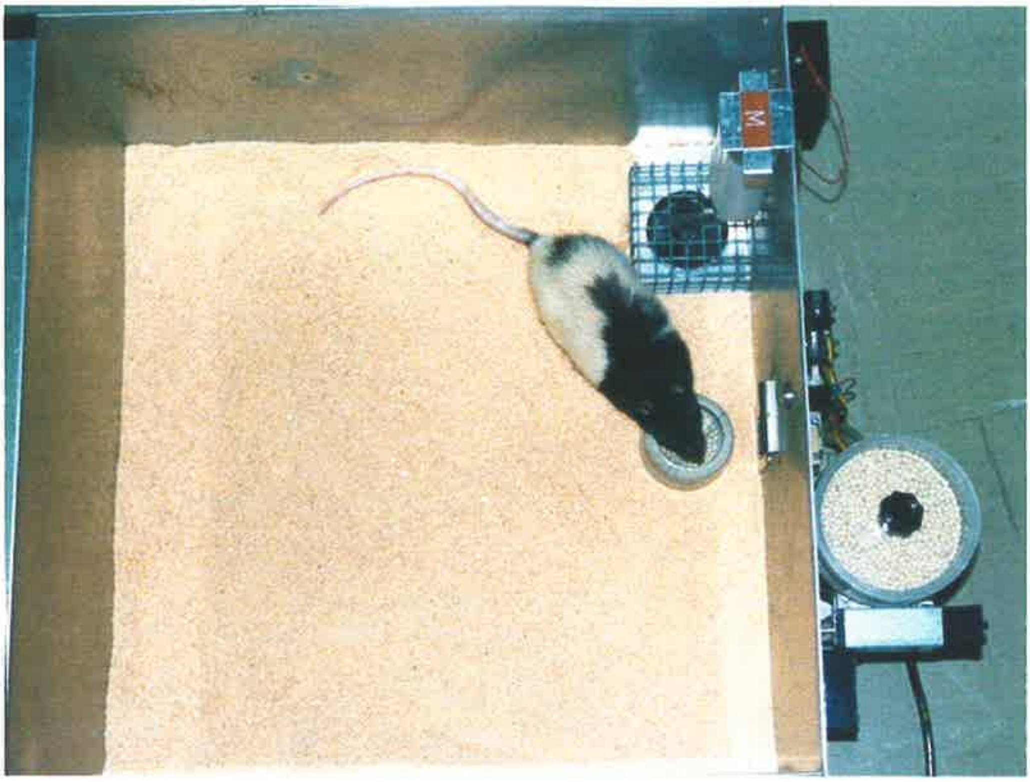


Figure 9.5. The ***mass reinforcement*** phase (food pellets in a ceramic dish)

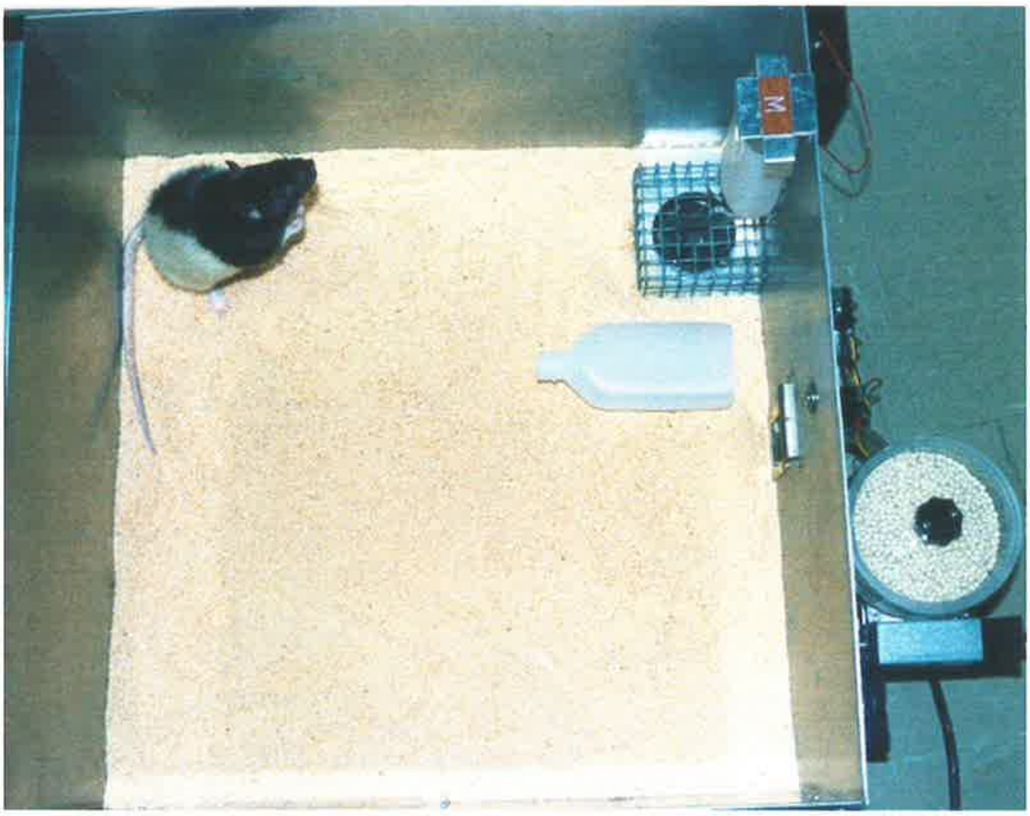


Figure 9.6. The final ***extinction*** session (with loose plastic water bottle housing)

9.2.3.2 HANDLING AND OBSERVATION SESSIONS

The experimental procedure consisted of two main phases: handling and observation, and was adhered to for all groups of rats. The observation phase included ***mass reinforcement***, ***conditioning*** and schedule running phases (***fixed-interval*** and ***extinction***).

HANDLING

Each rat was individually handled for the same amount of time before commencement of the experiment. All rats were handled on a daily basis for 7 days. Consequently, each rat received handling on seven separate occasions at the same time every day. Each handling session lasted for ten minutes, during which time the rat was removed from its home cage and gently stroked.

OBSERVATION

Throughout the experimental sessions the animals were maintained on a 23-hour food-deprivation schedule. The rats were observed on sixteen different occasions: two ***mass reinforcement*** sessions; one ***continuous reinforcement*** session; one ***extinction*** session; six FI60-s schedule sessions; six ***extinction*** sessions; and one ***extinction*** session, with a loose plastic water bottle present. Each observation session was of 3.5 hours duration (210 minutes), with the exception of ***conditioning*** sessions, which were of 30 minutes duration. During the observation sessions the stimulus objects were either present, or not present, according to the experimental conditions laid out in Table 9.1.

For the two ***mass reinforcement*** sessions, 210 food pellets were present in a small food dish located in front of the bar-area (Figure 9.5). The rat could consume these pellets at will over the 3.5-hour session. The number of pellets represented the number of pellets the rat could potentially receive during this period on a ***fixed-interval 60-seconds*** (FI60-s) schedule of reinforcement. During this phase, the rat was able to explore the box freely, which was devoid of stimulus objects.

Following the ***mass reinforcement*** sessions, ***bar pressing*** was shaped over a number of training sessions (varied according to the individual rat). No objects were present in the box during this period. The procedure of ***magazine training*** and ***shaping of the bar pressing response via successive approximations*** has been described previously for Experiment 1 and 2 (see section 6.2.3.2). These ***conditioning*** sessions were not video taped, and did not count as an observation session. Subsequently, all rats were placed on a ***continuous reinforcement*** (***CRF***) schedule of reinforcement. A minimum of 190 ***bar presses*** in 30 minutes was the criterion set before the next stage could be attempted. The duration of each training session was 30 minutes. Following ***CRF*** training, all rats were placed on a ***fixed-interval 60-seconds*** (FI60-s) schedule of reinforcement.

Table 9.1
The experimental design, showing which stimulus objects are present in each session (*i.e.*, objects from group A or B or none at all).

PHASE OF EXPERIMENT	**SESSION NUMBER**	**FIOS GROUP**	**FIOE GROUP**
Mass Reinforcement	1	No objects present	No objects present
Mass Reinforcement	2	No objects present	No objects present
Continuous Reinforcement	3	No objects present	No objects present
Extinction	4	No objects present	No objects present
Schedule (FI60)	5	No objects present	No objects present
Schedule (FI60)	6	No objects present	No objects present
Schedule (FI60)	7	No objects present	No objects present
Schedule (FI60) (Experimental **Session 1**)	8	**GROUP A OBJECTS**	No objects present
Schedule (FI60) (Experimental **Session 2**)	9	**GROUP A OBJECTS**	No objects present
Schedule (FI60) (Experimental **Session 3**)	10	**GROUP A OBJECTS**	No objects present
Extinction (Experimental **Session 4**)	11	**GROUP B OBJECTS**	**GROUP A OBJECTS**
Extinction (Experimental **Session 5**)	12	**GROUP B OBJECTS**	**GROUP A OBJECTS**
Extinction (Experimental **Session 6**)	13	**GROUP B OBJECTS**	**GROUP A OBJECTS**
Extinction	14	No objects present	No objects present
Extinction	15	No objects present	No objects present
Extinction	16	No objects present	No objects present
Extinction	17	**LOOSE BOTTLE**	**LOOSE BOTTLE**

All rats were run on the ***fixed-interval*** schedule for six sessions (once daily). For the first three ***fixed-interval*** sessions, no objects were present in the box. For the last three ***fixed-interval*** sessions, objects were present for rats in the FIOS group. Following this, they were placed on an ***extinction*** schedule for six sessions (once daily). Objects were present for the first three ***extinction*** sessions, but the boxes were devoid of objects in the last three ***extinction*** sessions. All rats were placed on a seventh day of ***extinction***, for the final session. The stimulus objects were not present, but a loose plastic water bottle (of the type used to house the perspex wall-mounted bottle) was placed between the bar and mounted water bottle areas (Figure 9.6). Only videotapes from the last three ***fixed-interval*** sessions and first three ***extinction*** sessions were scored.

Exploratory behaviour directed towards the objects, ***bar pressing***, ***drinking***, ***behaviour directed towards the water bottle***, and various other behaviours (to be detailed subsequently) were recorded under all the conditions specified.

Before the start of each session, 100 cm of water was measured into a measuring cylinder (glass) and transferred into the water bottle. This bottle was then placed into the protective plastic bottle surround, which was clipped into the wall mounts. The bottle wires were then connected to the lick counter, and the counter tested by tapping the index finger under the mouth of the bottle. It should be noted, that doing this wasted a couple of drops of water, but ensured that the apparatus was functional. At the end of each session, after the rat had been returned to its home-cage, the water bottle was unclipped, and the remaining water poured into the measuring cylinder.

This is <u>not</u> the most accurate way of measuring the water used. The method of weighing the water bottle and water inside it (subtract weight of container, leaving weight of water, which can be converted to an amount) at the start and finish of the session, is a more accurate measure. However, as the rats often destroyed the outer plastic bottle, a method that relied on the weight of the container remaining the same could not be employed (Figure 9.7).

Video recording commenced at the start of each observation session, as did the video camera timer. The rats were placed into the exploration box in such a way, that the body was side-on to the bar and object (1 or 4). As mentioned previously, this was to minimise positional biases. The perspex lid was then closed and the session commenced.

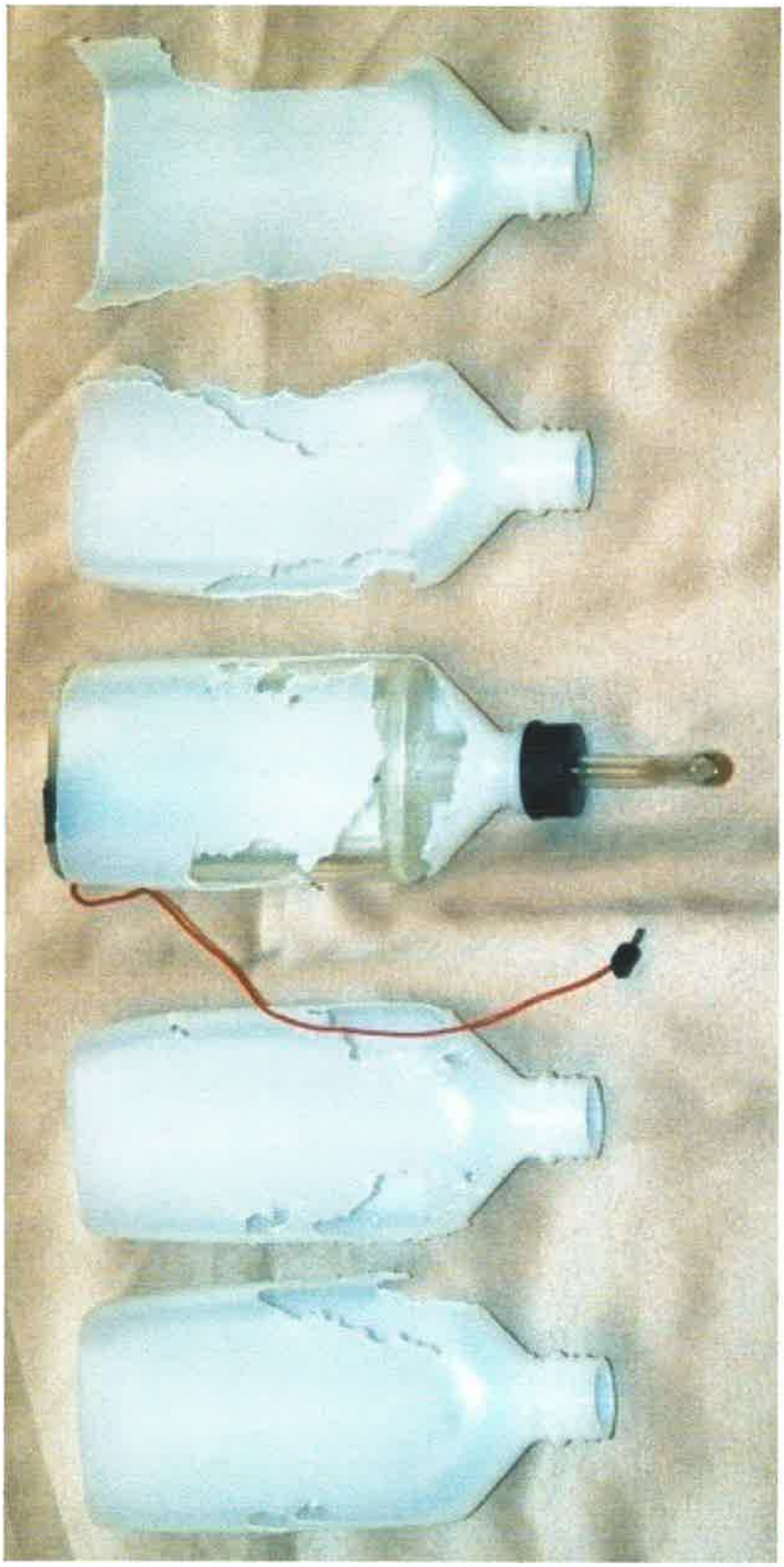


Figure 9.7. Some of the damaged white plastic water bottle housings, ranging from front and both sides completely chewed away (top) to housing slightly chewed (bottom). The center bottle shows damaged housing with the bottle still inside

The rat was left alone for the entire session. The experimenter was able to view the rat from behind the partition, via the video monitor. Since two-hour videotapes were used, different videotapes had to be inserted into the VCR after two hours. Thus, a few seconds of behavioural observation was lost every time the videotapes were changed. The rat was removed from the box at the end of 3.5 hours. Upon removal from the exploration box, the rat was returned to its home-cage where it received *ad libitum* food for one hour. Following each experimental session, the stimulus objects were wiped clean, and the sawdust was smoothed out to an even distribution, after faeces, pieces of chewed plastic bottle, and urine-soaked areas of sawdust were removed (and more sawdust added), if necessary.

Two experimental sessions were run almost simultaneously (except for conditioning sessions) in two adjacent rooms. One rat was always run a few minutes earlier than the second rat, since a few minutes was required to measure out the water, clip the bottles in, and place the rat in and out of the exploration box.

9.2.3.3 EVENT RECORDING

The observation sessions were all viewed upon completion of the experimental running. Scoring of the behavioural events was accomplished by means of an event-recording program, which was activated at the start of each session to be viewed. The event recorder consisted of a custom built board (fixed to the top of a table) with 15 buttons, each representing a different behavioural category. The program could be paused at any point during the event recording session, by pressing any button on the computer keyboard.

A number of the behavioural categories included are the same as those used in Experiment 1 (see section 6.2.3.3), namely: ***bar pressing***, ***bar-related behaviour***, ***sniff object***, ***sniff and touch object***, ***chew/bite object***, ***propping***, ***displacement***, and ***digging/burying*** (***rearing***, ***jump at lid*** & ***pica*** were not scored). A number of extra behavioural categories were also included. These were as follows:

Behaviour directed at the water bottle

- ***Sniffing water bottle*** (***i.e.***, ***sniff bottle***) - like ***sniff object***, this category includes orientation of the rat's snout towards the water bottle, without physical contact. Such ***sniff bottle*** occurs immediately prior to ***sniff and touch bottle***.

- ***Sniffing while touching or manipulating the water bottle*** **(*i.e., sniff and touch bottle*)** - involves physical contact with the water bottle, *i.e.*, touching, digging around the base or climbing upon the water bottle or wire-grid, while sniffing the water bottle. Like the ***sniff and touch object*** category, it does not include mouthing or biting of the water bottle. These behaviours fall into a separate category.

- ***Biting while touching or manipulating the water bottle*** **(*i.e., chew/bite bottle*)** -includes any mouthing, biting or chewing of the water bottle. The rat may also be touching the bottle or wire-grid with its paws or other parts of its body, whilst biting the water bottle.

- ***Drinking*** - involves the rat consuming water from the spout of the water bottle. The rat's forepaw(s) may be resting on the bottle itself, or on the wire-grid.

Other behavioural categories

- ***Resting / sleeping*** - includes lying down and remaining inert in one position (for more than 5 seconds), or asleep.

Frequency and duration measures were recorded for all behavioural events. The appropriate button was depressed for the full duration of each event, and released upon the completion of the behaviour. If instances of ***coprophagia*** (or other interesting behaviours that were not included in the list of behaviours scored) were observed during event recording, the tape was viewed again, and further notes were taken (*e.g.*, the number of bouts of ***coprophagia***, or ingestion of feces, were recorded).

9.2.3.4 INDEPENDENT JUDGING

The same method as in Experiment 1 and 2 was used to ensure observer reliability and replicability of behavioural findings. That is, three independent judges scored the behaviour of an animal chosen at random. The session was of 30 minutes duration. Prior to commencement of scoring, the independent judges were individually familiarised with the event recording apparatus. Each button was clearly labelled with the behaviour it represented. The behavioural categories were described, the task explained, and any ensuing questions pertaining to the behavioural scoring answered.

The independent judge was then given three ten-minute practice sessions, which had been selected at random from the remaining animals. The extra practice sessions were provided, since thirteen behavioural categories were to be scored. Previously, judges had only been required to score eleven categories. Subsequently, the judge was required to score the behaviours from the 30-minute session. The total frequency and duration of each behavioural category was then calculated, and compared with the behavioural measurements scored by the experimenter for the same session. In addition, the agreement amongst all the judges was examined.

9.3 RESULTS FOR EXPERIMENT 3

9.3.1 THE PRESENCE OF EXPLORATORY AND OTHER BEHAVIOURS DURING THE POST-REINFORCEMENT PAUSES

In order to test Hypothesis 13, a separate table of means for each frequency and duration measure was set up for subjects classified by the two grouping (or independent) variables, group and session. (These tables can be found in Appendix C). Each mean was based on the behavioural responses of four subjects, since there were four rats per group. The mean for each session was summed to give the sum of means for individual rats in the FIOS and FIOE groups for the three ***fixed-interval*** sessions combined. The same procedure was followed for the behavioural measures during the PRPs. This PRP sum of means value was then calculated as a percentage of the sum of means of that particular behavioural measure for the three ***fixed-interval*** sessions combined (*i.e.*, as a % of the total occurrence). Table 9.2 presents the sum of means and percentages of each frequency and duration measure for the two groups during the ***first 30 minutes*** of each session, and Table 9.3 and Table 9.4 for the ***middle 30 minutes*** and ***last 30 minutes*** of each session, respectively.

9.3.1.1 HYPOTHESIS THIRTEEN: PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

*Since **fixed-interval** schedules are characterised by the existence of regular PRPs, it is expected that a large proportion of **drinking** (Falk, 1971) and each of the other scored behaviours (hypothesis one) will occur during the PRPs.*

THE FIRST 30 MINUTES OF EACH SESSION

The frequency measures

In order of increasing percentage of total frequency, the behavioural measures for the FIOS group were: ***bar-related behaviour***; ***propping***; ***sniff and touch object***; ***sniff object***; ***sniff bottle***;

displacement; ***digging/burying***; ***sniff and touch bottle***; ***chew/bite object***; ***chew/bite bottle***; ***resting/sleeping***; and ***drinking*** (Table 9.2). The percentage of total frequency occurring during the PRPs ranged from 26.35% to 84.88%. Over a third of each behavioural category occurred during the PRPs (with the exception of ***bar-related behaviour***). Over 60% of ***chew/bite object***, ***chew/bite bottle*** (***aggression***), ***resting/sleeping*** (***inactivity***), and ***drinking*** (***polydipsia***) took place during the PRPs. That is, very large percentages of aberrant or ***schedule-induced behaviours*** took place during the PRPs.

Table 9.2

The mean frequency and duration of behaviours occurring during the PRPs (for the ***first 30 minutes*** of each session in the FIOS & FIOE groups) summed over the three ***fixed-interval*** sessions as a percentage of the (total) mean frequency and duration of behaviour (for the ***first 30 minutes*** of each session) summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS * FIOS GROUP	SUM OF MEANS * FIOE GROUP	SUM OF MEANS IN PRPs * FIOS GROUP	SUM OF MEANS IN PRPs * FIOE GROUP	% OF TOTAL * FIOS GROUP	% OF TOTAL * FIOE GROUP
FREQUENCIES						
Digging/Burying	41.25	92.75	23.5	55.75	56.97	60.11
Drinking	43	38.75	36.5	28	84.88	72.26
Chew/Bite Bottle	26.25	12.75	17	7.75	64.76	60.78
Sniff & Touch Bottle	81.75	119.25	48.5	75	59.33	62.89
Sniff Bottle	91.5	84.75	49.5	49.5	54.1	58.41
Propping	87.75	118.5	35	46.75	39.89	39.45
Displacement	84	97.25	46.5	52.5	55.36	53.98
Chew/Bite Object	22	no	13.5	no	61.36	no
Sniff & Touch Object	159.25	objects	71.5	objects	44.9	objects
Sniff Object	293.5	present	136.25	present	46.42	present
Bar-related Behaviour	564.5	717.5	148.75	209.5	26.35	29.2
Resting/Sleeping	1.5	4.75	1	2.5	66.67	52.63
DURATIONS (in seconds)						
Digging/Burying	53.81	108.84	37.06	70.16	68.87	64.46
Drinking	390.05	398.56	350.41	318.42	89.84	79.89
Chew/Bite Bottle	539.11	68.04	356.58	49.35	66.14	72.53
Sniff & Touch Bottle	111.7	268.76	69.35	160.83	62.09	59.84
Sniff Bottle	69.64	48	36.31	26.56	52.14	55.33
Propping	207.13	288.88	102.8	125.84	49.63	43.56
Displacement	333.7	556.43	242.61	405.73	72.7	72.92
Chew/Bite Object	341.43	no	294.78	no	86.34	no
Sniff & Touch Object	289.16	objects	115.91	objects	40.09	objects
Sniff Object	300.01	present	123.18	present	41.06	present
Bar-related Behaviour	392.71	535.66	141.48	188.02	36.03	35.1
Resting/Sleeping	9.86	42.04	6.96	15.15	70.59	36.04

In order of increasing percentage of total frequency, the behavioural measures for the FIOE group were: ***bar-related behaviour***; ***propping***; ***resting/sleeping***; ***displacement***; ***sniff bottle***; ***digging/burying***; ***chew/bite bottle***; ***sniff and touch bottle***; and ***drinking*** (Table 9.2). The percentage of total frequency occurring during the PRPs ranged from 29.2% to 72.26%. With the exception of ***bar-related behaviour*** and ***propping***, more than half of each of the behaviours occurred during the PRPs.

The duration measures

The behavioural measures for the FIOS group, in order of increasing percentage of total duration (in seconds) were: ***bar-related behaviour***; ***sniff and touch object***; ***sniff object***; ***propping***; ***sniff bottle***; ***sniff and touch bottle***; ***chew/bite bottle***; ***digging/burying***; ***resting/sleeping***; ***displacement***; ***chew/bite object***; and ***drinking*** (Table 9.2). The percentage of total duration occurring during the PRPs ranged from 36.03% to 89.84%. At least a third of each of the duration measures occurred during the PRPs. An exceptionally high percentage (almost 90%) of total duration of ***drinking*** (***polydipsia***) occurred during the PRPs, and over 70% of ***displacement***, ***chew/bite object*** (***aggression***), and ***resting/sleeping*** (***inactivity***) occurred during the PRPs.

The behavioural measures for the FIOE group, in order of increasing percentage of total duration (in seconds) were: ***bar-related behaviour***; ***resting/sleeping***; ***propping***; ***sniff bottle***; ***sniff and touch bottle***; ***digging/burying***; ***chew/bite bottle***; ***displacement***; and ***drinking*** (Table 9.2). The percentage of total duration occurring during the PRPs ranged from 35.1% to 79.89%. That is, over a third of each of the duration measures occurred during the PRPs. Over 70% of the time spent engaged in ***chew/bite bottle*** (***aggression***), ***displacement*** and ***drinking*** (***polydipsia***), took place during the PRPs.

THE MIDDLE 30 MINUTES OF EACH SESSION

The frequency measures

In order of increasing percentage of total frequency, the behavioural measures for the FIOS group were: ***bar-related behaviour***; *propping*; ***sniff and touch bottle***; ***sniff bottle***; ***sniff object***; ***displacement***; ***chew/bite bottle***; ***sniff and touch object***; ***resting/sleeping***; ***digging/burying***; ***drinking***; and ***chew/bite object*** (Table 9.3). The percentage of total frequency occurring during the PRPs ranged from 38.85% to 93.75%. With the exception of ***bar-related behaviour***, more than half of each behavioural category occurred during the PRPs. Over 80% of the frequency of ***digging/burying*** (possibly ***escape-directed behaviour***), ***drinking*** (***polydipsia***), ***chew/bite object*** and ***chew/bite bottle*** (***aggression***), ***sniff and touch object***, and ***resting/sleeping*** (***inactivity***) occurred during the PRPs.

Table 9.3
The mean frequency and duration of behaviours occurring during the PRPs, for the ***middle 30 minutes*** of each session in the FIOS and FIOE groups, summed over the three ***fixed-interval*** sessions (middle columns). This is then presented as a percentage of the (total) mean frequency and duration of behaviour for the ***middle 30 minutes*** of each session, summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS * FIOS GROUP**	**SUM OF MEANS * FIOE GROUP**	**SUM OF MEANS IN PRPs * FIOS GROUP**	**SUM OF MEANS IN PRPs * FIOE GROUP**	**% OF TOTAL * FIOS GROUP**	**% OF TOTAL * FIOE GROUP**
FREQUENCIES						
Digging/Burying	27.5	54.5	22.5	44.5	81.82	81.65
Drinking	32.75	19.5	29.75	19	90.84	97.44
Chew/Bite Bottle	6.25	6.75	5	6.5	80	96.3
Sniff & Touch Bottle	43.75	116.25	29.75	102	68	87.74
Sniff Bottle	69.5	72	49.5	55	71.22	76.39
Propping	113.25	61.25	70	36.25	61.81	59.18
Displacement	91.25	67	71	51.5	77.81	76.87
Chew/Bite Object	12	no	11.25	no	93.75	no
Sniff & Touch Object	81.75	objects	65.5	objects	80.12	objects
Sniff Object	189.5	present	144	present	75.99	present
Bar-related Behaviour	480.75	636.25	186.75	254.5	38.85	40
Resting/Sleeping	23.25	45	19	38.5	81.72	85.56
DURATIONS (in seconds)						
Digging/Burying	44.31	56.44	38.32	49.57	86.48	87.83
Drinking	360.49	246.38	341.36	246.1	94.69	99.89
Chew/Bite Bottle	64.01	169.81	51.05	167.16	79.75	98.44
Sniff & Touch Bottle	82.41	408.89	59.8	355.46	72.56	86.93
Sniff Bottle	47.76	40.28	36.71	31.19	76.86	77.43
Propping	318.93	204.91	196.62	140.17	61.65	68.41
Displacement	630.3	673.43	563.59	629.46	89.42	93.47
Chew/Bite Object	336.38	no	297.96	no	88.58	no
Sniff & Touch Object	168.94	objects	135.32	objects	80.1	objects
Sniff Object	145.69	present	109.08	present	74.87	present
Bar-related Behaviour	322.09	524.25	156.22	265.04	48.5	50.56
Resting/Sleeping	205.01	586.68	185.86	526.13	90.66	89.68

In order of increasing percentage of total frequency, the behavioural measures for the FIOE group were: ***bar-related behaviour***; ***propping***; ***sniff bottle***; ***displacement***; ***digging/burying***; ***resting/sleeping***; ***sniff and touch bottle***; ***chew/bite bottle***; and ***drinking*** (Table 9.3). The percentage of total frequency occurring during the PRPs ranged from 40% to 97.44%. Apart from ***bar-related behaviour*** and ***propping***, over 75% of the instances of each of the behaviours occurred during the PRPs. For ***chew/bite bottle*** (***aggression***) and ***drinking*** (***polydipsia***), these values were greater than 95%.

The duration measures

In order of increasing percentage of total duration (in seconds), the behavioural measures for the FIOS group were as follows: ***bar-related behaviour***; ***propping***; ***sniff and touch bottle***; ***sniff object***; ***sniff bottle***; ***chew/bite bottle***; ***sniff and touch object***; ***digging/burying***; ***chew/bite object***; ***displacement***; ***resting/sleeping***; and ***drinking*** (Table 9.3). The value for the percentage of total duration occurring during the PRPs ranged from 48.5% to 94.69%. With the exception of ***bar-related behaviour*** and ***propping,*** more than 70% of each duration measure occurred during the PRP's. Exceptionally high percentages of duration (>90%) of ***resting/sleeping*** (***inactivity***) and ***drinking*** (***polydipsia***) occurred during the PRPs.

In order of increasing percentage of total duration (in seconds), the behavioural measures for the FIOE group were as follows: ***bar-related behaviour***; ***propping***; ***sniff bottle***; ***sniff and touch bottle***; ***digging/burying***; ***resting/sleeping***; ***displacement***; ***chew/bite bottle***; and ***drinking*** (Table 9.3). The value for the percentage of total duration occurring during the PRPs ranged from 50.56% to 99.89%. Thus, more than half of each duration measure occurred during the PRPs and for ***displacement***, ***chew/bite bottle*** (***aggression***) and ***drinking*** (***polydipsia***) the values were over 90%. In fact, less than 2% of the time spent engaged in ***drinking*** and ***chew/bite object***, took place outside the PRPs.

THE LAST 30 MINUTES OF EACH SESSION

The frequency measures

In order of increasing percentage of total frequency, the behavioural measures for the FIOS group were: ***bar-related behaviour***; ***displacement***; ***chew/bite bottle***; ***propping***; ***sniff bottle***; ***sniff object***; ***sniff and touch object***; ***sniff and touch bottle***; ***drinking***; ***chew/bite object***; ***resting/sleeping***; ***digging/burying*** (Table 9.4). The value for percentage of total occurring during the PRPs ranged from 35.94% to 92.06%. With the exception of ***bar-related behaviour*** and ***displacement,*** over 70% of each behavioural category occurred during the PRPs. The instances of ***sniff and touch object*** and ***sniff and touch bottle*** (topographically similar behavioural categories) occurring during the PRPs were almost identical. Exceptionally high percentages (>90%) of ***drinking*** (***polydipsia***), ***chew/bite object*** (***aggression***), ***resting/sleeping*** (***inactivity***), and ***digging/burying*** (possibly ***escape-directed behaviour***) occurred during the PRPs.

In order of increasing percentage of total frequency, the behavioural measures for the FIOE group were: ***bar-related behaviour***; ***propping***; ***chew/bite bottle***; ***displacement***; ***sniff bottle***; ***digging/burying***; ***sniff and touch bottle***; ***drinking***; and ***resting/sleeping*** (Table 9.4). The value for percentage of total occurring during the PRPs ranged from 38.52% to 87.25%. With the exception of ***bar-related behaviour*** over 65% of the instances of these behaviours occurred during the PRPs.

Table 9.4
The mean frequency and duration of behaviours occurring during the PRPs, for the ***last 30 minutes*** of each session in the FIOS and FIOE groups, summed over the three ***fixed-interval*** sessions (middle column). This is then presented as a percentage of the (total) mean frequency and duration of behaviour for the ***last 30 minutes*** of each session, summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS * FIOS GROUP**	**SUM OF MEANS * FIOE GROUP**	**SUM OF MEANS IN PRPs * FIOS GROUP**	**SUM OF MEANS IN PRPs * FIOE GROUP**	**% OF TOTAL * FIOS GROUP**	**% OF TOTAL * FIOE GROUP**
FREQUENCIES						
Digging/Burying	31.5	49.25	29	37.5	92.06	76.14
Drinking	33.75	15.75	30.5	13.5	90.37	85.71
Chew/Bite Bottle	19.25	8.5	13.5	5.75	70.13	67.65
Sniff & Touch Bottle	51.75	103.5	42	85.5	81.16	82.61
Sniff Bottle	57.25	75.5	45	55.75	78.6	73.84
Propping	91.75	54.75	68.5	35.75	74.66	65.3
Displacement	101	66	68	47.5	67.33	71.97
Chew/Bite Object	16.75	no	15.25	no	91.05	no
Sniff & Touch Object	83.5	objects	67.75	objects	81.14	objects
Sniff Object	172.75	present	139.25	present	80.61	present
Bar-related Behaviour	368	613.25	132.25	236.25	35.94	38.52
Resting/Sleeping	23	49	21	42.75	91.3	87.25
DURATIONS (in seconds)						
Digging/Burying	43.41	54.56	41.75	44.44	96.18	81.45
Drinking	295.44	166.91	264.21	138.53	89.43	83
Chew/Bite Bottle	182.63	145.16	137.82	90.46	75.46	62.32
Sniff & Touch Bottle	91.76	322.96	73.29	277.45	79.87	85.91
Sniff Bottle	38.68	44.14	31.32	31.46	80.97	71.27
Propping	261.5	209.21	201.82	151.88	77.18	72.6
Displacement	572.16	734.43	482.53	600.81	84.33	81.81
Chew/Bite Object	413.5	no	389.33	no	94.16	no
Sniff & Touch Object	184.16	objects	152.59	objects	82.86	objects
Sniff Object	126.98	present	107.31	present	84.51	present
Bar-related Behaviour	195.16	508.96	86.68	258.65	44.42	50.82
Resting/Sleeping	462.31	822.64	445.85	762.81	96.44	92.73

The duration measures

In order of increasing percentage of total duration (in seconds), the behavioural measures for the FIOS group were: ***bar-related behaviour***; ***chew/bite bottle***; ***propping***; ***sniff and touch bottle***; ***sniff bottle***; ***sniff and touch object***; ***displacement***; ***sniff object***; ***drinking***; ***chew/bite object***; ***digging/burying***; and ***resting/sleeping*** (Table 9.4). The value for the percentage of total occurring during the PRPs ranged from 44.42% to 96.44%. With the exception of ***bar-related behaviour,*** more than 75% of time was spent engaged in all behaviours during the PRPs. Very high percentages of duration (> 94%) of ***chew/bite object*** (***aggression***), ***digging/burying*** (possibly ***escape-directed behaviour***) and ***resting/sleeping*** (***inactivity***) took place during the PRPs.

The behavioural measures in order of increasing percentage of total duration (in seconds) for the FIOE group were: ***bar-related behaviour***; ***chew/bite bottle***; ***sniff bottle***; ***propping***; ***digging/burying***; ***displacement***; ***drinking***; ***sniff and touch bottle***; and ***resting/sleeping*** (Table 9.4). The value for the percentage of total duration occurring during the PRPs ranged from 50.82% to 92.73%. Thus, more than half of each duration measure occurred during the PRPs. Most of the time (>90%) spent engaged in ***resting/sleeping*** occurred during the PRPs.

Summary

Table 9.5 provides a summary of the percentage of total mean frequency and duration of behaviours occurring during the PRPs (summed over the three ***fixed-interval*** sessions) for all three parts of session for both groups in Experiment 3 (taken from the last two columns of Table 9.2, 9.3 & 9.4).

The frequency measures

With respect to the frequency measures, ***Hypothesis 13 was supported***. That is, a large proportion of each of the scored behaviours occurred during the PRPs (ranging from 26.35% to 97.44%).

During the ***first 30 minutes***, more than a third of each frequency measure occurred during the PRPs for the FIOS group (except ***bar-related behaviour***, which was nevertheless >25%). For the FIOE group, more than 50% of frequency measures occurred during the PRPs (except ***bar-related behaviour*** & ***propping***, which were both >25%).

For the FIOS group, more than half of each frequency measure (except ***bar-related behaviour***), and in fact over 80% of the frequency of ***digging/burying***, ***drinking***, ***chew/bite object*** and

chew/bite bottle, ***sniff and touch object***, and ***resting/sleeping*** occurred during the PRPs of the ***middle 30 minutes***. For the FIOE group, over 75% of the frequency measures (except ***bar-related behaviour*** & ***propping***), and indeed more than 90% of frequency of ***chew/bite bottle*** and ***drinking*** took took place during the PRPs (Table 9.5).

Table 9.5

The percentage of the total mean frequency and duration of each behaviour occurring during the PRPs (summed over the three ***fixed-interval*** sessions) for all three parts of session for both groups.

BEHAVIOURAL MEASURE	**% OF TOTAL * first 30 minutes * FIOS GROUP**	**% OF TOTAL * first 30 minutes * FIOE GROUP**	**% OF TOTAL * mid 30 minutes * FIOS GROUP**	**% OF TOTAL * mid 30 minutes * FIOE GROUP**	**% OF TOTAL * last 30 minutes * FIOS GROUP**	**% OF TOTAL * last 30 minutes * FIOE GROUP**
FREQUENCIES						
Digging/Burying	56.97	60.11	81.82	81.65	92.06	76.14
Drinking	84.88	72.26	90.84	97.44	90.37	85.71
Chew/Bite Bottle	64.76	60.78	80	96.3	70.13	67.65
Sniff & Touch Bottle	59.33	62.89	68	87.74	81.16	82.61
Sniff Bottle	54.1	58.41	71.22	76.39	78.6	73.84
Propping	39.89	39.45	61.81	59.18	74.66	65.3
Displacement	55.36	53.98	77.81	76.87	67.33	71.97
Chew/Bite Object	61.36	no objects present	93.75	no objects present	91.05	no objects present
Sniff & Touch Object	44.9		80.12		81.14	
Sniff Object	46.42		75.99		80.61	
Bar-related Behaviour	26.35	29.2	38.85	40	35.94	38.52
Resting/Sleeping	66.67	52.63	81.72	85.56	91.3	87.25
DURATIONS (in seconds)						
Digging/Burying	68.87	64.46	86.48	87.83	96.18	81.45
Drinking	89.84	79.89	94.69	99.89	89.43	83
Chew/Bite Bottle	66.14	72.53	79.75	98.44	75.46	62.32
Sniff & Touch Bottle	62.09	59.84	72.56	86.93	79.87	85.91
Sniff Bottle	52.14	55.33	76.86	77.43	80.97	71.27
Propping	49.63	43.56	61.65	68.41	77.18	72.6
Displacement	72.7	72.92	89.42	93.47	84.33	81.81
Chew/Bite Object	86.34	no objects present	88.58	no objects present	94.16	no objects present
Sniff & Touch Object	40.09		80.1		82.86	
Sniff Object	41.06		74.87		84.51	
Bar-related Behaviour	36.03	35.1	48.5	50.56	44.42	50.82
Resting/Sleeping	70.59	36.04	90.66	89.68	96.44	92.73

During the ***last 30 minutes***, over 70% of each frequency measure (except ***bar-related behaviour*** & ***displacement***), and indeed more than 90% of frequency of ***chew/bite object***, ***resting/sleeping***, ***digging/burying*** and ***drinking*** for the FIOS group occurred during the PRPs. For the FIOE group, over 65% of frequency measures (except ***bar-related behaviour***) occurred during the PRPs (Table 9.5).

The duration measures

With respect to the duration measures, ***Hypothesis 13 was also supported***. That is, a large proportion of the time spent engaged in each of the scored behaviours occurred during the PRPs (ranging from 35.1% to 99.89%).

During the ***first 30 minutes***, more than a third of each of the duration measures took place during the PRPs for the FIOS group. Furthermore, almost 90% of total duration of ***drinking*** and more than 70% of duration of ***displacement***, ***chew/bite object***, and ***resting/sleeping*** occurred during the PRPs. For the FIOE group, more than a third of duration measures occurred during the PRPs. In addition, more than 70% of time spent engaged in ***chew/bite bottle***, ***displacement*** and ***drinking*** took place during the PRPs (Table 9.5).

For the FIOS group, more than 70% of duration measures (except ***bar-related behaviour & propping***) occurred during the PRPs during the ***middle 30 minutes***. Exceptionally high percentages of duration (>90%) of ***resting/sleeping*** and ***drinking*** occurred during the PRPs. For the FIOE group, more than 50% of each duration measure (>90% of duration of ***displacement)*** occurred during the PRPs. In fact, less than 2% of the time spent engaged in ***drinking*** and ***chew/bite object***, took place outside the PRPs (Table 9.5).

During the ***last 30 minutes***, more than 75% of each duration measure (except ***bar-related behaviour***), and in fact more than 90% of duration of ***chew/bite object***, ***resting/sleeping***, and ***digging/burying*** occurred during the PRPs for the FIOS group. For the FIOE group, more than 50% of duration measures occurred during the PRPs. Most of the time (>90%) spent engaged in ***resting/sleeping*** occurred during the PRPs (Table 9.5).

9.3.1.2 HYPOTHESIS FOURTEEN: EFFECT OF NOVEL STIMULUS OBJECTS ON PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

It is predicted that the presence or absence of novel stimulus objects during ***fixed-interval*** *running may have an effect on the proportions of behaviours (including* ***drinking****) occurring during the PRPs. Thus, it is expected that there will be a difference between the FIOS group (objects present) and the FIOE group (objects absent) during* ***fixed-interval*** *sessions.*

The frequency measures

There was ***partial support for Hypothesis 14***, with respect to the frequency measures. The presence or absence of objects during ***fixed-interval*** sessions had an effect on the proportion of frequency of some of the non object-directed behaviours that occurred during PRPs (as shown in Table 9.5).

During the ***first 30 minutes***, when objects were absent (FIOE group), the proportions were lower (>10% difference) for frequency of ***drinking*** and ***resting/sleeping***. However, the proportions were very similar (<5% difference) irrespective of presence or absence of objects for the frequency of all other behavioural categories (Table 9.5).

For the ***middle 30 minutes***, when objects were absent (FIOE group), the proportions were higher (between 5% & 20%) for the frequency of ***drinking***, ***chew/bite bottle***, ***sniff and touch bottle***, and ***sniff bottle***. However, the proportions were very similar (<5% difference) irrespective of presence or absence of objects for the frequency of ***digging/burying***, ***displacement***, ***bar-related behaviour***, ***resting/sleeping*** and ***propping*** (Table 9.5).

During the ***last 30 minutes***, when objects were absent (FIOE group), the proportions were lower (by up to 16%) for frequency of ***digging/burying*** and ***propping***. However, the proportions were very similar (<5% difference) irrespective of presence or absence of objects for the frequency of all other behavioural categories (Table 9.5).

The duration measures

There was also ***partial support for Hypothesis 14***, with respect to the duration measures. The presence or absence of objects during ***fixed-interval*** sessions had an effect on the proportion of duration of some of the non object-directed behaviours that occurred during PRPs (see Table 9.5).

During the ***first 30 minutes***, when objects were absent (FIOE group), the proportions were lower (>6% difference) for duration of ***drinking***, ***propping*** and ***resting/sleeping*** (almost 35% lower). For this same group, the proportion was higher (about 6.5%) for the duration of ***chew/bite bottle***. However, the proportions were very similar (<5% difference) irrespective of presence or absence of objects for the duration of ***digging/burying***, ***sniff and touch bottle***, ***sniff bottle***, ***displacement*** and ***bar-related behaviour*** (Table 9.5).

For the ***middle 30 minutes***, when objects were absent (FIOE group), the proportions were higher (between 5% & 20%) for the duration of ***drinking***, ***chew/bite bottle***, ***sniff and touch bottle***, and ***propping***. However, the proportions were very similar (<5% difference) irrespective of presence or absence of objects for the duration of ***digging/burying***, ***displacement***, ***bar-related behaviour*** and ***resting/sleeping*** and ***sniff bottle*** (Table 9.5).

During the ***last 30 minutes***, when objects were absent (FIOE group), the proportions were lower (by up to 15%) for the duration of ***digging/burying***, ***drinking***, ***chew/bite bottle*** and ***sniff bottle***, but the proportions were higher (by about 6%) for duration of ***sniff and touch bottle*** and ***bar-related behaviour***. However, the proportions were very similar (<5% difference) irrespective of presence or absence of objects for the duration of ***propping***, ***displacement***, ***bar-related behaviour*** and ***resting/sleeping*** (Table 9.5).

9.3.1.3 HYPOTHESIS FIFTEEN: WITHIN-SESSION CHANGES IN PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

*There may be within-session changes in the proportions of behaviours occurring during the PRPs. That is, the proportions may differ depending on the part of session (**first**, **middle** or **last 30 minutes**). Higher percentages of total frequency and duration may occur during the PRPs as the session continues, since PRPs may stabilise over the 3.5-hour session. Thus, it is expected that percentage of frequency and duration occurring during PRPs will be higher in the **last 30 minutes** than in the **first 30 minutes**.*

Hypothesis 15 was supported, with respect to the frequency measures. That is, the percentage of total frequency occurring during PRPs was greater in the ***last 30 minutes*** than in the ***first 30 minutes*** for all the behavioural categories scored in the FIOS and FIOE groups (Table 9.6). The percentages during the ***first 30 minutes*** ranged from 26.35% to 84.88% for the FIOS group and from 29.2% to 72.26% for the FIOE group. During the ***last 30 minutes***, the percentages ranged from 35.94% to 92.06% for the FIOS group and from 38.52% to 87.25% for the FIOE group. Notably, the percentage of frequency of ***resting/sleeping*** and ***object-directed behaviours*** (for the FIOS group) occurring during the PRPs increased substantially over the session.

Hypothesis 15 was also supported, with respect to the duration measures (with two exceptions). That is, the percentage of total duration occurring during PRPs was greater in the ***last 30 minutes*** than in the ***first 30 minutes*** for most of the behavioural categories scored in the FIOS and FIOE groups (Table 9.6). The exceptions were for ***drinking*** in the FIOS group, which was almost the same, and ***chew/bite bottle*** in the FIOE group. The percentages during the ***first 30 minutes*** ranged from 36.03% to 89.84% for the FIOS group and from 35.1% to 79.89% for the FIOE group. During the ***last 30 minutes***, the percentages ranged from 44.42% to 96.44% for the FIOS group and from 50.82% to 92.73% for the FIOE group.

Table 9.6

The percentage of total mean frequency and duration of behaviours occurring during the PRPs (for the ***first, middle & last 30 minutes*** of each session for the FIOS & FIOE groups).

BEHAVIOURAL MEASURE	**% OF TOTAL * FIOS GROUP * first 30 minutes**	**% OF TOTAL * FIOS GROUP * middle 30 minutes**	**% OF TOTAL * FIOS GROUP * last 30 minutes**	**% OF TOTAL * FIOE GROUP * first 30 minutes**	**% OF TOTAL * FIOE GROUP * middle 30 minutes**	**% OF TOTAL * FIOE GROUP * last 30 minutes**
FREQUENCIES						
Digging/Burying	56.97	81.82	92.06	60.11	81.65	76.14
Drinking	84.88	90.84	90.37	72.26	97.44	85.71
Chew/Bite Bottle	64.76	80	70.13	60.78	96.3	67.65
Sniff & Touch Bottle	59.33	68	81.16	62.89	87.74	82.61
Sniff Bottle	54.1	71.22	78.6	58.41	76.39	73.84
Propping	39.89	61.81	74.66	39.45	59.18	65.3
Displacement	55.36	77.81	67.33	53.98	76.87	71.97
Chew/Bite Object	61.36	93.75	91.05	no objects present	no objects present	no objects present
Sniff & Touch Object	44.9	80.12	81.14			
Sniff Object	46.42	75.99	80.61			
Bar-related Behaviour	26.35	38.85	35.94	29.2	40	38.52
Resting/Sleeping	66.67	81.72	91.3	52.63	85.56	87.25
DURATIONS (in seconds)						
Digging/Burying	68.87	86.48	96.18	64.46	87.83	81.45
Drinking	89.84	94.69	89.43	79.89	99.89	83
Chew/Bite Bottle	66.14	79.75	75.46	72.53	98.44	62.32
Sniff & Touch Bottle	62.09	72.56	79.87	59.84	86.93	85.91
Sniff Bottle	52.14	76.86	80.97	55.33	77.43	71.27
Propping	49.63	61.65	77.18	43.56	68.41	72.6
Displacement	72.7	89.42	84.33	72.92	93.47	81.81
Chew/Bite Object	86.34	88.58	94.16	no objects present	no objects present	no objects present
Sniff & Touch Object	40.09	80.1	82.86			
Sniff Object	41.06	74.87	84.51			
Bar-related Behaviour	36.03	48.5	44.42	35.1	50.56	50.82
Resting/Sleeping	70.59	90.66	96.44	36.04	89.68	92.73

9.3.2 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE DURING THE PRPs, OVER SCHEDULE SESSIONS, BETWEEN PART OF SESSION, AND BETWEEN GROUPS

The changes in each behavioural measure (frequency & duration) occurring during the PRPs over the three ***fixed-interval*** sessions are presented graphically in Figures 9.8- 9.12(III) inclusive. The scores for the ***first***, ***middle*** and ***last 30 minutes*** of each session are plotted on each graph (separately for the two groups), allowing a visual comparison in trends across the sessions. Patterns of change will be presented for each of the behaviours in turn. It should be noted that only the patterns of change during the PRPs are covered in this section. Section 9.3.6 presents the overall patterns of change for each session, not just during the PRPs.

No firm expectations are held concerning patterns of change within PRPs over the three ***fixed-interval*** sessions, or within sessions (***first***, ***middle*** or ***last 30 minutes***). However, the frequency and duration of ***behaviour directed at the stimulus objects*** during the PRPs may reflect the expected overall decrease over and within sessions as a result of habituation to the objects.

9.3.2.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

For the FIOE group, the highest mean frequency and duration of ***bar-related behaviour*** during the PRPs was observed in the ***middle 30 minutes*** of session 1, whilst the lowest occurred during the ***first 30 minutes*** of session 3 (Figure 9.8). The frequency and duration scores showed an overall decrease across the three sessions for all parts of session (***first***, ***middle*** & ***last 30 minutes***).

For the FIOS group, the highest mean frequency and duration scores of ***bar-related behaviour*** during the PRPs occurred during the ***middle 30 minutes*** of all three sessions, with the highest score recorded in session 1 (Figure 9.8). The mean scores for both measures were lower than in the FIOE group, but the pattern was similar, with an overall decrease across the three sessions for all parts of session (***first***, ***middle*** & ***last 30 minutes***). The frequency and duration scores in session 3 were noticeably similar for all three parts of session.

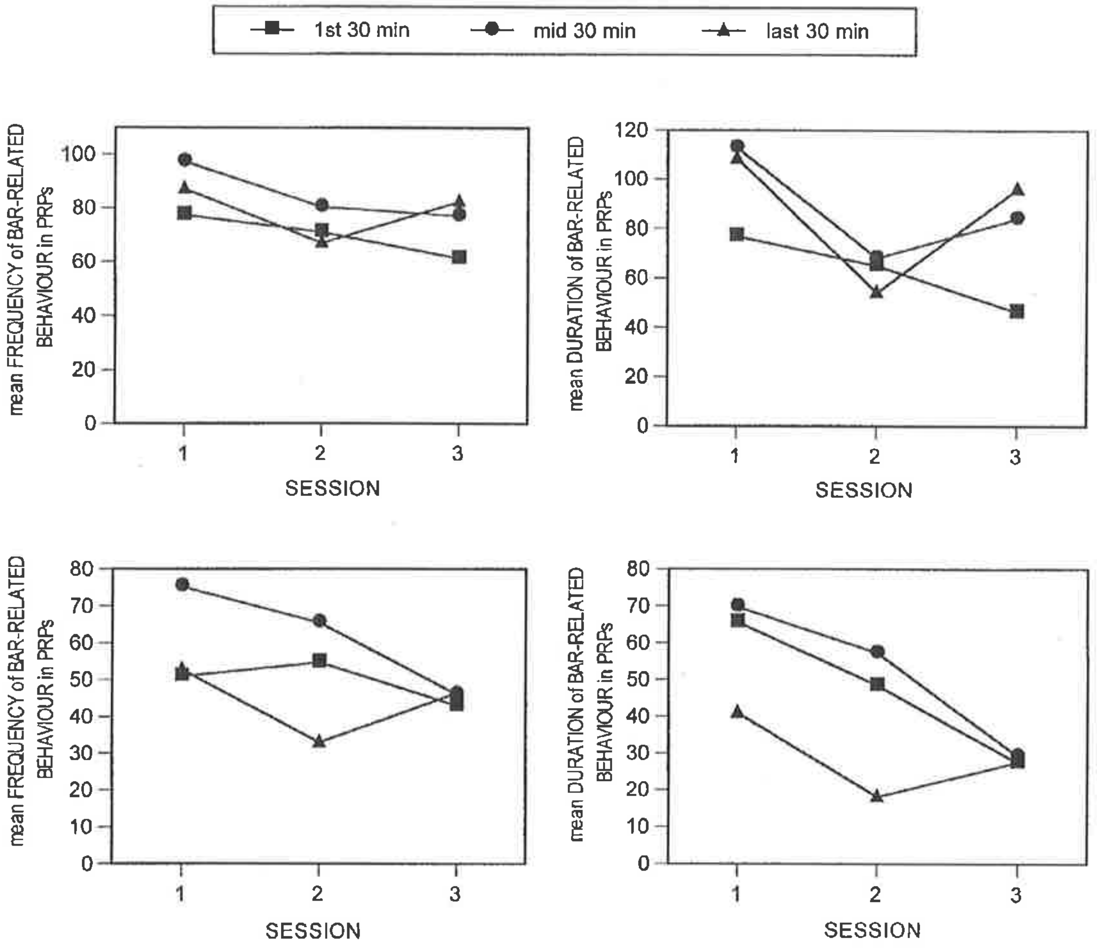


Figure 9.8. Mean frequency (left) and duration (right) scores of ***bar-related behaviour*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

9.3.2.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

The behavioural categories discussed in this section are only relevant to the FIOS group, since only rats in this group had stimulus objects present during the three ***fixed-interval*** sessions.

The highest frequency and duration score of ***sniff object*** during the PRPs, occurred during the ***last 30 minutes*** of session 3 and ***first*** 30 minutes of session 1 respectively (Figure 9.9). The lowest frequency and duration scores occurred during the ***middle 30 minutes*** of session 1 and ***first 30 minutes*** of session 3 respectively. The frequency and duration scores for the ***first 30 minutes*** decrease over the three sessions, but these same measures show an increase over the three sessions for the ***middle*** and ***last 30 minutes***.

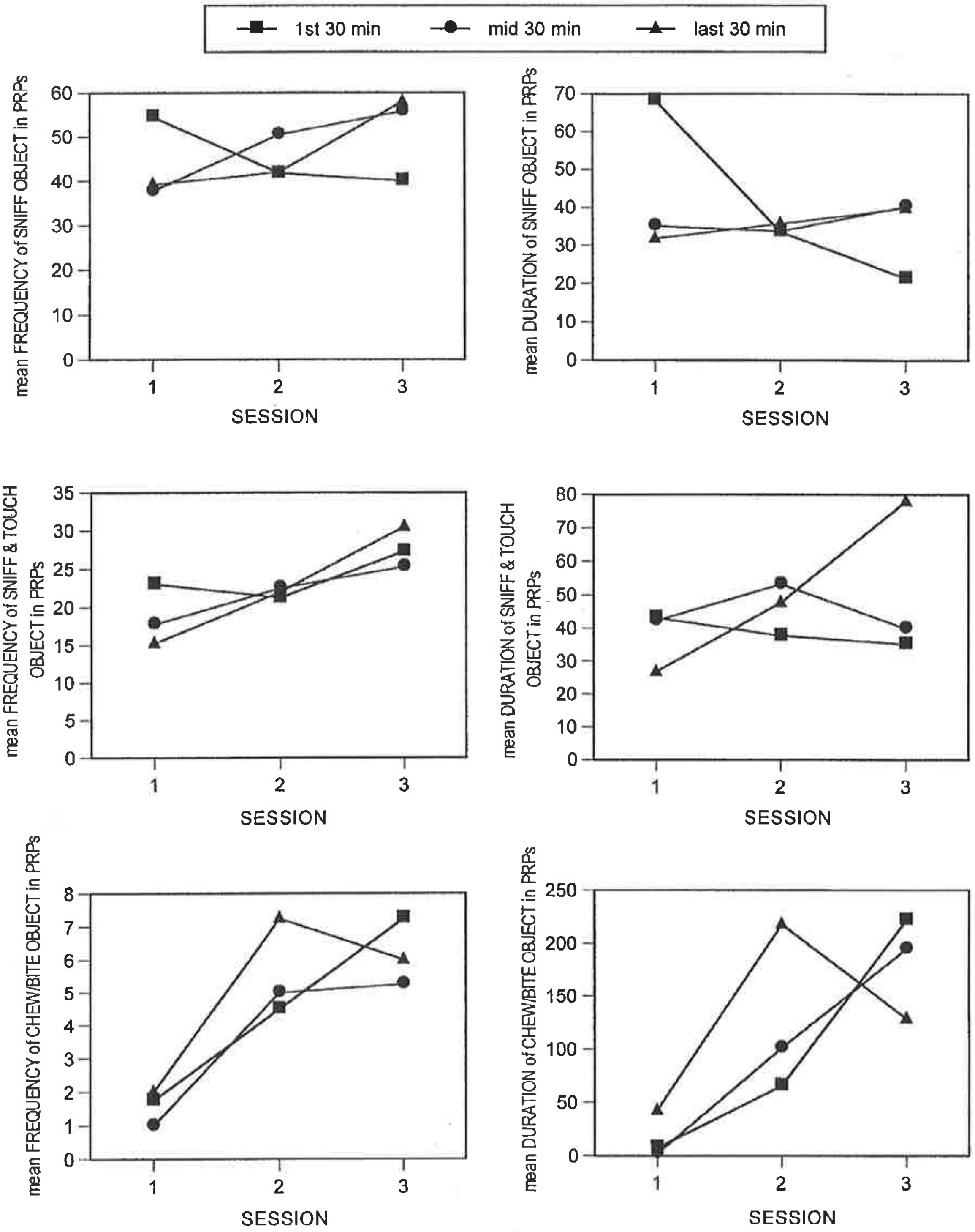


Figure 9.9. Mean frequency (left) and duration (right) scores of ***behaviour directed at the stimulus objects*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session (top- ***sniff object***, middle- ***sniff & touch object***, & bottom- ***chew/bite object***)

The highest and lowest mean frequency and duration scores of ***sniff and touch object*** during the PRPs occurred during the ***last 30 minutes*** of session 3 and session 1 respectively (Figure 9.9). The frequency scores for all three parts of session show an overall increase across the three sessions. The mean duration score increases significantly for the ***last 30 minutes*** over the three sessions, but demonstrates a slight overall decrease in the ***first*** and ***middle 30 minutes*** over these same sessions. Thus, more bouts of this behaviour occur but of shorter duration for these two parts of session.

The mean frequency scores of ***chew/bite object*** during the PRPs over the three sessions are low (<10), whilst the duration scores are only noticeably low in the first session. The highest frequency and duration scores occur during the ***first 30 minutes*** of session 3 (Figure 9.9). The mean frequency and duration scores demonstrate an overall increase over the three sessions for all three parts of session. Thus, few instances of this behaviour occur in any session, but the duration of bouts increases markedly over the three sessions.

9.3.2.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

For the FIOE group, the highest mean frequency and duration scores of ***propping*** during the PRPs were observed during the ***first*** and ***last 30 minutes*** of session 2 respectively (Figure 9.10). The lowest frequency score occurred during the ***last 30 minutes*** of session 3, and the lowest duration was recorded during the ***first 30 minutes*** of session 1. The frequency and duration scores show an overall increase for the ***first 30 minutes*** across the three sessions. However, the pattern in these measures reflects an overall decrease for the ***middle*** and ***last 30 minutes*** over these same sessions.

For the FIOS group, the highest mean frequency and duration scores of ***propping*** during the PRPs were observed during the ***last 30 minutes*** of session 3 (Figure 9.10). The lowest mean frequency and duration scores occurred during the ***first 30 minutes*** of session 1. The most extreme variation in frequency and duration scores over the three sessions is observed in the ***last 30 minutes***. The frequency and duration scores show an overall increase across the three sessions for all parts of session.

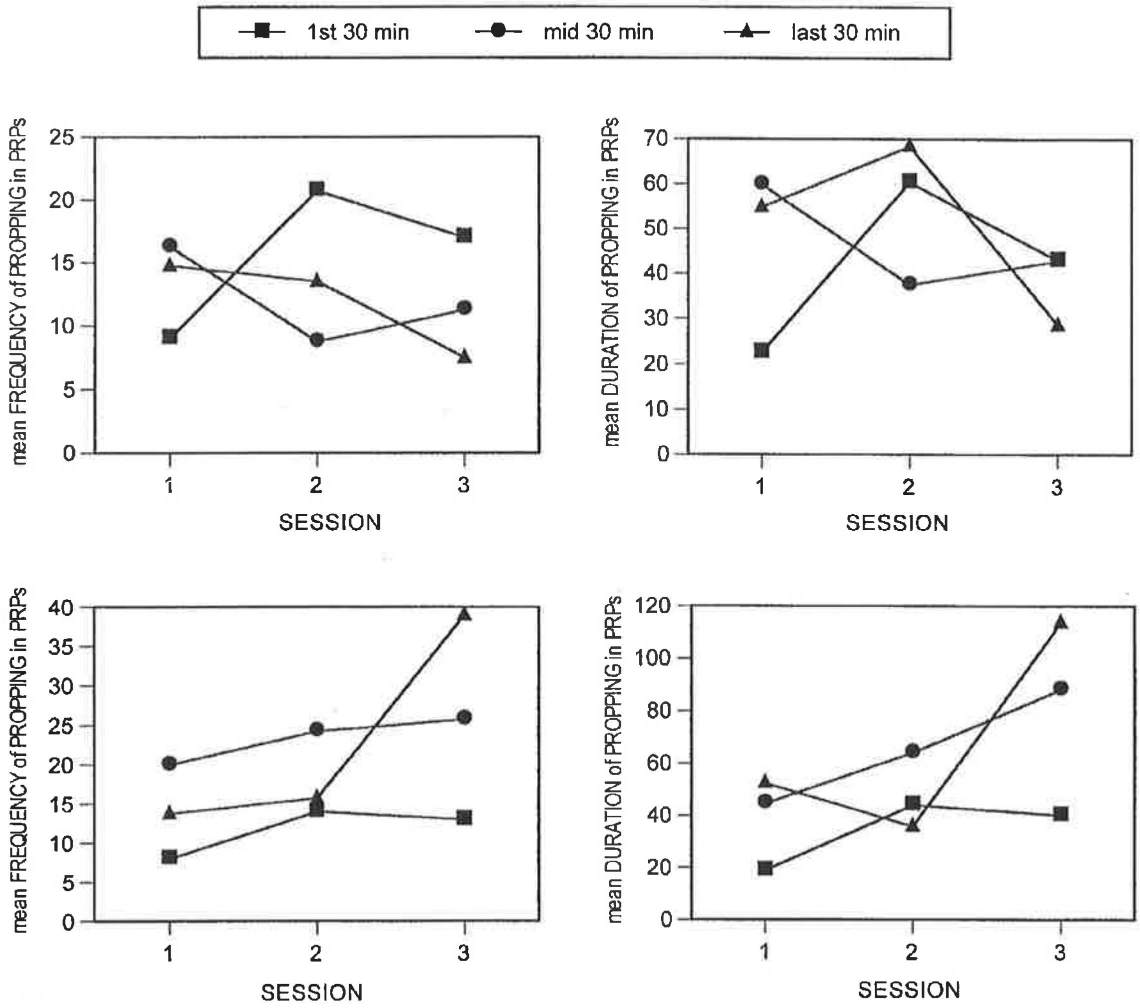


Figure 9.10. Mean frequency (left) and duration (right) scores of ***propping*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

9.3.2.4 BEHAVIOUR DIRECTED AT THE WATER BOTTLE

For the FIOE group, the highest mean frequency and duration scores of ***sniff bottle*** during the PRPs were observed in the ***middle 30 minutes*** of session 3 (Figure 9.11:I). The lowest frequency occurred during the ***first 30 minutes*** of session 1, and the lowest duration was recorded in the ***first 30 minutes*** of session 2. The frequency and duration scores demonstrate an overall increase across the three sessions for all parts of session. Overall there were relatively few bouts of this behaviour, and all of short duration.

For the FIOS group, the highest mean frequency scores of ***sniff bottle*** during the PRPs were observed during the ***first*** and ***middle 30 minutes*** of session 3, whilst the highest duration was observed in the ***first 30 minutes*** of session 1 (Figure 9.11:I). The lowest frequency and duration scores occurred during the ***last 30 minutes*** of session 2. An increase in frequency scores with a corresponding decrease in duration scores was recorded for the ***first*** and ***middle 30 minutes*** across the three sessions. For the ***last 30 minutes***, on the other hand, there was a slight overall decrease in frequency scores, but an overall increase in duration scores. As with the FIOE group, there were relatively few bouts of this behaviour, and all of short duration.

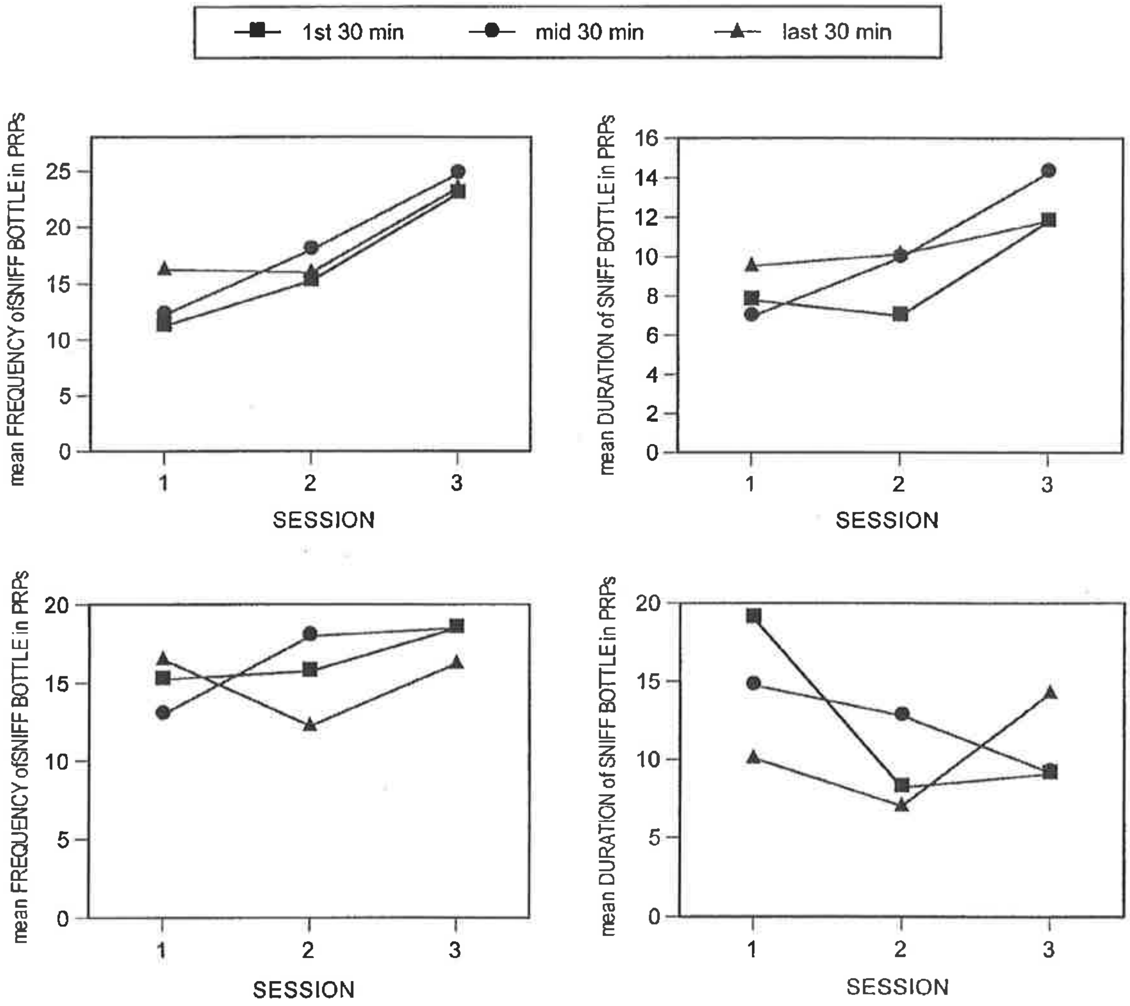


Figure 9.11 (I). Mean frequency (left) and duration (right) scores of ***sniff bottle*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

For the FIOE group, the highest mean frequency and duration scores of ***sniff and touch bottle*** during the PRPs occurred during the ***middle 30 minutes*** of every session, with the highest overall scores recorded in session 3 (Figure 9.11:II). The lowest frequency and duration value in each session is for the ***first 30 minutes***. Both measures increase over the three sessions for all parts of session (***first***, ***middle*** & ***last 30 minutes***).

For the FIOS group, the lowest mean frequency scores of ***sniff and touch bottle*** during the PRPs were obtained in the ***middle 30 minutes*** of every session. The highest overall frequency occurred in the ***first 30 minutes*** of session 3, and the highest duration was recorded during the ***last 30***

minutes of the same session. The lowest overall frequency and duration scores were recorded in the ***middle 30 minutes*** of session 1 and the ***first 30 minutes*** of session 2 respectively. Visual inspection shows an overall increase in frequency scores over the three sessions for all parts of session. The duration scores demonstrate an overall increase across sessions for the ***first*** and ***last 30 minutes***, but the value for the ***middle 30 minutes*** decreases over the three sessions. For ***sniff and touch bottle***, the duration scores for all parts of session were much lower for the FIOS group (all <30 seconds) than for the FIOE group (most >50 seconds & one up to almost 140 seconds). The frequency scores were also lower in the FIOS group.

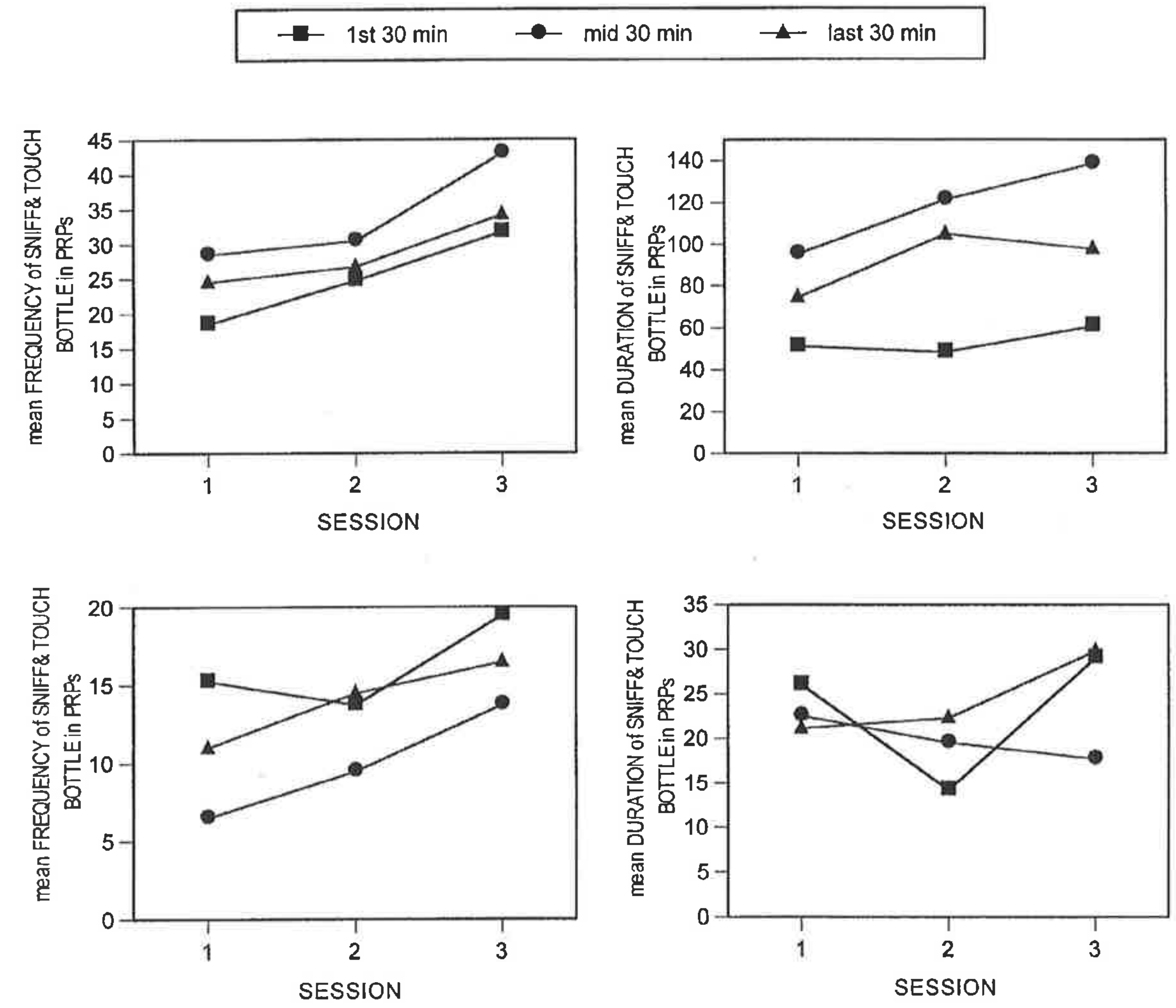


Figure 9.11 (II). Mean frequency (left) and duration (right) scores of ***sniff and touch bottle*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

As Figure 9.11 (III) indicates, for the FIOE group, the frequency values of ***chew/bite bottle*** during the PRPs were very low overall (<6 in all cases). During the ***middle 30 minutes*** of session 3, less than six bouts of this behaviour were engaged in for more than 160 seconds. However, overall the duration scores were also relatively low. An overall increase in frequency and duration scores was observed for all parts of session across the three ***fixed-interval*** sessions. The most dramatic increase in duration occurred during the ***middle 30 minutes***.

For the FIOS group, the frequency scores of ***chew/bite bottle*** during the PRPs were also low (<9 in all cases). The highest mean duration scores were observed during the ***first 30 minutes*** of each session (Figure 9.11:III). Seven bouts of ***chew/bite bottle*** took up more than 160 seconds during the ***first 30 minutes*** of session 2. The duration scores for the ***middle*** and ***last 30 minutes*** of every session were relatively low. Overall, the frequency and duration scores increase over sessions for the ***first*** and ***middle 30 minutes***, whereas these measures show an overall decrease for the ***last 30 minutes***.

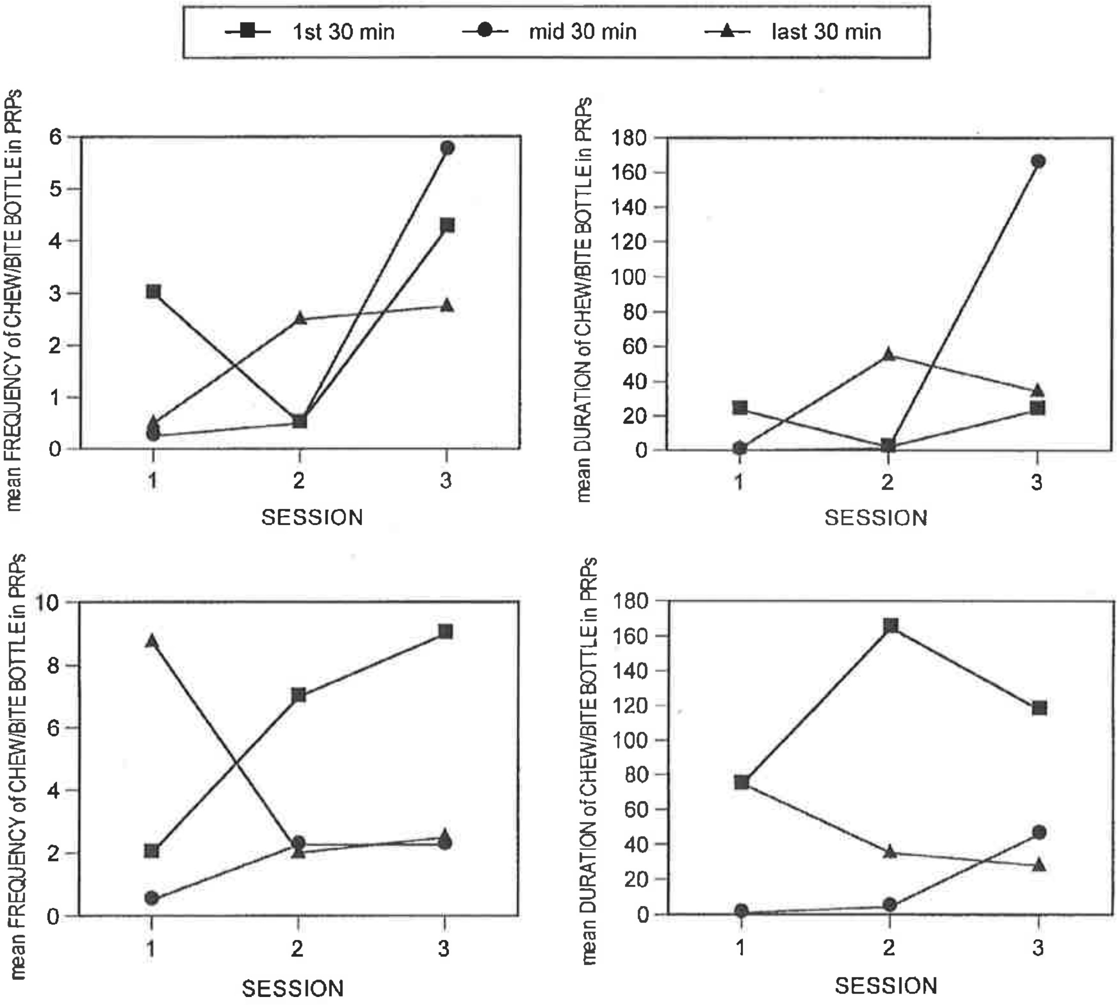
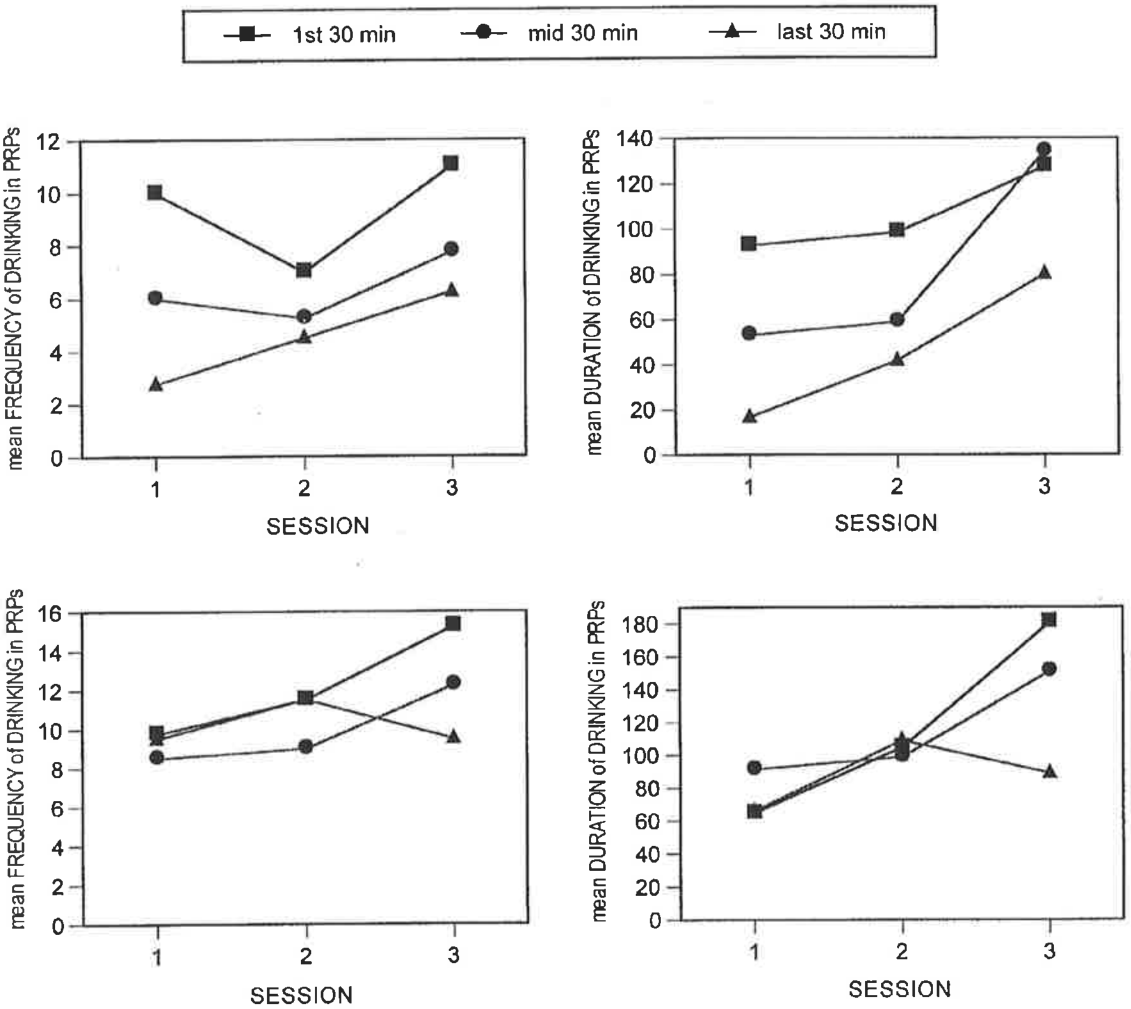


Figure 9.11 (III). Mean frequency (left) and duration (right) scores of ***chew/bite bottle*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

For the FIOE group, the lowest mean frequency and duration scores of ***drinking*** during the PRPs were observed during the ***last 30 minutes*** of each session (Figure 9.11:IV). The highest frequency and duration scores were observed during the ***first 30 minutes*** of most sessions (except duration in session 3). Only few instances of ***drinking*** took place during the PRPs (<12 in all cases). An overall increase in frequency and duration scores over sessions was recorded for all parts of session.



<u>Figure 9.11 (IV).</u> Mean frequency (left) and duration (right) scores of ***drinking*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

For the FIOS group, the highest mean <u>frequency</u> scores of ***drinking*** during the PRPs were observed during the ***first 30 minutes*** of each session, but frequency scores were fairly low (<16 in all cases). The overall highest frequency and duration was obtained during the ***first 30 minutes*** of session 3 (Figure 9.11:IV). The lowest overall scores for both measures occurred during session 1. There was an overall increase in frequency scores across sessions for the ***first*** and ***middle 30 minutes***. There was little change over sessions for the frequency score during the ***last 30 minutes***. Visual inspection shows an overall increase over the three sessions for all parts of session (***first***, ***middle*** & ***last 30 minutes***). In most cases, the frequency and duration scores were higher for the FIOS group. Thus, if objects were present, more bouts occurred and more time was spent ***drinking*** during the PRPs.

9.3.2.5 OTHER BEHAVIOURAL CATEGORIES

For the FIOE group, the mean frequency scores of ***displacement*** during the PRPs changed little over the three sessions, or between the different parts of session (***first***, ***middle*** & ***last 30 minutes***). Relatively few (<22) bouts occurred. The duration values, on the other hand, did change quite substantially over the three sessions, and parts of session (Figure 9.12:I). The lowest duration score in every session occurred during the ***first 30 minutes***. The highest overall frequency and duration scores were observed in the ***first*** and ***last 30 minutes*** of session 3 respectively. An overall increase in frequency and duration scores across sessions was observed in the ***first*** and ***last 30 minutes***. For the ***middle 30 minutes***, the frequency decreased, whilst the duration increased over the three sessions.

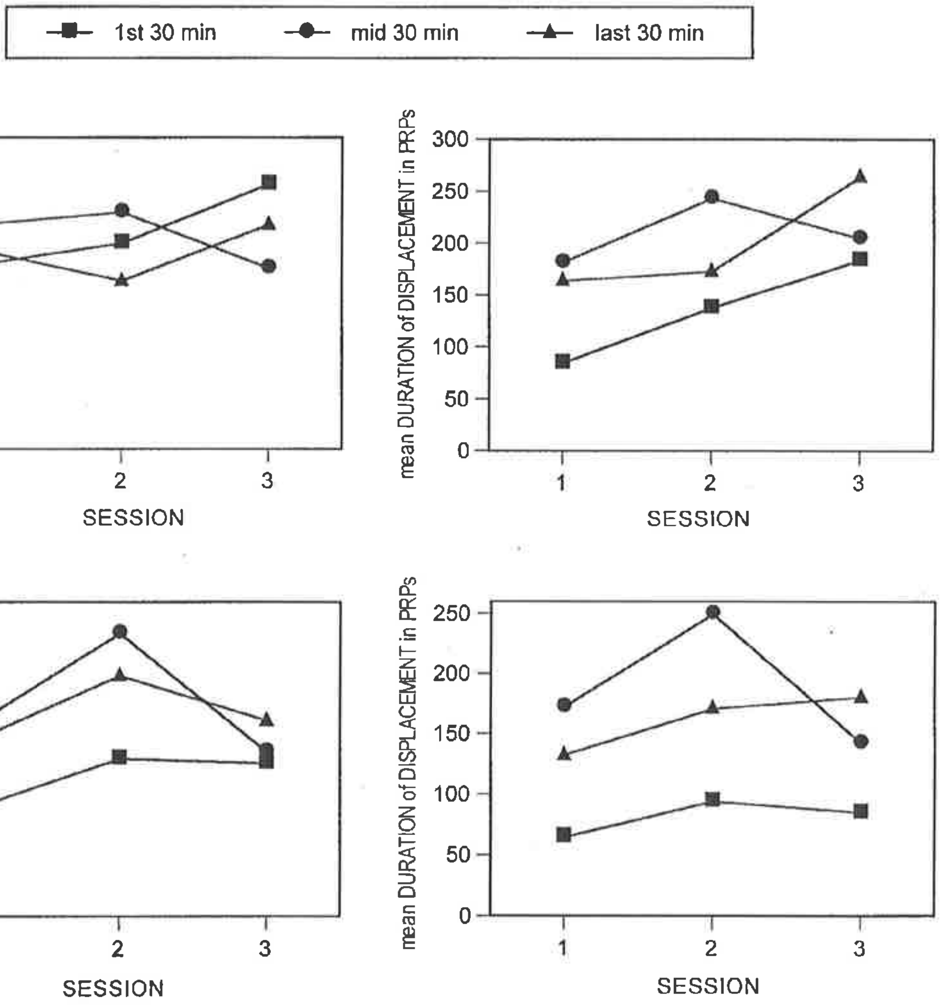


Figure 9.12 (I). Mean frequency (left) and duration (right) scores of ***displacement*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

For the FIOS group, the overall highest mean frequency and duration scores of ***displacement*** during the PRPs were observed during the ***middle 30 minutes*** of session 2 (Figure 9.12:I). The lowest measures in every session occurred during the ***first 30 minutes***. Both measures increased noticeably in session 2 for all parts of session. An overall increase across sessions occurred during the ***first*** and ***last 30 minutes***, whereas an overall decrease over the three sessions was recorded for the ***middle 30 minutes***. In most cases, the mean frequency and duration scores for all parts of session were higher if objects were present (FIOS group).

For the FIOE group, the highest overall mean frequency and duration of ***digging/burying*** during the PRPs was observed during the ***last*** and ***first 30 minutes*** of session 1 respectively (Figure 9.12:II). The mean frequency scores were relatively low (<25), as were the duration scores (<32 seconds). For all parts of session, an overall decrease across the three sessions was observed.

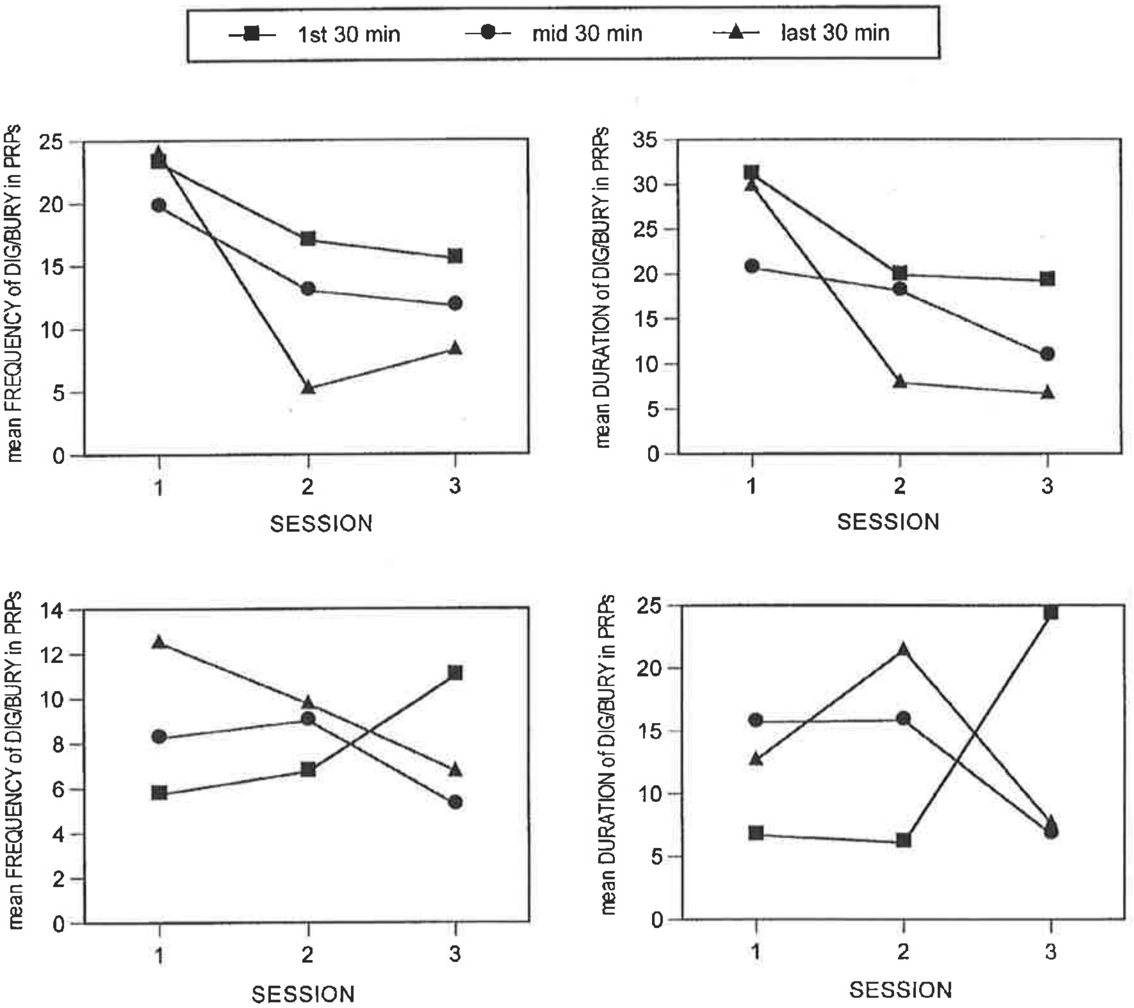


Figure 9.12 (II). Mean frequency (left) and duration (right) scores of ***digging/burying*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

For the FIOS group, the highest overall mean frequency of ***digging/burying*** during the PRPs was observed during the ***last 30 minutes*** of session 1, whilst the highest duration occurred during the ***first 30 minutes*** of session 3 (Figure 9.12:II). The frequency and duration scores during the ***first*** and ***middle 30 minutes*** were lower than for the FIOE group. Overall, the frequency scores were low (<13). The duration scores were also low (<25 seconds). The frequency and duration scores for the ***first 30 minutes*** showed an overall increase across sessions, whereas these measures decreased overall for the ***middle*** and ***last 30 minutes***.

For the FIOE group, almost negligible mean frequency and duration scores of ***resting/sleeping*** during the PRPs were observed during the ***first 30 minutes*** of each session (Figure 9.12:III). The highest overall frequency occurred during the ***middle 30 minutes*** of session 2, whilst the highest overall duration was recorded during the ***last 30 minutes*** of session 3. The frequency and duration scores for the ***first*** and ***last 30 minutes*** showed an overall increase across sessions, whereas an overall decrease in these measures occurred during the ***middle 30 minutes*** (after a sharp increase in session 2). Whilst the frequency scores were relatively low (<18), some of the duration scores were high (270 - 350 seconds).

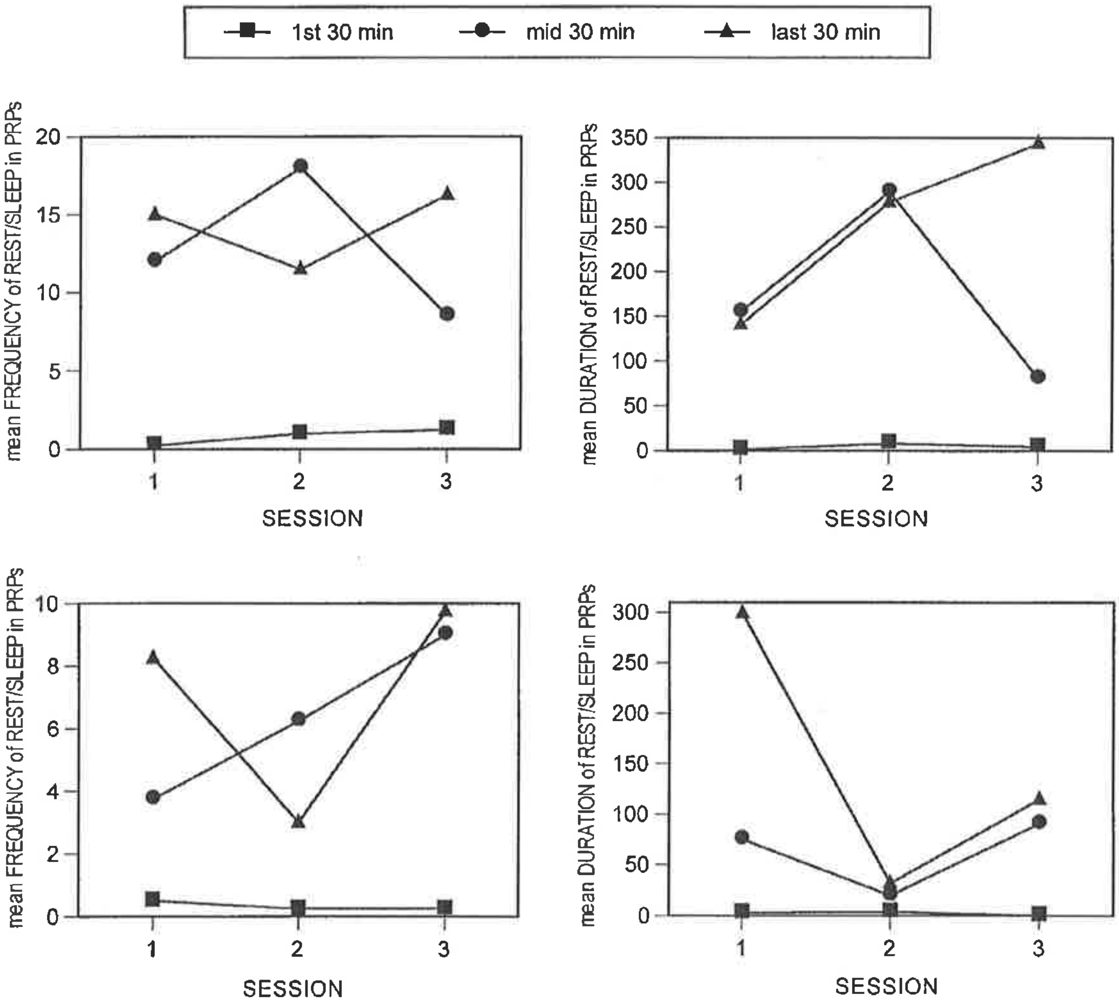


Figure 9.12 (III). Mean frequency (left) and duration (right) scores of ***resting/sleeping*** during the PRPs for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each ***fixed-interval*** session

Almost negligible mean frequency and duration scores of ***resting/sleeping*** during the PRPs were observed during the ***first 30 minutes*** of each session for the FIOS group (Figure 9.12:III), with a slight overall decrease across sessions. The highest overall mean frequency and duration scores were observed during the ***last 30 minutes*** of session 3 and session 1 respectively. The frequency and duration scores show an overall increase across sessions for the ***middle 30 minutes***. For the ***last 30 minutes***, the frequency scores increase overall and the duration scores decrease overall (after both measures drop noticeably in session 2). In most cases, the frequency and duration scores are lower than for the FIOE group.

9.3.3 CHANGES IN BEHAVIOURS DURING PRPs OVER SCHEDULE SESSIONS, BETWEEN PART OF SESSION, AND BETWEEN OBJECT CONDITIONS

The previous section presented the mean frequency and duration of the scored behaviours exhibited by the four groups of rats graphically. Since the sample sizes were small, the data have been primarily analysed by description. Bearing this in mind, the data are now analysed by means of statistical testing. As with Experiment 1 (section 6.3.3) and Experiment 2 (section 7.3.3), a multivariate analysis of variance (MANOVA) was performed for each of the frequency and duration measures, occurring during the PRPs. For each MANOVA there were three independent (or grouping) variables: object (objects present or absent), session and part of session (***first***, ***middle*** or ***last 30 minutes***). In each case there was one dependent variable: the frequency or duration measure of a particular behavioural category.

It should be noted that there were no objects present in one of the two groups (FIOE) during ***fixed-interval*** sessions. Therefore, the grouping variable ***object*** has an obvious effect on ***object-directed behaviours*** in these three sessions. If the other independent variables (session or part of session) have a ***main effect*** on the frequency or duration of ***object-directed behaviours***, it is only relevant for the group with objects present during ***fixed-interval*** sessions (FIOS).

For the frequency measures of behavioural categories, during the PRPs, no statistically significant ***main effects*** of object, session or part of session were found. In addition, there were no statistically significant ***interaction effects*** between any of the grouping variables.

Main effect of *session*

Statistically significant differences over the three ***fixed-interval*** sessions (*i.e.*, a ***session*** main effect) were only reflected in one measure, namely the duration of ***drinking*** [*F* (2,10)=4.10, *p*=.05] during the PRPs. As shown in Figure 9.13 (I), the time spent ***drinking*** during PRPs increased substantially over the three ***fixed-interval*** sessions.

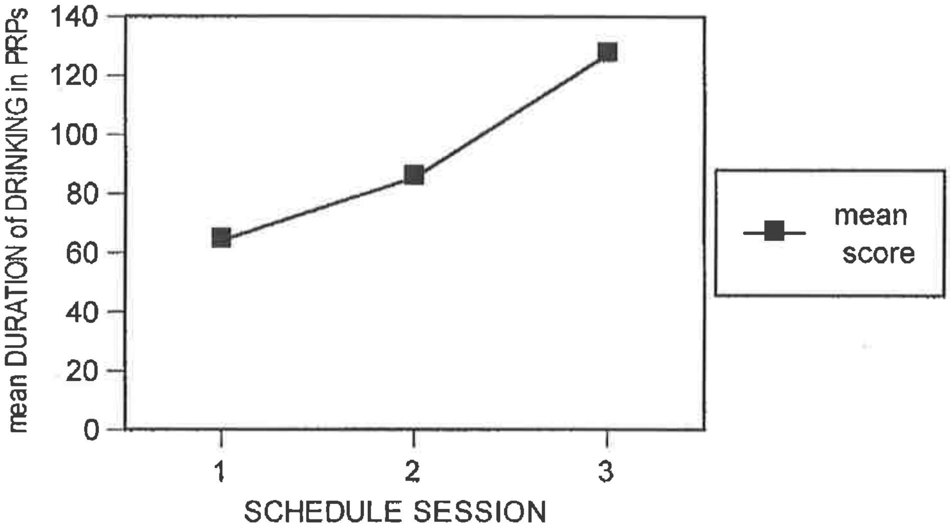


Figure 9.13 (I). Mean duration of ***drinking*** during the PRPs for the "session" grouping variable

Object x part of session x session interaction effect

The MANOVA for the duration of ***sniff and touch object*** [*F* (4,20)=2.87, *p*=.05] yielded a statistically significant ***object*** x ***part of session*** x ***session*** interaction. This measure was affected by all three grouping variables during ***fixed-interval*** sessions. It should be noted that objects were only present in the FIOS group. Visual inspection of Figure 9.13 (II) indicates that there was a slight increase in time spent engaged in ***sniff and touch object*** during the PRPs over the three ***fixed-interval*** sessions. However, whilst this increase was marked during the ***last 30 minutes***, a slight decrease actually occurred during the ***first*** and ***middle 30 minutes*** over these sessions. Obviously, there was an ***object*** effect, since stimulus objects were only present in the FIOS group during these sessions.

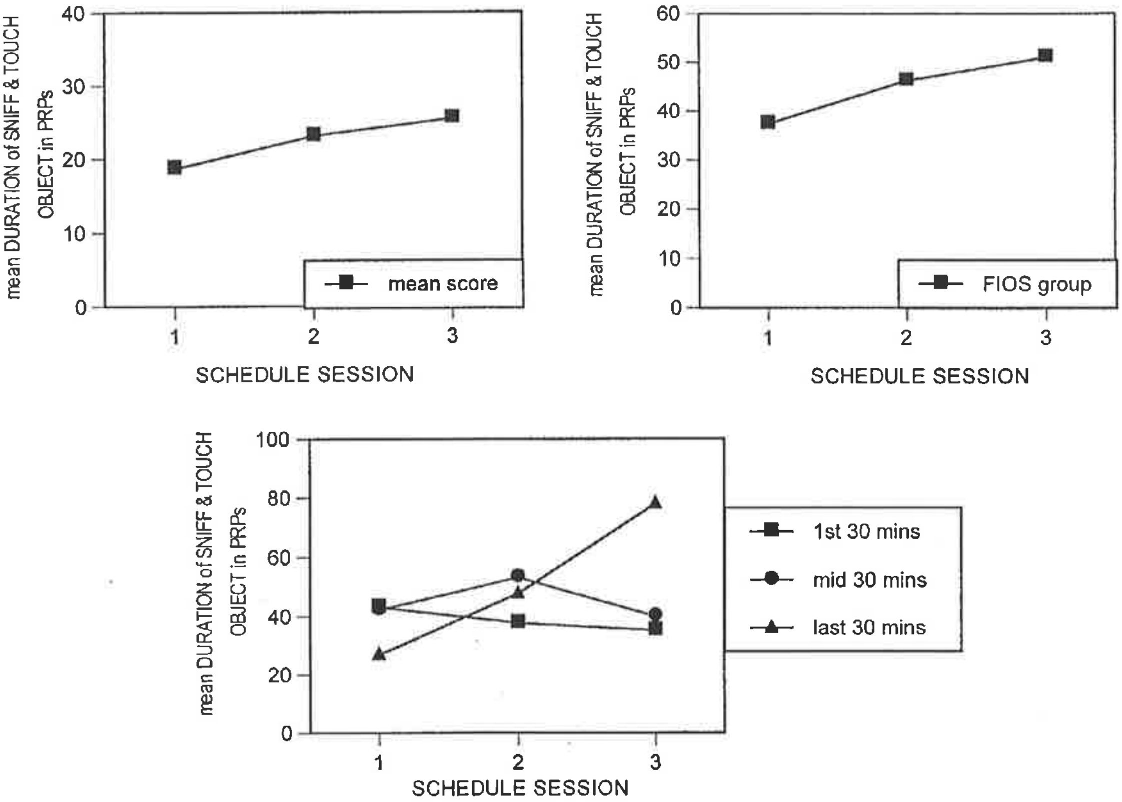


Figure 9.13 (II). Mean duration of ***sniff and touch object*** during the PRPs was affected by all three grouping variables for the FIOS group (top left- "session" grouping variable, top right- "object" grouping variable, & bottom- "part of session" grouping variable)

9.3.4 THE MOST FREQUENTLY OCCURRING BEHAVIOURS, AND ONES OF LONGEST DURATION IN SCHEDULE AND EXTINCTION SESSIONS

In order to test Hypotheses 16 and 17, it was necessary to determine which behavioural events occurred most frequently in each group, for the ***fixed-interval*** and ***extinction*** sessions (separately). The mean values for each frequency measure were summed over the three ***fixed-interval*** sessions, and summed over the three ***extinction*** sessions (separately). Similarly, the mean values for each duration measure were summed over the three ***fixed-interval*** and ***extinction*** sessions (separately), and then used to determine which behavioural measures were of longest duration in each group during ***fixed-interval*** and ***extinction*** sessions.

9.3.4.1 HYPOTHESIS SIXTEEN: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

*If objects are absent during **fixed-interval** sessions, more time and effort can be devoted to behaviours that are not object-directed. Thus, it is expected that higher frequencies and durations of non-object behaviours will be observed in the FIOE group during **fixed-interval** sessions. In addition, without objects present to "distract" them during **fixed-interval** sessions, the frequency and duration of **bar-pressing** and **drinking** scores is expected to be higher in the FIOE group.*

THE FIRST 30 MINUTES OF EACH SESSION

The frequency measures

In increasing order, the mean frequency of each behavioural category for the FIOS group (summed over the three ***fixed-interval*** sessions) was, ***resting/sleeping***; ***chew/bite object***; ***chew/bite bottle***; ***digging/burying***; ***drinking***; ***sniff and touch bottle***; ***displacement***; ***propping***; ***sniff bottle***; ***sniff and touch object***; ***sniff object***; ***bar-related behaviour***; and ***bar pressing*** (Table 9.7). These values ranged from 1.5 to 1109.5. The behaviour to occur most frequently (apart from ***bar pressing***) was ***bar-related behaviour***, followed by ***sniff object***. Few instances (<23) of ***resting/sleeping*** and ***chew/bite object*** were observed.

The mean frequency of each behavioural category for the FIOE group, summed over the three ***fixed-interval*** sessions, in increasing order was: ***resting/sleeping***; ***chew/bite bottle***; ***drinking***; ***sniff bottle***; ***digging/burying***; ***displacement***; ***propping***; ***sniff and touch bottle***; ***bar-related behaviour***; and ***bar pressing*** (Table 9.7). These values ranged from 4.75 to 1002.75. The behaviour to occur most frequently (apart from ***bar pressing***) was ***bar-related behaviour***, followed by ***sniff and touch bottle*** and ***propping***. Few instances (<13) of ***resting/sleeping*** and ***chew/bite bottle*** were observed.

The duration measures

In increasing order of duration for the FIOS group for the ***fixed-interval*** sessions, these measures were: ***resting/sleeping***; ***digging/burying***; ***sniff bottle***; ***sniff and touch bottle***; ***propping***; ***sniff and touch object***; ***sniff object***; ***displacement***; ***chew/bite object***; ***drinking***; ***bar-related behaviour***; ***bar pressing***; and ***chew/bite bottle*** (Table 9.7). These values ranged from 9.86 seconds to 539.11 seconds. Most time was spent engaged in ***chew/bite bottle***, followed by ***bar pressing***, ***bar-related behaviour***, and ***drinking***. Almost the same time was spent engaged in ***bar pressing***, ***bar-related***

behaviour and ***drinking***. The next highest duration was for ***chew/bite object***, which was topographically similar to the highest duration measure (***chew/bite bottle***)- another ***aggressive behaviour***. Least time (<70 seconds) was spent engaged in ***resting/sleeping***, ***digging/burying*** and ***sniff bottle***.

Table 9.7
The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***first 30 minutes*** of each session, summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR SCHEDULE SESSIONS * FIOS GROUP**	**SUM OF MEANS FOR SCHEDULE SESSIONS * FIOE GROUP**
FREQUENCIES		
Digging/Burying	41.25	92.75
Drinking	43	38.75
Chew/Bite Bottle	26.25	12.75
Sniff & Touch Bottle	81.75	119.25
Sniff Bottle	91.5	84.75
Propping	87.75	118.5
Displacement	84	97.25
Chew/Bite Object	22	no objects present
Sniff & Touch Object	159.25	
Sniff Object	293.5	
Bar pressing	1109.5	1002.75
Bar-related Behaviour	564.5	717.5
Resting/Sleeping	1.5	4.75
DURATIONS (in seconds)		
Digging/Burying	53.81	108.84
Drinking	390.05	398.56
Chew/Bite Bottle	539.11	68.04
Sniff & Touch Bottle	111.7	268.76
Sniff Bottle	69.64	48
Propping	207.13	288.88
Displacement	333.7	556.43
Chew/Bite Object	341.43	no objects present
Sniff & Touch Object	289.16	
Sniff Object	300.01	
Bar pressing	395.29	272.3
Bar-related Behaviour	392.71	535.66
Resting/Sleeping	9.86	42.04

In increasing order of duration for the ***fixed-interval*** sessions, for the FIOE group, these measures were: ***resting/sleeping***; ***sniff bottle***; ***chew/bite bottle***; ***digging/burying***; ***sniff and touch bottle***; ***bar pressing***; ***propping***; ***drinking***; ***bar-related behaviour***; and ***displacement*** (Table 9.7). These values ranged from 42.04 seconds to 556.43 seconds. Most time was spent engaged in ***displacement***, followed by ***bar-related behaviour***, and ***drinking***. Least time (<50 seconds) was spent engaged in ***resting/sleeping*** and ***sniff bottle***.

THE MIDDLE 30 MINUTES OF EACH SESSION

The frequency measures

In increasing order of frequency for the FIOS group for the ***fixed-interval*** sessions, these measures were: ***chew/bite bottle***; ***chew/bite object***; ***resting/sleeping***; ***digging/burying***; ***drinking***; ***sniff and touch bottle***; ***sniff bottle***; ***sniff and touch object***; ***displacement***; ***propping***; ***sniff object***; ***bar-related behaviour***; and ***bar pressing*** (Table 9.8). These values ranged from 6.25 to 1175. ***Bar-related behaviour*** was the most frequently occurring behaviour (apart from ***bar pressing***), followed by ***sniff object*** and ***propping***. Few instances (<13) of ***chew/bite bottle*** and ***chew/bite object*** were observed.

In increasing order, the mean frequency of each behavioural category for the FIOE group, for the ***fixed-interval*** sessions was: ***chew/bite bottle***; ***drinking***; ***resting/sleeping***; ***digging/burying***; ***propping***; ***displacement***; ***sniff bottle***; ***sniff and touch bottle***; ***bar-related behaviour***; and ***bar-pressing*** (Table 9.8). These values ranged from 6.75 to 904.25. ***Bar-related behaviour*** was the most frequently occurring behaviour (apart from ***bar pressing***), followed by ***sniff and touch bottle***. Few instances (<20) of ***chew/bite bottle*** and ***drinking*** were observed.

The duration measures

In increasing order of duration, the measures for the FIOS group during ***fixed-interval*** sessions were: ***digging/burying***; ***sniff bottle***; ***chew/bite bottle***; ***sniff and touch bottle***; ***sniff object***; ***sniff and touch object***; ***resting/sleeping***; ***bar pressing***; ***propping***; ***bar-related behaviour***; ***chew/bite object***; ***drinking***; and ***displacement*** (Table 9.8). These values ranged from 44.31 seconds to 630.3 seconds. Most time was spent engaged in ***displacement***, followed by ***drinking*** and ***chew/bite object***. Least amount of time (<85 seconds) was spent engaged in ***digging/burying*** and the three ***bottle-directed behaviours***.

For the FIOE group, in increasing order of duration, these measures summed over the three ***fixed-interval*** sessions were: ***sniff bottle***; ***digging/burying***; ***chew/bite bottle***; ***propping***; ***drinking***; ***bar pressing***; ***sniff and touch bottle***; ***bar-related behaviour***; ***resting/sleeping***; and ***displacement*** (Table 9.8). These values ranged from 40.28 seconds to 673.43 seconds. Most time was spent engaged in ***displacement***, followed by ***resting/sleeping*** and ***bar-related behaviour***. Least amount of time (<60 seconds) was spent engaged in ***sniff bottle*** and ***digging/burying***.

Table 9.8
The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***middle 30 minutes*** of each session, summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR SCHEDULE SESSIONS * FIOS GROUP	SUM OF MEANS FOR SCHEDULE SESSIONS * FIOE GROUP
FREQUENCIES		
Digging/Burying	27.5	54.5
Drinking	32.75	19.5
Chew/Bite Bottle	6.25	6.75
Sniff & Touch Bottle	43.75	116.25
Sniff Bottle	69.5	72
Propping	113.25	61.25
Displacement	91.25	67
Chew/Bite Object	12	no
Sniff & Touch Object	81.75	objects
Sniff Object	189.5	present
Bar pressing	1175	904.25
Bar-related Behaviour	480.75	636.25
Resting/Sleeping	23.25	45
DURATIONS (in seconds)		
Digging/Burying	44.31	56.44
Drinking	360.49	246.38
Chew/Bite Bottle	64.01	169.81
Sniff & Touch Bottle	82.41	408.89
Sniff Bottle	47.76	40.28
Propping	318.93	204.91
Displacement	630.3	673.43
Chew/Bite Object	336.38	no
Sniff & Touch Object	168.94	objects
Sniff Object	145.69	present
Bar pressing	264.75	251.73
Bar-related Behaviour	322.09	524.25
Resting/Sleeping	205.01	586.68

THE LAST 30 MINUTES OF EACH SESSION

The frequency measures

For the FIOS group, in increasing order, the mean frequency of each behavioural category summed over ***fixed-interval*** sessions was: ***chew/bite object***; ***chew/bite bottle***; ***resting/sleeping***; ***digging/burying***; ***drinking***; ***sniff and touch bottle***; ***sniff bottle***; ***sniff and touch object***; ***propping***; ***displacement***; ***sniff object***; ***bar-related behaviour***; and ***bar pressing*** (Table 9.9). The values ranged from 16.75 to 1178.75. After ***bar pressing***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***sniff object***. The least frequently occurring behaviours (<20) were ***chew/bite object*** and ***chew/bite bottle***.

Table 9.9
The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***last 30 minutes*** of each session, summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR SCHEDULE SESSIONS * FIOS GROUP	SUM OF MEANS FOR SCHEDULE SESSIONS * FIOE GROUP
FREQUENCIES		
Digging/Burying	31.5	49.25
Drinking	33.75	15.75
Chew/Bite Bottle	19.25	8.5
Sniff & Touch Bottle	51.75	103.5
Sniff Bottle	57.25	75.5
Propping	91.75	54.75
Displacement	101	66
Chew/Bite Object	16.75	no
Sniff & Touch Object	83.5	objects
Sniff Object	172.75	present
Bar pressing	1178.75	815
Bar-related Behaviour	368	613.25
Resting/Sleeping	23	49
DURATIONS (in seconds)		
Digging/Burying	43.41	54.56
Drinking	295.44	166.91
Chew/Bite Bottle	182.63	145.16
Sniff & Touch Bottle	91.76	322.96
Sniff Bottle	38.68	44.14
Propping	261.5	209.21
Displacement	572.16	734.43
Chew/Bite Object	413.5	no
Sniff & Touch Object	184.16	objects
Sniff Object	126.98	present
Bar pressing	257.26	224.5
Bar-related Behaviour	195.16	508.96
Resting/Sleeping	462.31	822.64

For the FIOE group, in increasing order, the mean frequency of each behavioural category summed over the ***fixed-interval*** sessions was: ***chew/bite bottle***; ***drinking***; ***resting/sleeping***; ***digging/burying***; ***propping***; ***displacement***; ***sniff bottle***; ***sniff and touch bottle***; ***bar-related behaviour***; and ***bar pressing*** (Table 9.9). The values ranged from 8.5 to 815. After ***bar pressing***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***sniff and touch bottle***. The least frequently (<16) occurring behaviours were ***chew/bite bottle*** and ***drinking***. Similar values (<6 difference) were found for ***resting/sleeping***, ***digging/burying*** and ***propping***.

The duration measures

In increasing order of duration for the FIOS group during ***fixed-interval*** sessions, these measures were: ***sniff bottle***; ***digging/burying***; ***sniff and touch bottle***; ***sniff object***; ***chew/bite bottle***; ***sniff***

and touch object; ***bar-related behaviour***; ***bar pressing***; ***propping***; ***drinking***; ***chew/bite object***; ***resting/sleeping***; and ***displacement*** (Table 9.9). These values ranged from 38.68 seconds to 572.16 seconds. Most time was spent engaged in ***displacement***, followed by ***resting/sleeping*** and ***chew/bite object***. Least time (<45 seconds) was spent engaged in ***sniff bottle*** and ***digging/burying***.

The mean values for each of the duration measures summed over the three ***fixed-interval*** sessions for the FIOE group are given in Table 9.9. In increasing order of duration, these measures were: ***sniff bottle***; ***digging/burying***; ***chew/bite bottle***; ***drinking***; ***propping***; ***bar-pressing***; ***sniff and touch bottle***; ***bar-related behaviour***; ***displacement***; and ***resting/sleeping***. These values ranged from 44.14 seconds to 822.64 seconds. Most time was spent engaged in ***resting/sleeping***, followed by ***displacement*** and then ***bar-related behaviour***. Least time (<55 seconds) was spent engaged in ***sniff bottle*** and ***digging/burying***.

Summary

Hypothesis 16 was supported, with respect to the frequency and duration measures for most of the non object-directed behaviours during all three parts of session (the ***first***, ***middle & last 30 minutes***). Without objects to "distract" them during ***fixed-interval*** sessions, the FIOE rats were able to engage in more non-object behaviours (than the FIOS rats). However, during the ***first 30 minutes***, the frequency and duration of ***chew/bite bottle*** was markedly lower and the ***sniff bottle*** measures were also lower. During the ***middle 30 minutes***, the frequency and duration of ***propping*** was markedly lower, whilst the frequency of ***displacement*** and duration of ***sniff bottle*** was also lower. During the ***last 30 minutes***, the frequency and duration of ***chew/bite bottle*** was markedly lower. In addition, the frequency and duration of ***propping*** and frequency of ***displacement*** was also lower.

However, ***Hypothesis 16 was not supported***, with respect to the ***bar pressing*** and ***drinking*** measures. It was predicted that without objects present to "distract" them during ***fixed-interval*** sessions, the FIOE group would also have higher frequency and duration scores for ***bar pressing*** and ***drinking.*** This was not the case. Instead, during the ***first 30 minutes***, these measures were lower for this group (with the exception of duration of ***drinking***, which was slightly higher). During the ***middle 30 minutes***, the frequency and duration of ***bar pressing*** and ***drinking*** was lower (noticeably so for ***drinking***), and markedly so for the ***last 30 minutes***.

9.3.4.2 HYPOTHESIS SEVENTEEN: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

When objects are first encountered during ***extinction****, it is expected that* <u>*higher*</u> *frequencies and durations of object-directed behaviours will be observed. That is, the* ***FIOE*** *group will direct more behaviour towards novel stimulus objects during* ***extinction*** *sessions than the* ***FIOS*** *group. No firm expectations are held for the other behavioural categories.*

THE FIRST 30 MINUTES OF EACH SESSION

The frequency measures

Table 9.10 provides the mean values for each frequency measure summed over the three ***extinction*** sessions, for the FIOS group. In increasing order, these categories were: ***resting/sleeping***; ***drinking***; ***chew/bite bottle***; ***chew/bite object***; ***sniff bottle***; ***displacement***; ***digging/burying***; ***sniff and touch bottle***; ***propping***; ***bar pressing***; ***sniff and touch object***; ***bar-related behaviour***; and ***sniff object***. These values ranged from 4.25 to 252.25. Apart from ***sniff object***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***sniff and touch object***. Only few instances (<16) of ***resting/sleeping*** and ***drinking*** were observed.

In increasing order of frequency for the FIOE group for the ***extinction*** sessions, these measures were: ***resting/sleeping***, ***drinking***, ***chew/bite object***, ***chew/bite bottle***, ***sniff bottle***, ***sniff and touch bottle***, ***displacement***, ***propping***, ***digging/burying***, ***bar pressing***, ***sniff and touch object***, ***bar-related behaviour*** and ***sniff object*** (Table 9.10). These values ranged from 2.75 to 317.25. Apart from ***sniff object***, the behaviour to occur most frequently was ***bar-related behaviour***, followed by ***sniff and touch object***. Only few instances (<11) of ***resting/sleeping*** and ***drinking*** were observed.

The duration measures

In increasing order of duration for the ***extinction*** sessions, the behavioural measures for the FIOS group were: ***sniff bottle***; ***bar pressing***; ***drinking***; ***resting/sleeping***; ***digging/burying***; ***sniff and touch bottle***; ***bar-related behaviour***; ***sniff object***; ***propping***; ***sniff and touch object***; ***chew/bite object***; ***chew/bite bottle***; and ***displacement*** (Table 9.10). These values ranged from 31.73 seconds to 980.28 seconds. Most time was spent engaged in ***displacement***, followed by ***chew/bite bottle***, ***chew/bite object*** and ***sniff and touch object***. The least amount of time (<50 seconds) was spent engaged in ***sniff bottle*** and ***bar pressing***.

Table 9.10

The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***first 30 minutes*** of each session, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	**SUM OF MEANS FOR EXTINCTION SESSIONS * FIOS GROUP**	**SUM OF MEANS FOR EXTINCTION SESSIONS * FIOE GROUP**
FREQUENCIES		
Digging/Burying	83.5	114.25
Drinking	15	10.5
Chew/Bite Bottle	30.75	23.25
Sniff & Touch Bottle	91.75	76.75
Sniff Bottle	63.75	63.75
Propping	122.25	100.75
Displacement	69.25	78.5
Chew/Bite Object	55.25	18.75
Sniff & Touch Object	206	201.5
Sniff Object	252.25	317.25
Bar pressing	193.5	135.25
Bar-related Behaviour	215	209
Resting/Sleeping	4.25	2.75
DURATIONS (in seconds)		
Digging/Burying	115.58	109.59
Drinking	84.26	92.23
Chew/Bite Bottle	575.41	614.33
Sniff & Touch Bottle	147.94	171.89
Sniff Bottle	31.73	41.73
Propping	367.38	302.06
Displacement	980.28	887.78
Chew/Bite Object	544.39	240.86
Sniff & Touch Object	520.03	596.98
Sniff Object	184.41	339.18
Bar pressing	45.86	38.01
Bar-related Behaviour	163.78	210.48
Resting/Sleeping	106.58	84.96

In increasing order of duration for the ***extinction*** sessions, the behavioural measures for the FIOE group were: ***bar pressing***; ***sniff bottle***; ***resting/sleeping***; ***drinking***; ***digging/burying***; ***sniff and touch bottle***; ***bar-related behaviour***; ***chew/bite object***; ***propping***; ***sniff object***; ***sniff and touch object***; ***chew/bite bottle***; and ***displacement*** (Table 9.10). These values ranged from 38.01 seconds to 887.78 seconds. Most time was spent engaged in ***displacement***, followed by ***chew/bite bottle*** and ***sniff and touch object***. The least amount of time (<45 seconds) was spent engaged in ***bar pressing*** and ***sniff bottle***.

THE MIDDLE 30 MINUTES OF EACH SESSION

The frequency measures

For the FIOS group, in increasing order, the mean frequency of each behavioural category over ***extinction*** sessions was: ***drinking***; ***chew/bite object***; ***chew/bite bottle***; ***sniff bottle***; ***bar pressing***; ***resting/sleeping***; ***digging/burying***; ***sniff and touch bottle***; ***displacement***; ***propping***; ***sniff and touch object***; ***bar-related behaviour***; and ***sniff object*** (Table 9.11). These values ranged from 4.5 to 156.25. The most frequently occurring behaviour was ***sniff object***, followed by ***bar-related behaviour***, ***sniff and touch object***, and ***propping***. The least frequently (<15) occurring behaviours were ***drinking***, ***chew/bite object*** and ***chew/bite bottle***.

Table 9.11
The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***middle 30 minutes*** of each session, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR EXTINCTION SESSIONS * FIOS GROUP	SUM OF MEANS FOR EXTINCTION SESSIONS * FIOE GROUP
FREQUENCIES		
Digging/Burying	51.25	26
Drinking	4.5	1
Chew/Bite Bottle	14.5	3.25
Sniff & Touch Bottle	52.75	40
Sniff Bottle	27.75	35.5
Propping	94.75	60.25
Displacement	59	38.75
Chew/Bite Object	8	2.25
Sniff & Touch Object	98.75	90
Sniff Object	156.25	130
Bar pressing	38.75	38
Bar-related Behaviour	140	187.25
Resting/Sleeping	48.75	44
DURATIONS (in seconds)		
Digging/Burying	68.53	26.36
Drinking	24.63	29.78
Chew/Bite Bottle	255.4	36.75
Sniff & Touch Bottle	169.25	156.26
Sniff Bottle	18.73	38.58
Propping	397.48	247.35
Displacement	1219.18	686.68
Chew/Bite Object	78.68	21.01
Sniff & Touch Object	376.34	747.51
Sniff Object	157.94	291.5
Bar pressing	12.08	14.89
Bar-related Behaviour	156.86	370.1
Resting/Sleeping	1137.98	1860.96

In increasing order for the FIOE group, the mean frequency of each behavioural category for the ***extinction*** sessions was: ***drinking***; ***chew/bite object***; ***chew/bite bottle***; ***digging/burying***; ***sniff bottle***; ***bar pressing***; ***displacement***; ***sniff and touch bottle***; ***resting/sleeping***; ***propping***; ***sniff and touch object***; ***sniff object***; and ***bar-related behaviour*** (Table 9.11). These values ranged from 1 to 187.25. The most frequently occurring behaviours were ***bar-related behaviour***, ***sniff object***, and ***sniff and touch object***. Few instances (<4) of ***drinking***, ***chew/bite object*** and ***chew/bite bottle*** were observed.

The duration measures

In increasing order of duration, the measures for the FIOS group during the ***extinction*** sessions were: ***bar pressing***; ***sniff bottle***; ***drinking***; ***digging/burying***; ***chew/bite object***; ***bar-related behaviour***; ***sniff object***; ***sniff and touch bottle***; ***chew/bite bottle***; ***sniff and touch object***; ***propping***; ***resting/sleeping***; and ***displacement*** (Table 9.11). These values ranged from 12.08 seconds to 1219.18 seconds. Most time was spent engaged in ***displacement***, ***resting/sleeping*** and ***propping***. Low amounts of time (<25 seconds) were spent engaged in ***bar pressing***, ***sniff bottle*** and ***drinking***.

For the FIOE group, in increasing order of duration, these measures summed over the three ***extinction*** sessions were: ***bar pressing***; ***chew/bite object***; ***digging/burying***; ***drinking***; ***chew/bite bottle***; ***sniff bottle***; ***sniff and touch bottle***; ***propping***; ***sniff object***; ***bar-related behaviour***; ***displacement***; ***sniff and touch object***; and ***resting/sleeping*** (Table 9.11). These values ranged from 14.89 seconds to 1860.96 seconds. A substantial amount of time (>1800 seconds) was spent engaged in ***resting/sleeping***. The next highest amounts of time were spent engaged in ***sniff and touch object*** and ***displacement***. Low amounts of time (<30 seconds) were spent engaged in ***bar pressing***, ***chew/bite object***, ***digging/burying*** and ***drinking***.

THE LAST 30 MINUTES OF EACH SESSION

The frequency measures

In increasing order for the FIOS group, the mean frequency of each behavioural category for the ***extinction*** sessions was: ***drinking*** and ***chew/bite object*** (identical scores); ***chew/bite bottle***; ***bar pressing***; ***sniff bottle***; ***displacement***; ***digging/burying***; ***sniff and touch bottle***; ***resting/sleeping***; ***sniff and touch object***; ***propping***; ***sniff object***; and ***bar-related behaviour*** (Table 9.12). These values ranged from 2.5 to 159.25. The most frequently occurring behaviours were ***bar-related***

behaviour, ***sniff object*** and ***propping***. The least frequent (<18) behaviours were ***drinking*** and ***chew/bite object*** and ***chew/bite bottle***.

Table 9.12
The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***last 30 minutes*** of each session, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR EXTINCTION SESSIONS * FIOS GROUP	SUM OF MEANS FOR EXTINCTION SESSIONS * FIOE GROUP
FREQUENCIES		
Digging/Burying	42.25	28
Drinking	2.5	2
Chew/Bite Bottle	17.75	4.75
Sniff & Touch Bottle	56.75	46.5
Sniff Bottle	28.75	41.25
Propping	98.5	65.5
Displacement	39.25	49.25
Chew/Bite Object	2.5	1.25
Sniff & Touch Object	84.5	88.25
Sniff Object	130	142
Bar pressing	27.75	41.25
Bar-related Behaviour	159.25	229.5
Resting/Sleeping	63.25	66.75
DURATIONS (in seconds)		
Digging/Burying	41.6	26.93
Drinking	11.48	5.8
Chew/Bite Bottle	380.85	55.01
Sniff & Touch Bottle	187.09	164.99
Sniff Bottle	23.95	39
Propping	359.03	273.91
Displacement	438.29	972.14
Chew/Bite Object	10.13	5.4
Sniff & Touch Object	409.11	717.66
Sniff Object	148.73	162.08
Bar pressing	9.43	12.9
Bar-related Behaviour	286.5	574.38
Resting/Sleeping	2064.48	1593.16

For the FIOE group, in increasing order, the mean frequency of each behavioural category summed over the ***extinction*** sessions was: ***chew/bite object***; ***drinking***; ***chew/bite bottle***; ***digging/burying***; ***sniff bottle***; ***bar pressing***; ***sniff and touch bottle***; ***displacement***; ***propping***; ***resting/sleeping***; ***sniff and touch object***; ***sniff object***; and ***bar-related behaviour*** (Table 9.12). These values ranged from 1.25 to 229.5. The most frequently occurring behaviours were ***bar-related behaviour***, ***sniff object*** and ***sniff and touch object***. Few instances (<5) of ***chew/bite object***, ***drinking*** and ***chew/bite bottle*** were observed. Identical scores were found for ***bar***

pressing and ***sniff bottle***, and the values for ***sniff and touch bottle*** and ***displacement*** were similar (<3 difference).

The duration measures

In increasing order of duration for the FIOS group during the ***extinction*** sessions, the behavioural measures were: ***bar pressing***; ***chew/bite object***; ***drinking***; ***sniff bottle***; ***digging/burying***; ***sniff object***; ***sniff and touch bottle***; ***bar-related behaviour***; ***propping***; ***chew/bite bottle***; ***sniff and touch object***; ***displacement***; and ***resting/sleeping*** (Table 9.12). These values ranged from 9.43 seconds to 2064.48 seconds. A large amount of session time was spent engaged in ***resting/sleeping***. When active, the most time was spent engaged in ***displacement*** and ***sniff and touch object***. Least time (<12 seconds) was spent engaged in ***bar pressing***, ***chew/bite object*** and ***drinking***. Whilst very little time was spent engaged in ***chew/bite object***, a substantial amount of time (>380 seconds) was spent engaged in ***chew/bite bottle***. Though topographically similar, the ***aggressive behaviour*** was directed at the water-source rather than at objects in general.

In increasing order of duration for the ***extinction*** sessions, the behavioural measures for the FIOE group were: ***chew/bite object***; ***drinking***; ***bar pressing***; ***digging/burying***; ***sniff bottle***; ***chew/bite bottle***; ***sniff object***; ***sniff and touch bottle***; ***propping***; ***bar-related behaviour***; ***sniff and touch object***; ***displacement***; and ***resting/sleeping*** (Table 9.12). These values ranged from 5.4 seconds to 1593.16 seconds. A large amount of session time was spent engaged in ***resting/sleeping***. When active, the most time was spent engaged in ***displacement*** and ***sniff and touch object***. Least time (<13 seconds) was spent engaged in ***chew/bite object***, ***drinking*** and ***bar pressing***. Whilst very little time was spent engaged in ***chew/bite object***, a larger amount of time (about 55 seconds) was spent engaged in ***chew/bite bottle***. Though topographically similar, the ***aggressive behaviour*** was directed at the water-source rather than at objects in general.

Summary

There was some support for Hypothesis 17, with respect to the frequency and duration of ***object-directed behaviours*** during ***extinction***. The main exception was frequency and duration of ***chew/bite object***, which was lower for the FIOE group. Since this was the FIOE rats' first encounter with novel stimulus objects, it was expected that they would direct more behaviour towards the objects than the FIOS rats (*i.e.*, higher frequency & duration scores).

During the ***first 30 minutes***, the frequency and duration of ***sniff object*** and the duration of ***sniff and touch object*** was indeed much higher for the FIOE group. However, the frequency of ***sniff***

and touch object was slightly less, and the frequency and duration of ***chew/bite object*** was markedly lower.

For the ***middle 30 minutes***, the frequency of all three ***object-directed behaviours*** was lower for the FIOE group (*i.e.*, Hypothesis 17 was not supported). By contrast, duration of ***sniff and touch object*** was much higher in this group, as was duration of ***sniff object*** (as predicted). However, the duration of ***chew/bite object*** was markedly lower. Thus, there were fewer bouts but of longer duration for ***sniff object*** and ***sniff and touch object***.

During the ***last 30 minutes***, frequency and duration of ***sniff object*** and ***sniff and touch object*** was higher for the FIOE group (as predicted). However, the frequency and duration of ***chew/bite object*** was lower.

No firm expectations were held for the other non-object behaviours. During the ***first 30 minutes***, the FIOE frequency scores were lower for all the other behaviours, except ***digging/burying*** and ***sniff bottle*** (identical score in both groups). The FIOE duration scores were lower for ***digging/burying***, ***propping***, ***displacement***, ***bar pressing*** and ***resting/sleeping***. Thus, for many of the non object-directed behaviours in the FIOE group, there were fewer bouts but of longer duration during the ***first 30 minutes*** of ***extinction***.

During the ***middle 30 minutes*** of ***extinction***, the FIOE frequency scores were lower for all but ***sniff bottle*** and ***bar-related behaviour***. The frequency of ***bar pressing*** was similar in both groups. The FIOE duration scores were lower for some of the other behaviours, except ***drinking***, ***sniff bottle***, ***propping***, ***bar-related behaviour*** and ***resting/sleeping***. The duration of ***bar pressing*** was similar in both groups. The duration of ***resting/sleeping*** was particularly high for the FIOE group.

For the other behaviours during the ***last 30 minutes*** of ***extinction***, the FIOE frequency scores were lower for all other behaviours except ***sniff bottle***. The FIOE duration scores were lower for ***digging/burying***, ***drinking***, ***chew/bite bottle***, ***sniff and touch bottle***, ***propping***, and ***resting/sleeping***. Duration scores of ***resting/sleeping*** were very high for both groups, but noticeably higher for the FIOS group.

9.3.4.3 HYPOTHESIS EIGHTEEN: WITHIN-SESSION CHANGES IN BEHAVIOUR DURING FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

*Within-session changes in behaviour may be observed during **fixed-interval** sessions. That is, the frequency and duration scores may differ depending on the part of session (**first**, **middle** or **last 30 minutes**).*

- *It is expected that late session decreases in **bar pressing** may occur (and fewer reinforcers may be obtained) as a result of satiation or habituation to the reinforcer (McSweeney and Roll, 1998).*
- *Late session decreases in exploratory behaviour directed at the stimulus objects (**sniff object**, **sniff and touch object** and **chew/bite object**) may be observed as a result of habituation to the objects.*
- *Other behaviours may peak at different times throughout the session (**first**, **middle**, **last 30 minutes**).*

With respect to the frequency and duration of ***bar pressing***, there was ***partial support for Hypothesis 18***. It was expected that late session decreases in ***bar pressing*** would occur during ***fixed-interval*** sessions. However, a habituation or satiation effect was only experienced if objects were absent during the 3.5 hour long ***fixed-interval*** sessions. When objects were present during ***fixed-interval*** sessions (FIOS group), there were no late session decreases in frequency of ***bar pressing*** (the duration scores did decrease). Furthermore, the number of reinforcers obtained did not decrease (there was a minimal increase during the ***middle & last 30 minutes***). These rats did not appear to satiate or habituate to the reinforcer over the 3.5-hour long session. By contrast, when objects were absent during ***fixed-interval*** sessions (FIOE group), there was a late session decrease in frequency and duration of ***bar pressing***, as well as a decrease in the number of reinforcers obtained (Table 9.13).

There was some support for Hypothesis 18, with respect to the ***object-directed behaviours***. As expected, there were late session decreases in some of the ***object-directed behaviours***. There was a noticeable decrease in ***sniff object*** and ***sniff and touch object*** over the 3.5-hour long ***fixed-interval*** session (Table 9.13). However, whilst the frequency of ***chew/bite object*** also showed a late session decrease, the duration of this behaviour in fact increased. The topography of the response towards the stimulus appeared to come into play. The time spent engaged in ***aggressive behaviour*** directed at the objects (***chew/bite object***), increased over the session, whereas ***exploratory sniffing and manipulation*** responses decreased.

Table 9.13

The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***first, middle*** and ***last 30 minutes*** of each session, summed over the three ***fixed-interval*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR SCHEDULE SESSIONS * **FIOS GROUP** * **first 30 minutes**	SUM OF MEANS FOR SCHEDULE SESSIONS * **FIOS GROUP** * **middle 30 minutes**	SUM OF MEANS FOR SCHEDULE SESSIONS * **FIOS GROUP** * **last 30 minutes**	SUM OF MEANS FOR SCHEDULE SESSIONS * **FIOE GROUP** * **first 30 minutes**	SUM OF MEANS FOR SCHEDULE SESSIONS * **FIOE GROUP** * **middle 30 minutes**	SUM OF MEANS FOR SCHEDULE SESSIONS * **FIOE GROUP** * **last 30 minutes**
FREQUENCIES						
Digging/Burying	41.25	27.5	31.5	92.75	54.5	49.25
Drinking	43	32.75	33.75	38.75	19.5	15.75
Chew/Bite Bottle	26.25	6.25	19.25	12.75	6.75	8.5
Sniff & Touch Bottle	81.75	43.75	51.75	119.25	116.25	103.5
Sniff Bottle	91.5	69.5	57.25	84.75	72	75.5
Propping	87.75	113.25	91.75	118.5	61.25	54.75
Displacement	84	91.25	101	97.25	67	66
Chew/Bite Object	22	12	16.75	no objects present	no objects present	no objects present
Sniff & Touch Object	159.25	81.75	83.5			
Sniff Object	293.5	189.5	172.75			
Bar pressing	1109.5	1175	1178.75	1002.75	904.25	815
Bar-related Behaviour	564.5	480.75	368	717.5	636.25	613.25
Resting/Sleeping	1.5	23.25	23	4.75	45	49
Reinforcers received	84	86	84.5	84	82.25	79
DURATIONS (in seconds)						
Digging/Burying	53.81	44.31	43.41	108.84	56.44	54.56
Drinking	390.05	360.49	295.44	398.56	246.38	166.91
Chew/Bite Bottle	539.11	64.01	182.63	68.04	169.81	145.16
Sniff & Touch Bottle	111.7	82.41	91.76	268.76	408.89	322.96
Sniff Bottle	69.64	47.76	38.68	48	40.28	44.14
Propping	207.13	318.93	261.5	288.88	204.91	209.21
Displacement	333.7	630.3	572.16	556.43	673.43	734.43
Chew/Bite Object	341.43	336.38	413.5	no objects present	no objects present	no objects present
Sniff & Touch Object	289.16	168.94	184.16			
Sniff Object	300.01	145.69	126.98			
Bar pressing	395.29	264.75	257.26	272.3	251.73	224.5
Bar-related Behaviour	392.71	322.09	195.16	535.66	524.25	508.96
Resting/Sleeping	9.86	205.01	462.31	42.04	586.68	822.64

There was also ***partial support for Hypothesis 18***, with respect to the prediction that different behaviours might peak at different times throughout the ***fixed-interval*** session. Although the frequency and duration measures for most of the behavioural categories peaked during the ***first 30 minutes***, there were a number of measures that peaked later in the session in both groups (Table 9.13).

For the FIOS group, the frequency score for most of the behaviours peaked during the ***first 30 minutes*** (Table 9.13). The exceptions were ***propping*** (peaked in the ***middle 30 minutes***), ***displacement*** and ***bar pressing*** (peaked in the ***last 30 minutes***). The frequency of ***resting/sleeping*** was similarly high during the ***middle*** and ***last 30 minutes***. The duration scores also peaked during the ***first 30 minutes*** for most of the behavioural categories. However, the duration of ***propping*** and ***displacement*** peaked during the ***middle 30 minutes***, whilst ***chew/bite object*** and ***resting/sleeping*** peaked in the ***last 30 minutes***.

For the FIOE group, the frequency of all behaviours peaked during the ***first 30 minutes***, with the exception of ***resting/sleeping***, which peaked during the ***last 30 minutes*** (Table 9.13). Most of the duration scores also peaked during the ***first 30 minutes***. However, the duration of ***chew/bite bottle*** and ***sniff and touch bottle*** peaked during the ***middle 30 minutes***, whereas duration of ***displacement*** and ***resting/sleeping*** peaked during the ***last 30 minutes***.

9.3.4.4 HYPOTHESIS NINETEEN: WITHIN-SESSION CHANGES IN BEHAVIOUR DURING EXTINCTION (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Within-session changes in behaviour may also be observed during ***extinction*** *sessions. That is, the frequency and duration scores may differ depending on the part of session (****first****,* ***middle*** *or* ***last 30 minutes****).*

- *It is predicted that late session decreases in* ***bar pressing*** *may occur as the response extinguishes.*
- *Late session decreases in exploratory behaviour directed at the stimulus objects (****sniff object****,* ***sniff and touch object*** *and* ***chew/bite object****) may be observed as a result of habituation to the objects.*
- *Other behaviours may peak at different times throughout the session (****first****,* ***middle****,* ***last 30 minutes****).*

Hypothesis 19 was supported, with respect to the frequency and duration of ***bar pressing***. As expected, there was a late session decrease in frequency and duration of ***bar pressing*** for both groups, as the ***bar pressing*** response extinguished over the 3.5-hour long session (Table 9.14).

Hypothesis 19 was also supported, with respect to most of the measures of ***object-directed behaviours***. For the group that first encountered objects during ***extinction*** (FIOE group), there were late session decreases in most of the ***object-directed behaviours*** (Table 9.14). However, whilst the frequency of ***sniff and touch object*** showed a late session decrease, the duration of this behaviour in fact increased quite noticeably. Thus, the time spent engaged in ***sniffing and touching the objects*** by the FIOE rats did not show a habituation effect. For the FIOS group, which first encountered objects during ***fixed-interval*** sessions, there were the expected late session decreases in the frequency and duration of all ***object-directed behaviours***, suggesting that these rats did habituate to the objects.

Table 9.14
The mean frequency and duration of behaviours in the FIOS and FIOE groups, for the ***first, middle*** and ***last 30 minutes*** of each session, summed over the three ***extinction*** sessions.

BEHAVIOURAL MEASURE	SUM OF MEANS FOR EXTINCTION SESSIONS * **FIOS GROUP** * **first 30 minutes**	SUM OF MEANS FOR EXTINCTION SESSIONS * **FIOS GROUP** * **middle 30 minutes**	SUM OF MEANS FOR EXTINCTION SESSIONS * **FIOS GROUP** * **last 30 minutes**	SUM OF MEANS FOR EXTINCTION SESSIONS * **FIOE GROUP** * **first 30 minutes**	SUM OF MEANS FOR EXTINCTION SESSIONS * **FIOE GROUP** * **middle 30 minutes**	SUM OF MEANS FOR EXTINCTION SESSIONS * **FIOE GROUP** * **last 30 minutes**
FREQUENCIES						
Digging/Burying	83.5	51.25	42.25	114.25	26	28
Drinking	15	4.5	2.5	10.5	1	2
Chew/Bite Bottle	30.75	14.5	17.75	23.25	3.25	4.75
Sniff & Touch Bottle	91.75	52.75	56.75	76.75	40	46.5
Sniff Bottle	63.75	27.75	28.75	63.75	35.5	41.25
Propping	122.25	94.75	98.5	100.75	60.25	65.5
Displacement	69.25	59	39.25	78.5	38.75	49.25
Chew/Bite Object	55.25	8	2.5	18.75	2.25	1.25
Sniff & Touch Object	206	98.75	84.5	201.5	90	88.25
Sniff Object	252.25	156.25	130	317.25	130	142
Bar pressing	193.5	38.75	27.75	135.25	38	41.25
Bar-related Behaviour	215	140	159.25	209	187.25	229.5
Resting/Sleeping	4.25	48.75	63.25	2.75	44	66.75
DURATIONS (in seconds)						
Digging/Burying	115.58	68.53	41.6	109.59	26.36	26.93
Drinking	84.26	24.63	11.48	92.23	29.78	5.8
Chew/Bite Bottle	575.41	255.4	380.85	614.33	36.75	55.01
Sniff & Touch Bottle	147.94	169.25	187.09	171.89	156.26	164.99
Sniff Bottle	31.73	18.73	23.95	41.73	38.58	39
Propping	367.38	397.48	359.03	302.06	247.35	273.91
Displacement	980.28	1219.18	438.29	887.78	686.68	972.14
Chew/Bite Object	544.39	78.68	10.13	240.86	21.01	5.4
Sniff & Touch Object	520.03	376.34	409.11	596.98	747.51	717.66
Sniff Object	184.41	157.94	148.73	339.18	291.5	162.08
Bar pressing	45.86	12.08	9.43	38.01	14.89	12.9
Bar-related Behaviour	163.78	156.86	286.5	210.48	370.1	574.38
Resting/Sleeping	106.58	1137.98	2064.48	84.96	1860.96	1593.16

There was also ***partial support for Hypothesis 19***, with respect to the prediction that different behaviours might peak at different times throughout the session. The frequency and duration measures for most of the behavioural categories peaked during the ***first 30 minutes***, but there were a few measures that peaked later in the session in both groups (Table 9.14).

For the FIOS group, the frequency of each of the behaviours scored peaked during the ***first 30 minutes*** (except ***resting/sleeping***, which peaked in the ***last 30 minutes***). The duration scores also peaked during the ***first 30 minutes*** for most of the behavioural categories (Table 9.14). However, the duration of ***propping*** and ***displacement*** peaked during the ***middle 30 minutes***, whilst ***sniff and touch bottle***, ***bar-related behaviour*** and ***resting/sleeping*** peaked in the ***last 30 minutes***.

For the FIOE group, the frequency of all behaviours peaked during the ***first 30 minutes***, with the exception of ***bar-related behaviour*** and ***resting/sleeping***, which peaked during the ***last 30 minutes*** (Table 9.14). Most of the duration scores also peaked during the ***first 30 minutes***. However, the duration of ***sniff and touch object*** and ***resting/sleeping*** peaked during the ***middle 30 minutes***, whilst duration of ***displacement*** and ***bar-related behaviour*** peaked during the ***last 30 minutes***.

9.3.5 PERCENTAGE OF HALF-HOUR SESSION SEGMENT TIME SPENT ENGAGED IN EACH BEHAVIOURAL CATEGORY, OVER SESSIONS, AND BETWEEN GROUPS

Graphical representations for the mean percentage of time spent engaged in each behavioural category are provided in Figures 9.13 (I - III). A substantial percentage of ***not scored*** exists for both groups. As Table 9.15 indicates, between 7.59% and 55.94% of session time was spent engaged in behavioural activities that were not scored. Most of the ***not scored*** category is likely to represent ***general ambulatory behaviour***, or movement between the bar area, objects, bottle and peripheral areas of the box. However, this category also includes some interesting behaviours such as ***coprophagia***, ***pushing at the lid with the snout*** and ***escape*** from the apparatus, details of which are presented in section 9.3.7.4.

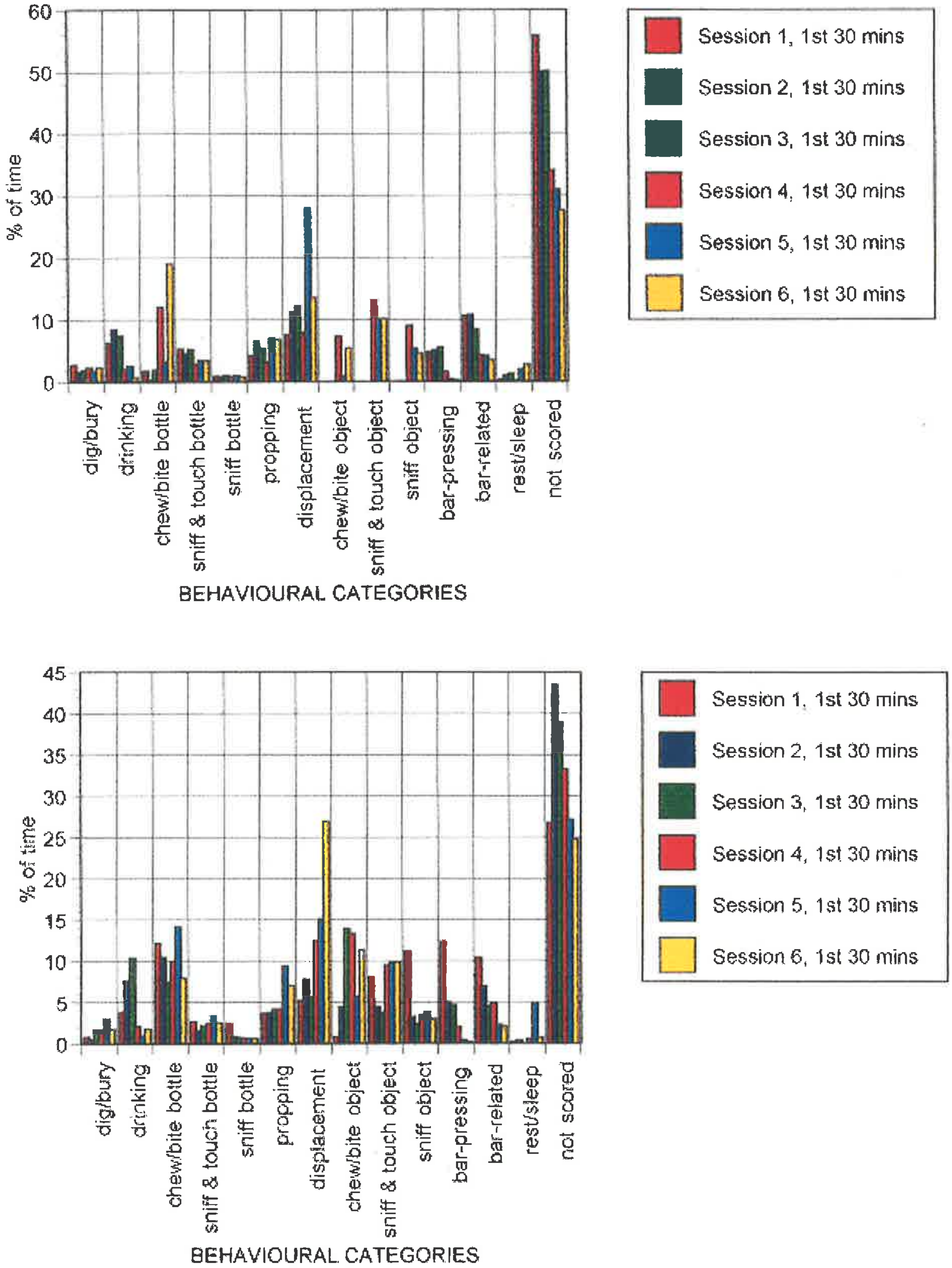


Figure 9.14 (I). Mean percentage of time spent engaged in each behavioural category for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes*** of each session. (Calculated as mean time in seconds spent engaged in behaviour, as a percentage of the ***first 30 minutes***, i.e., 1800 seconds).

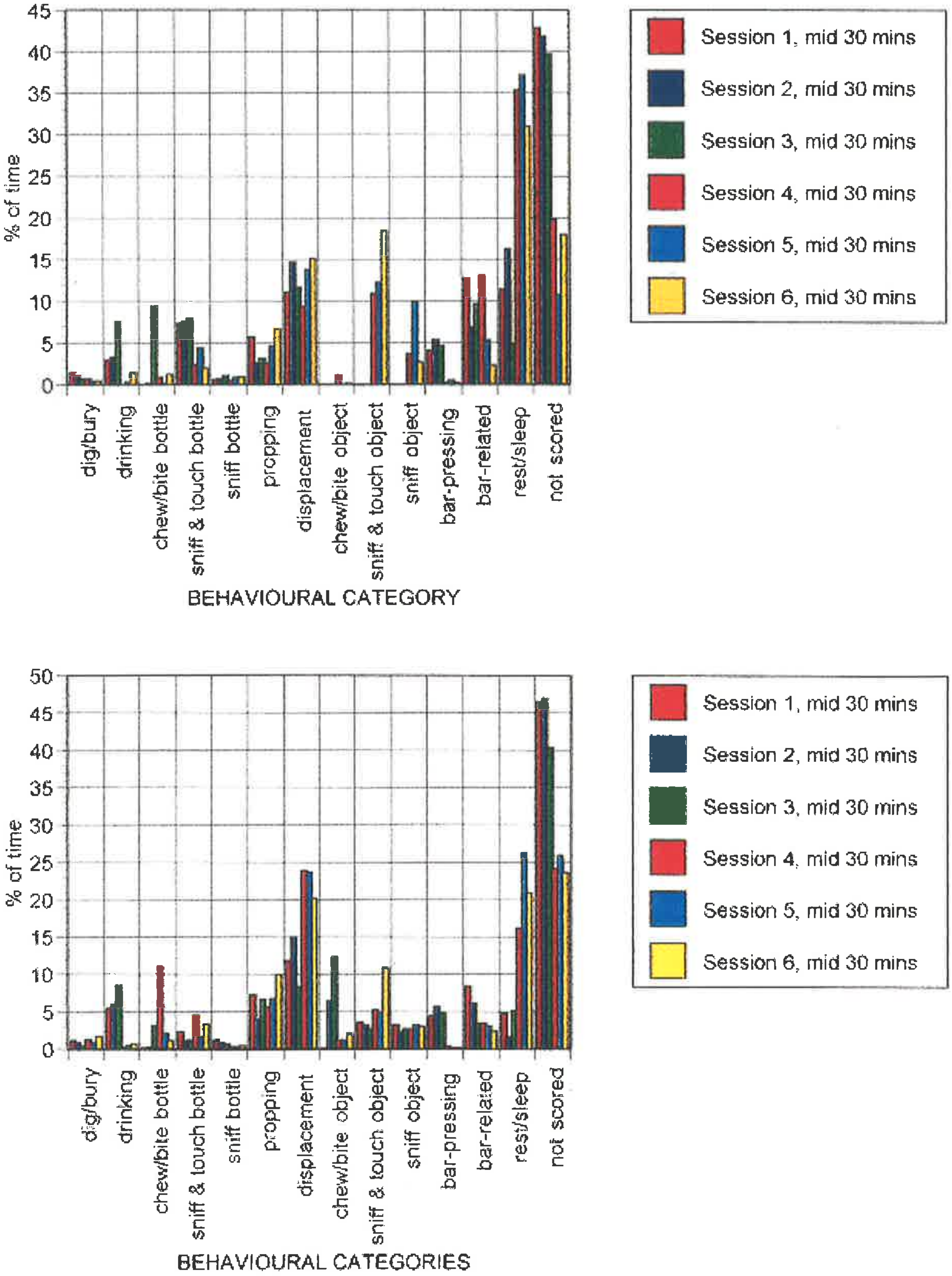


Figure 9.14 (II). Mean percentage of time spent engaged in each behavioural category for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***middle 30 minutes*** of each session. (Calculated as mean time in seconds spent engaged in behaviour, as a percentage of the ***middle 30 minutes***, i.e., 1800 seconds).

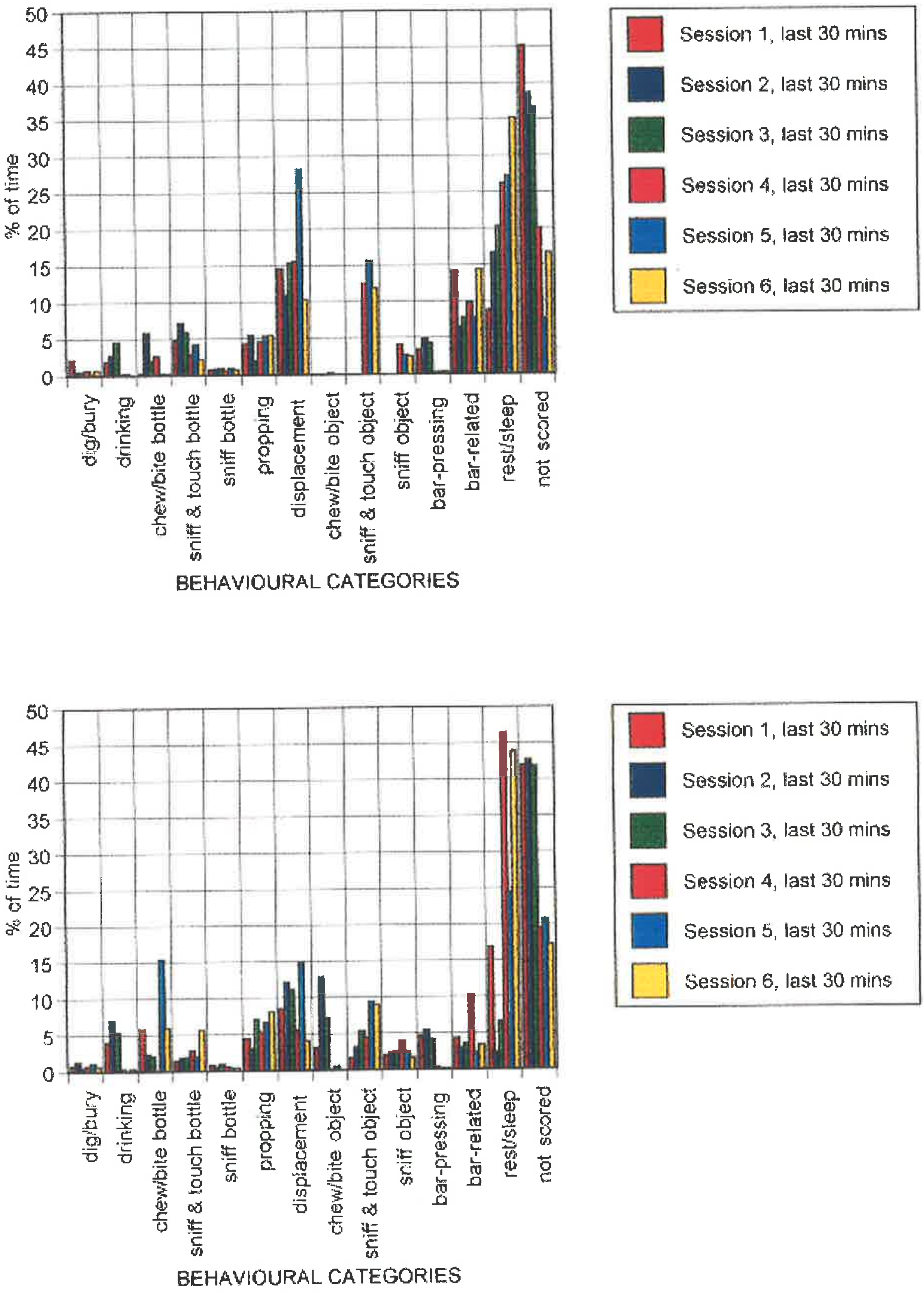


Figure 9.14 (III). Mean percentage of time spent engaged in each behavioural category for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***last 30 minutes*** of each session. (Calculated as mean time in seconds spent engaged in behaviour, as a percentage of the ***last 30 minutes***, i.e., 1800 seconds).

Table 9.15

The percentage of half-hour session segment spent (1800 seconds) engaged in behaviour that was ***not scored***.

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS						
1st 30 min	26.79 %	43.56 %	38.89 %	33.28 %	27.1 %	24.74 %
mid 30 min	46.5 %	46.95 %	40.39 %	24.2 %	25.88 %	23.64 %
last 30 min	41.92 %	42.66 %	41.81 %	19.44 %	20.63 %	17.11 %
FIOE						
1st 30 min	55.94 %	50.13 %	50.18 %	34.11 %	30.98 %	27.68 %
mid 30 min	42.81 %	41.8 %	39.68 %	19.76 %	10.73 %	17.97 %
last 30 min	45.17 %	38.61 %	36.58 %	19.98 %	7.59 %	16.68 %

Overall, there was a decrease across the six sessions in the percentage of total session spent engaged in behaviours that were not scored, for both groups and all parts of session (Table 9.15). The percentages were noticeably higher during ***fixed-interval*** sessions for both groups (except for the ***first 30 minutes*** of session 1 in the FIOS group). The percentages for the FIOS group were all lower in the ***first 30 minutes*** of each session, but higher in the ***middle 30 minutes*** of each session. No such clear-cut pattern of differences existed for the ***last 30 minutes***. Overall within-session decreases occurred in all sessions for the FIOE group, and in all ***extinction*** sessions as well as session 2 for the FIOS group.

9.3.5.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

During ***fixed-interval*** sessions, the FIOS group spent between 7.74% and 22.67% of total session time engaged in ***behaviour directed at the bar and food-trough area*** (Table 9.16). By contrast, these behaviours represented between 11.3% and 17.45% of total session time for the FIOE group. Thus, ***behaviour directed at the bar and food-trough area*** took up less than 23% of total session time in all cases, but never represented less than 7% of total session time during ***fixed-interval*** sessions. Within-session decreases were observed in every session for the FIOS group, whereas no clear-cut pattern emerged for the FIOE group. The percentages were higher in every part of every session when objects were absent during ***fixed-interval*** sessions (except for the ***first 30 minutes*** of session 1).

Table 9.16
The percentage of half-hour session segment spent (1800 seconds) engaged in ***behaviour directed at the bar and food-trough area*** (***bar-pressing*** + ***bar-related behaviour***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS						
1st 30 min	22.67 %	11.98 %	9.13 %	6.78 %	2.62 %	2.25 %
mid 30 min	12.77 %	11.67 %	8.16 %	3.73 %	3.18 %	2.48 %
last 30 min	8.98 %	8.42 %	7.74 %	10.47 %	2.48 %	3.49 %
FIOE						
1st 30 min	15.31 %	15.71 %	13.87 %	5.67 %	4.47 %	3.66 %
mid 30 min	16.72 %	12.08 %	14.31 %	13.18 %	5.69 %	2.51 %
last 30 min	17.45 %	11.30 %	12 %	10.07 %	7.97 %	14.59 %

During ***extinction*** sessions, the FIOS group spent between 2.25% and 10.47% of total session time engaged in ***behaviour directed at the bar and food-trough area*** (Table 9.16). The FIOE group spent between 2.51% and 14.59% of ***extinction*** sessions engaged in these behaviours. ***Behaviour directed at the bar and food-trough area*** took up less than 15% of total session time, but never represented less than 2% of total session time during ***extinction***. The percentages were higher for the group with objects first present during ***extinction*** (FIOE) in most parts of session (except the ***first*** and ***last 30 minutes*** of session 4). Within-session changes occurred in ***extinction*** sessions for both groups, but with no clear-cut pattern emerging.

The overall pattern across sessions is similar for both groups (Table 9.16). The percentages show an overall decrease over the three ***fixed-interval*** sessions for all parts of session. The percentages then continue to decrease over the ***extinction*** sessions (except the ***last 30 minutes*** for the FIOE group, & the ***last 30 minutes*** of session 4 increased in the FIOS group).

9.3.5.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

During ***fixed-interval*** sessions, the FIOS group spent between 6.73% and 19.92% of total session time engaged in ***behaviour directed at the stimulus objects*** (Table 9.17). An overall increase in percentages was observed for all parts of session (more marked in the ***middle & last 30 minutes***) across the three ***fixed-interval*** sessions.

During ***extinction*** sessions, between 9.07% and 26.16% of the FIOS group's time was spent engaged in ***object-directed behaviours***, whereas the FIOE percentages were slightly higher, ranging from 14.22% to 29.32% (Table 9.17). For both groups, there was an overall decrease across sessions for the ***first 30 minutes*** and an overall increase for the ***middle 30 minutes***. For the ***last 30 minutes***, the percentages showed an overall increase across sessions for the FIOS group and a decrease for the FIOE group. In most cases, there was a within-session decrease in percentage of time spent engaged in ***object-directed behaviours***.

Table 9.17
The percentage of half-hour session segment spent (1800 seconds) engaged in ***behaviour directed at the stimulus objects*** (***chew/bite object*** + ***sniff object*** + ***sniff and touch object***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS **1st 30 min** **mid 30 min** **last 30 min**	19.86 % 6.84 % 6.73 %	11.92 % 11.76 % 18.42 %	19.92 % 17.56 % 15.11 %	26.16 % 9.07 % 8.64 %	19.18 % 9.18 % 12.33 %	24.04 % 15.80 % 10.58 %
FIOE **1st 30 min** **mid 30 min** **last 30 min**	NO OBJECTS PRESENT	NO OBJECTS PRESENT	NO OBJECTS PRESENT	29.32 % 15.64 % 16.73 %	16.21 % 22.19 % 18.22 %	19.85 % 21.06 % 14.22 %

Overall, the percentage of session time spent engaged in ***behaviour directed at stimulus objects*** did not exceed 30% (Table 9.17). For the group with objects first present during ***fixed-interval*** sessions (FIOS), there was an overall increase across the six sessions for all parts of session. Further, there was an increase across ***fixed-interval*** sessions and an increase across ***extinction*** sessions (except during the ***first 30 minutes***). There was, however, a within-session decrease. Thus, a habituation effect was observed within sessions, but the rats actually directed more ***behaviour towards the objects*** over sessions, suggesting that objects had "regained novelty" between sessions. During ***extinction***, more ***object-directed exploratory behaviour*** occurred as the ***bar pressing*** response extinguished.

For the group with objects first present during ***extinction*** (FIOE), the highest score was obtained in the first ***extinction*** session only for the ***first 30 minutes*** (Table 9.17). For the ***middle*** and ***last 30 minutes***, the highest score occurred during the second ***extinction*** session. There was an overall decrease across sessions for the ***first*** and ***last 30 minutes***, suggesting a habituation effect in these parts of session. Overall within-session decreases were observed in two of the three ***extinction*** sessions. The scores for the FIOE group (their first encounter with novel objects) were higher in most cases (excluding the ***first 30 minutes*** of sessions 4 & 5).

For the FIOE group, the ***chew/bite object*** category, which might be ***object-directed aggression***, took up less than 8% of total session time during the ***first 30 minutes*** and less than 1.5% of total time during the ***middle*** and ***last 30 minutes*** of ***extinction*** sessions (see Appendix A). For the FIOS group, the percentages were higher. For the first session, less than 3.5% of total session time was spent engaged in this behaviour (in all parts of session). Between 4.34% and 13.9% of total session time was spent in ***chew/bite object*** for the next two ***fixed-interval*** sessions. The percentages were still quite high (between 5.67% & 13.28%) during the ***first 30 minutes*** of ***extinction*** sessions, but these values fell to below 2.4% for the ***middle*** and ***last 30 minutes*** of ***extinction*** sessions.

9.3.5.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

The ***propping*** category took up less than 10% of total session time in all cases. For the FIOS group, the percentages ranged between 3.06% and 7.19% during ***fixed-interval*** sessions and between 4.13% and 8.08% during ***extinction*** sessions (Table 9.18). The FIOE percentages, on the other hand, were slightly lower, ranging between 1.92% and 6.48% during ***fixed-interval*** sessions and between 2.57% and 6.93% during ***extinction*** sessions.

Table 9.18
The percentage of half-hour session segment spent (1800 seconds) engaged in ***propping.***

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS						
1st 30 min	3.62 %	3.76 %	4.13 %	4.15 %	9.3 %	6.97 %
mid 30 min	7.19 %	3.93 %	6.6 %	5.61 %	6.67 %	9.79 %
last 30 min	4.43 %	3.06 %	7.04 %	5.23 %	6.63 %	8.09 %
FIOE						
1st 30 min	4.16 %	6.48 %	5.41 %	3.12 %	6.93 %	6.73 %
mid 30 min	5.68 %	2.61 %	3.09 %	2.57 %	4.57 %	6.61 %
last 30 min	4.26 %	5.44 %	1.92 %	4.51 %	5.29 %	5.42 %

For the ***first 30 minutes*** of each session, the percentages were higher for the FIOE group during ***fixed-interval*** sessions, but lower during ***extinction*** sessions (Table 9.18). For the ***middle*** and ***last 30 minutes***, the FIOS group percentages were higher in every session (except the ***last 30 minutes*** of session 2). An overall increase across the six sessions occurred for all parts of session, for both groups. There was no clear-cut pattern for within-session changes.

9.3.5.4 BEHAVIOUR DIRECTED AT THE WATER BOTTLE

During ***fixed-interval*** sessions, the FIOS group spent between 2.26% and 17.12% of total session time engaged in ***behaviour directed at the water bottle*** (Table 9.19). These percentages were slightly higher for the VIOS group (between 5.53% and 18.28%). During ***extinction*** sessions, between 3.38% and 18.1% of the FIOS group's time was directed at the water bottle, whereas the percentages ranged from 2.97% to 23% for the FIOE group. Within-session decreases occurred in all but the last session for the FIOS group. For the FIOE group, within-session decreases occurred in all ***extinction*** sessions and also in session 1.

Overall, less than 25% of total session time was spent engaged in ***bottle-directed behaviours*** (Table 9.19). If objects were absent during ***fixed-interval*** sessions (FIOE group), an overall increase in these behaviours across ***fixed-interval*** sessions was observed (for all parts of session). When objects were present, the percentages decreased overall across ***fixed-interval*** sessions in the ***first*** and ***last 30 minutes***. Over ***extinction*** sessions, the percentages decreased across sessions in the ***first*** and ***middle 30 minutes*** for the FIOS group, whilst they increased for the FIOE group. That is, the pattern was reversed. Over the six sessions, the percentages decreased for the ***first*** and ***middle 30 minutes*** in the FIOS group and decreased for the ***middle*** and ***last 30 minutes*** in the FIOE group.

Table 9.19
The percentage of half-hour session segment spent (1800 seconds) engaged in ***behaviour directed at the water bottle*** (***chew/bite bottle*** + ***sniff bottle*** + ***sniff and touch bottle***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS						
1st 30 min	17.12 %	12.68 %	10.23 %	12.94 %	18.1 %	10.91 %
mid 30 min	3.58 %	2.26 %	4.94 %	15.89 %	3.91 %	4.83 %
last 30 min	7.99 %	4.6 %	4.81 %	3.38 %	17.61 %	11.89 %
FIOE						
1st 30 min	7.79 %	5.53 %	8.06 %	15.58 %	7.41 %	23.0 %
mid 30 min	7.92 %	8.17 %	18.28 %	3.64 %	5.23 %	3.99 %
last 30 min	5.83 %	13.87 %	8.77 %	6.12 %	5.3 %	2.97 %

For the FIOE group, the ***chew/bite bottle*** category, which might be ***bottle-directed aggression***, took up less than 2% of total session time during the ***first 30 minutes***, less than 10% of total time during the ***middle*** and ***last 30 minutes*** of ***fixed-interval*** sessions (see Appendix A). During ***extinction*** sessions, up to 18.98% of total session time during the ***first 30 minutes*** was spent in

chew/bite bottle, whilst less than 3% of session time was taken up by this behaviour during the ***middle*** and ***last 30 minutes***. For the FIOS group, the percentages were higher during the ***first 30 minutes*** of ***fixed-interval*** sessions. During the ***last 30 minutes*** of ***extinction*** sessions, the percentages varied dramatically from one session to the next. No time at all was spent engaged in ***chew/bite bottle*** during session 4, whereas more than 15% of total session time was devoted to this behaviour in the next session.

During ***fixed-interval*** sessions, the FIOS group spent between 3.78% and 10.34% of total time engaged in ***drinking***, whereas the FIOE group spent between 1.92% and 8.46% ***drinking*** (Table 9.20). During ***extinction*** sessions, the percentage of total session time spent engaged in ***drinking*** was lower. Both groups spent less than 2.6% of ***extinction*** time engaged in ***drinking***. For the FIOE group, there were two parts of session where no ***drinking*** took place at all.

Table 9.20
The percentage of half-hour session segment spent (1800 seconds) engaged in ***drinking***.

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS						
1st 30 min	3.78 %	7.55 %	10.34 %	2.07 %	0.9 %	1.71 %
mid 30 min	5.47 %	6.02 %	8.54 %	0.27 %	0.42 %	0.68 %
last 30 min	4.02 %	7.03 %	5.37 %	0.29 %	0.01 %	0.34 %
FIOE						
1st 30 min	6.3 %	8.46 %	7.38 %	1.93 %	2.51 %	0.69 %
mid 30 min	2.96 %	3.28 %	7.45 %	0 %	0.27 %	1.38 %
last 30 min	1.92 %	2.75 %	4.6 %	0.13 %	0.19 %	0 %

An overall increase in total time spent ***drinking*** across ***fixed-interval*** sessions occurred for all parts of session, for both groups (Table 9.20). Over the six sessions, there was an overall decrease for both groups and all parts of session. There was no clear-cut pattern across ***extinction*** sessions. For both groups, there was an overall within-session decrease in every session.

9.3.5.5 "AGGRESSIVE" BEHAVIOURS

Overall, the percentage of session time spent engaged in ***aggressive behaviour*** directed at the water bottle and stimulus objects did not exceed 25% (Table 9.21). However, the values fluctuated greatly, with almost negligible percentages of total session time spent engaged in these behaviours in a number of cases.

For the group with objects first present during ***fixed-interval*** sessions (FIOS), there was an overall increase in percentages across the six sessions for the ***first*** and ***middle 30 minutes***, and an overall decrease across these same sessions for the ***last 30 minutes*** (Table 9.21). All parts of session demonstrated an increase over ***fixed-interval*** sessions. There was an overall within-session decrease for all sessions with the exception of session 2.

For the FIOE group, there are no ***chew/bite object*** scores included during ***fixed-interval*** sessions (Table 9.21). The percentage of total session time spent engaged in ***chew/bite bottle*** increases across ***fixed-interval*** sessions for all parts of session. In most cases this percentage was less than 2%, but for the ***middle 30 minutes*** of session 3 was more than 9%. During ***extinction***, when objects are first present, the percentage of total session time spent engaged in ***aggressive behaviours*** varied between 0.08% and 24.29%. The highest percentages occurred during the ***first 30 minutes*** of ***extinction*** sessions. There was an overall within-session decrease for extinction sessions. The percentages decreased over ***extinction*** sessions for the ***middle*** and ***last 30 minutes***.

Table 9.21
The percentage of half-hour session segment spent (1800 seconds) engaged in ***aggressive behaviours*** (***chew/bite object*** + ***chew/bite bottle***).

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS						
1st 30 min	12.83 %	14.73 %	21.36 %	23.21 %	19.83 %	19.17 %
mid 30 min	0.26 %	6.62 %	15.36 %	12.27 %	3.14 %	3.14 %
last 30 min	8.84 %	15.13 %	9.15 %	0.08 %	15.75 %	5.89 %
FIOE	No objects present	No objects present	No objects present			
1st 30 min	1.67 %	0.23 %	1.88 %	19.23 %	4 %	24.29 %
mid 30 min	0 %	0.08 %	9.35%	1.90 %	0.08 %	1.23 %
last 30 min	0.26 %	5.82 %	1.99 %	2.92 %	0.28 %	0.16 %

During ***extinction*** sessions, the percentage of time spent engaged in ***aggressive behaviours*** was higher in most cases for the FIOS group (except the ***first 30 minutes*** of session 4 and the ***last 30 minutes*** of session 6).

9.3.5.6 OTHER BEHAVIOURAL CATEGORIES

During ***fixed-interval*** sessions, the FIOS group spent between 5.21% and 14.93% of total time engaged in ***displacement***, whereas the FIOE group spent between 7.51% and 15.39% engaged in this behaviour (Table 9.22). During ***extinction*** sessions, the percentage of total session time spent engaged in ***displacement*** varied more. The FIOS group spent between 4.02% and 26.98% involved in ***displacement*** activities, whilst the percentages ranged from 7.89% to 28.14% for the FIOE group. During ***extinction***, the percentages were greater than 20% in a number of cases. For both groups, there was an overall increase in percentages over the six sessions for the ***first*** and ***middle 30 minutes***. For the FIOS group, there was an overall within-session increase during the ***fixed-interval*** sessions, which changed to a decrease during ***extinction*** sessions. For the FIOE group, there was an overall within-session increase for four of the six sessions.

Table 9.22
The percentage of half-hour session segment spent (1800 seconds) engaged in ***displacement.***

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS						
1st 30 min	5.21 %	7.73 %	5.61 %	12.42 %	15.05 %	26.98 %
mid 30 min	11.82 %	14.93 %	8.26 %	23.87 %	23.64 %	20.23 %
last 30 min	8.48 %	12.17 %	11.14 %	5.53 %	14.8 %	4.02 %
FIOE						
1st 30 min	7.51 %	11.24 %	12.16 %	7.89 %	27.94 %	13.49 %
mid 30 min	11.1 %	14.66 %	11.65 %	9.29 %	13.75 %	15.11 %
last 30 min	14.53 %	10.89 %	15.39 %	15.6 %	28.14 %	10.27 %

Both groups spent less than 3% of total session engaged in ***digging/burying*** in all sessions (Table 9.23). There was a within-session decrease for both groups (except in session 2 for the FIOS group). That is, slightly more time was spent ***digging/burying*** in the earlier part of each session. There was a small overall decrease in percentages across the six sessions for the FIOE group for all parts of session, whereas an overall decrease was only observed in the ***last 30 minutes*** for the FIOS group.

Table 9.23

The percentage of half-hour session segment spent (1800 seconds) engaged in ***digging/burying.***

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS **1st 30 min** **mid 30 min** **last 30 min**	 0.76 % 1.11 % 0.7 %	 0.51 % 0.88 % 1.28 %	 1.72 % 0.47 % 0.43 %	 1.68 % 1.25 % 0.66 %	 2.97 % 0.92 % 1.03 %	 1.77 % 1.64 % 0.62 %
FIOE **1st 30 min** **mid 30 min** **last 30 min**	 2.72 % 1.42 % 2.09 %	 1.55 % 1.08 % 0.52 %	 1.78 % 0.64 % 0.43 %	 2.18 % 0.63 % 0.68 %	 1.67 % 0.42 % 0.13 %	 2.24 % 0.41 % 0.69 %

For the FIOS group, the percentage of time spent ***resting/sleeping*** ranged from 0.03% to 16.76% during ***fixed-interval*** sessions and between 0.52% and 46.36% during ***extinction*** (Table 9.24). For the FIOE group these percentages ranged from 0.27% to 20.32% during ***fixed-interval*** sessions and between 0.19% and 37.14% during ***extinction***. Thus, the variation was large (from almost negligible to almost 50%).

Table 9.24

The percentage of half-hour session segment spent (1800 seconds) engaged in ***resting/sleeping.***

GROUP	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FIOS **1st 30 min** **mid 30 min** **last 30 min**	 0.2 % 4.72 % 16.76 %	 0.32 % 1.6 % 2.37 %	 0.03 % 5.07 % 6.55 %	 0.52 % 16.12 % 46.36 %	 4.77 % 26.19 % 24.49 %	 0.63 % 20.91 % 43.85 %
FIOE **1st 30 min** **mid 30 min** **last 30 min**	 0.27 % 11.38 % 8.75 %	 0.90 % 16.32 % 16.63 %	 1.17 % 4.9 % 20.32 %	 0.19 % 35.29 % 26.18 %	 1.87 % 37.14 % 27.17 %	 2.66 % 30.96 % 35.17 %

Overall, for both groups and all parts of sessions, the percentage of total session spent engaged in ***resting/sleeping*** increases across the six sessions (Table 9.24). This increase is marked for the ***middle*** and ***last 30 minutes***. There was a clear within-session increase for both groups for all sessions, and the increase from ***first*** to ***last 30 minutes*** was particularly noticeable during the ***extinction*** sessions. Thus, rats were more likely to ***rest/sleep*** during the latter stages of each session.

9.3.6 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE OVER SESSIONS, AND BETWEEN GROUPS

The changes in each behavioural measure (frequency & duration) over the three ***fixed-interval*** (sessions 1 to 3), and three ***extinction*** sessions (sessions 4 to 6) are presented graphically in Figures 9.15 (I) – 9.19 (III), inclusive. The scores for the ***first***, ***middle*** and ***last 30 minutes*** of each session are plotted on each graph (separately for the two groups), allowing a visual comparison of trends across the six sessions. Patterns of change will be presented for each of the behaviours in turn.

9.3.6.1 BEHAVIOUR DIRECTED AT THE MANIPULANDUM AND FOOD-TROUGH AREA

As Figure 9.15 (I) indicates, for the FIOE group, both the frequency and duration of ***bar pressing*** followed a similar pattern across the six sessions, for the three parts of session (***first***, ***middle*** & ***last 30 minutes***). The mean duration scores were much lower than the frequency scores, since little time was needed to completely depress the manipulandum. There was an overall increase in frequency and duration scores across the three ***fixed-interval*** sessions for all parts of session. In each session the scores for the ***last 30 minutes*** were lowest. The mean scores for all three parts of session plummeted dramatically in the first ***extinction*** session (session 4). The scores for the ***first 30 minutes*** were substantially higher in this session. This is not surprising, since it was the early part of the first ***extinction*** session. The mean scores varied little over the three ***extinction*** sessions, for the ***middle*** and ***last 30 minutes***. The mean score for the ***first 30 minutes*** decreased in session 5 and 6, to a value that was similar to the value observed in the latter parts of session. (The mean frequency scores were all < 380 & the mean duration scores were all < 100 seconds).

As with the FIOE group, both the frequency and duration of ***bar pressing*** for the FIOS group, followed a similar pattern across the six sessions, for the three parts of session (Figure 9.15:I), with the exception of the duration score in session 1, for the ***first 30 minutes***. Again, the mean duration scores were much lower than the frequency scores. For all parts of session, an overall increase in frequency occurred over the three ***fixed-interval*** sessions. For the ***middle 30 minutes***, the mean duration scores showed a slight overall increase across ***fixed-interval*** sessions, whereas an overall decrease occurred for the other parts of session. For the ***first 30 minutes***, the duration score in session 1 was strikingly high, before decreasing dramatically in session 2. As with the FIOE group, the mean scores for all three parts of session decreased sharply in the first ***extinction*** session (session 4). The scores for the ***first 30 minutes*** were noticeably higher. This is not surprising, since the ***first 30 minutes*** of session 4 were the earliest part of the first ***extinction*** session. The mean scores varied little over the three ***extinction*** sessions, for the ***middle*** and ***last***

30 minutes. The mean score for the ***first 30 minutes*** decreased in session 5 and 6, to a value that was similar to the value observed in the latter parts of session. (The mean frequency scores were all < 480 & the mean duration scores were all < 230 seconds).

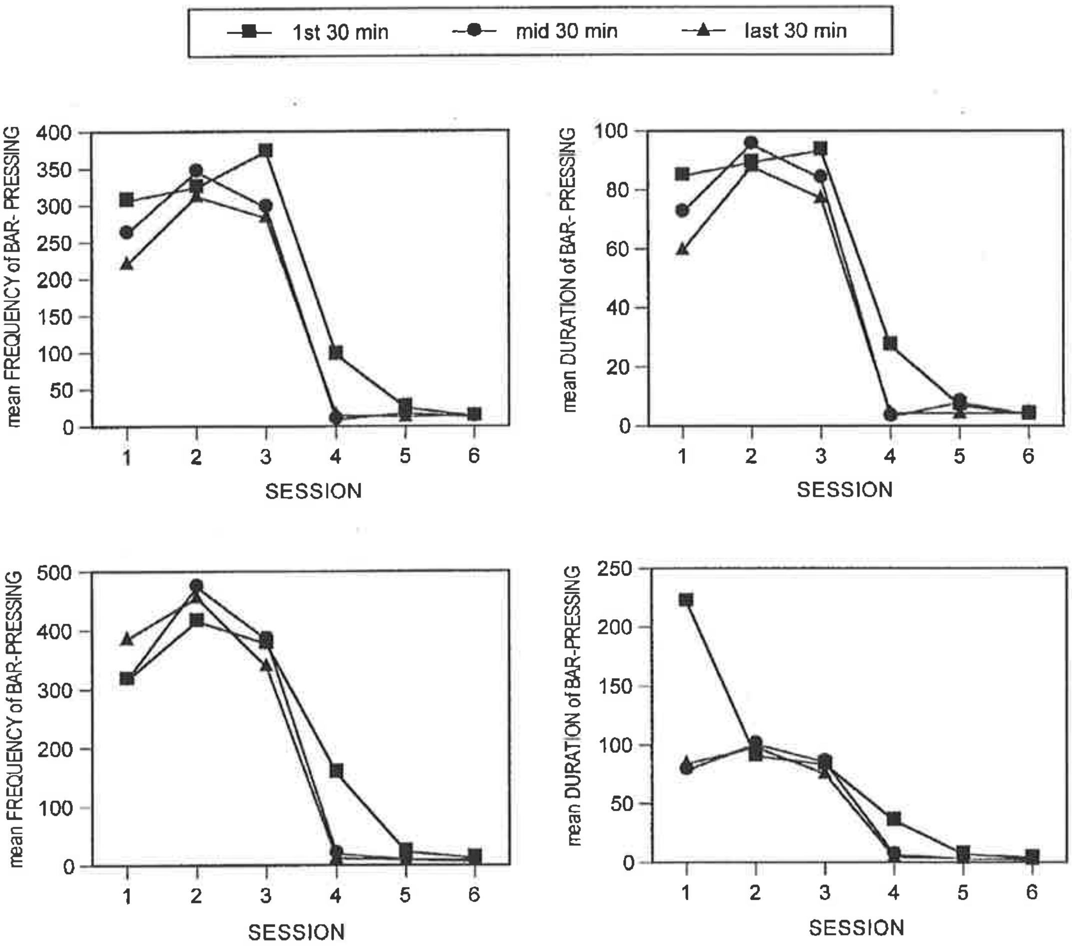


Figure 9.15 (I). Mean frequency (left) and duration (right) scores of ***bar pressing*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOE group, the frequency of ***bar-related behaviour*** for all parts of session showed an overall decrease across the six sessions, with a marked decrease in the first ***extinction*** session (Figure 9.15:II). The duration scores also reflected this trend, for the ***first 30 minutes*** of each session. For the ***middle*** and ***last 30 minutes*** of each session, both measures decreased markedly from session 1 to 2 (to almost the same value). For the ***middle*** and ***last 30 minutes*** of each session, the mean duration scores followed a similar pattern across the first five sessions. The scores decreased dramatically from session 1 to 2, and then increased in an almost linear fashion to session 4. The mean score for the ***middle 30 minutes*** of session 4 was slightly higher than the score in session 1. For the ***middle 30 minutes***, the mean duration scores decreased sharply from session 4 to 5, before decreasing again in session 6 to the lowest overall score. For the ***last 30***

minutes, the mean duration scores also decreased from session 4 to 5, before increasing markedly in session 6 to the highest overall score. The overall decrease in mean frequency scores over the six sessions was very dramatic for all three parts of session. The overall decrease in mean duration scores over the six sessions was also marked for the ***first*** and ***middle 30 minutes*** of each session. (The mean frequency scores were all < 280 & the mean duration scores were all < 260 seconds).

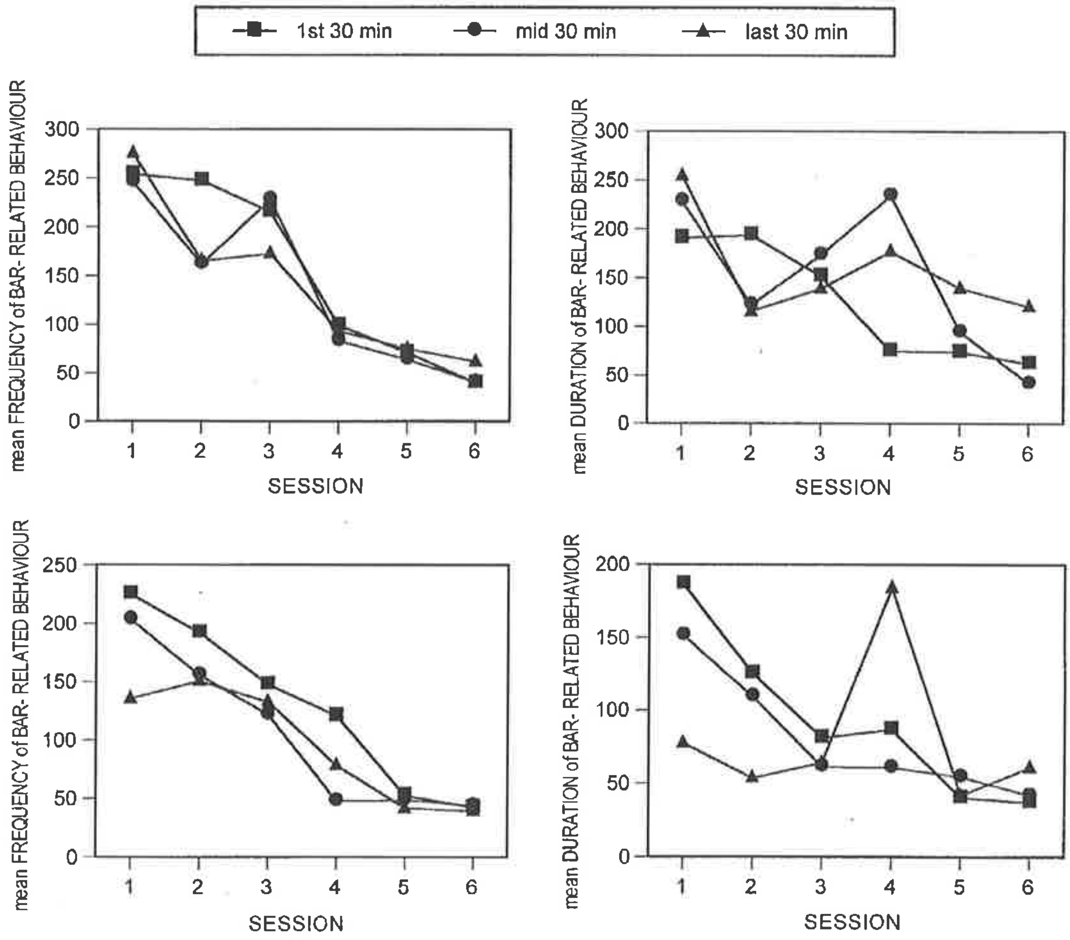


Figure 9.15 (II). Mean frequency (left) and duration (right) scores of ***bar-related behaviour*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOS group, the frequency scores of ***bar-related behaviour*** showed a dramatic overall decrease across the six sessions, and the scores for the last two sessions were very similar, for all three parts of session (Figure 9.15:II). Whereas, the frequency scores for the FIOE group were similar in both the first and last session, for all three parts of session, those for the FIOS group were noticeably different in the first session, but similar in the last session, for all three parts of session. The duration scores showed a dramatic decrease across the six sessions for the ***first*** and ***middle 30 minutes*** of each session. For the ***last 30 minutes*** of each session, a small overall decrease was observed across the six sessions, but with a large (threefold) increase in session 4, the first ***extinction*** session. (The mean frequency scores were all < 230 & the mean duration scores were all < 190 seconds).

9.3.6.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

It should be noted that objects were first present during ***extinction*** for the FIOE group. Thus, there are only three points of reference on each graph for this group.

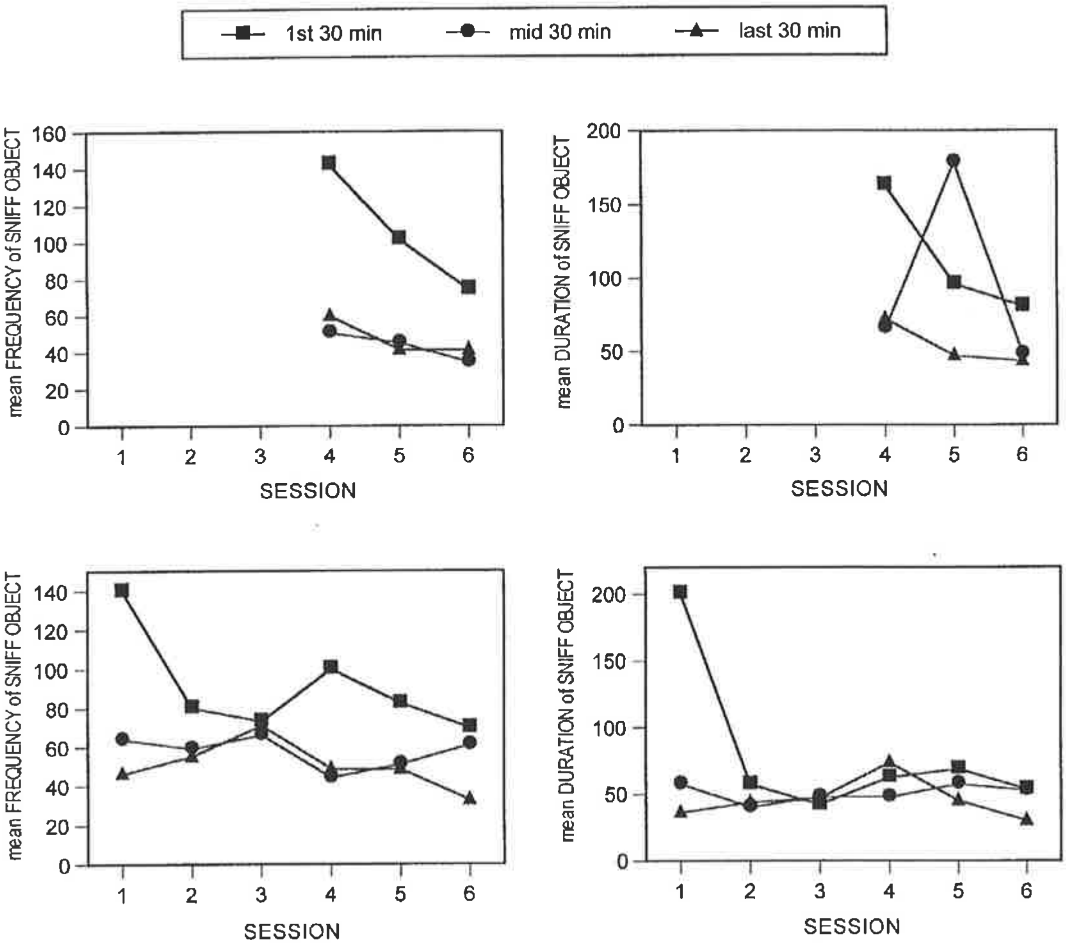


Figure 9.16 (I). Mean frequency (left) and duration (right) scores of ***sniff object*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOE group, the frequency scores of ***sniff object*** for the ***first 30 minutes*** were markedly higher (more than double for the first two ***extinction*** sessions) than those for the other two parts of session (Figure 9.16:I). For the ***middle*** and ***last 30 minutes*** of each session, the mean frequency scores were similar in all three sessions. For all parts of session, the frequency scores decreased over ***extinction***. Similarly, a decrease in duration scores over ***extinction*** was observed for the ***first*** and ***last 30 minutes*** of each session (the values were much higher for the ***first 30 minutes***). For the ***middle 30 minutes*** of each session, a dramatic inverted "V" pattern was obtained. The scores for session 4 and 6 were similar to those obtained for the ***last 30 minutes***, but the score for session 5 was the highest value obtained overall, and far higher than the scores for the other two parts of session 5. (The mean frequency scores were all < 150 & the mean duration scores were all < 180 seconds.).

For the FIOS group, the frequency scores of ***sniff object*** were highest for the ***first 30 minutes*** of all six sessions (Figure 9.16:I). In session 1 and 4, the mean score was more than double the score for the other two parts of session. The scores for the ***first 30 minutes*** decreased over the first three sessions (markedly from session 1- 2), increased in session 4 (to a higher value than observed in session 1 & 2), and then decreased over ***extinction***. The final score was approximately half the score obtained in session 1. For the ***middle*** and ***last 30 minutes***, there was a small overall increase in frequency across the ***fixed-interval*** sessions, and a decrease in the first ***extinction*** session. For the ***middle 30 minutes***, the frequency gradually increased over ***extinction***. Interestingly, the final score is similar to those obtained in the first 3 sessions. For the ***last 30 minutes***, the frequency decreased over ***extinction***. The highest duration was obtained in the ***first 30 minutes*** of session 1 (more than triple the next highest score). This value then decreased dramatically (more than threefold) to a value that was similar to those obtained for the other two parts of session. Except for the ***first 30 minutes*** of session 1, the other mean scores for all three parts of session do not differ noticeably over the six sessions. There is an overall decrease across the six sessions for all parts of session (very slight for the ***middle & last 30 minutes***). The lowest overall score was obtained in the ***last 30 minutes*** of session 6. (All mean frequencies were < 140 & the mean duration scores were all < 200 seconds).

As Figure 9.16 (II) shows, for the FIOE group the mean frequency scores of ***sniff and touch object*** followed the pattern observed for the ***sniff object*** scores (almost exactly), although the actual values were lower (especially for the ***first 30 minutes*** of each session). The scores for the ***first 30 minutes*** of each session were markedly higher (almost triple for the first ***extinction*** session) than those for the other two parts of session. The frequency scores decreased over ***extinction*** for all parts of session. The mean duration scores showed an overall decrease for the ***first*** and ***last 30 minutes*** of session, whereas this measure increased quite dramatically over ***extinction*** for the ***middle 30 minutes***. (The mean frequency scores were all < 90 & the mean duration scores were all < 340 seconds).

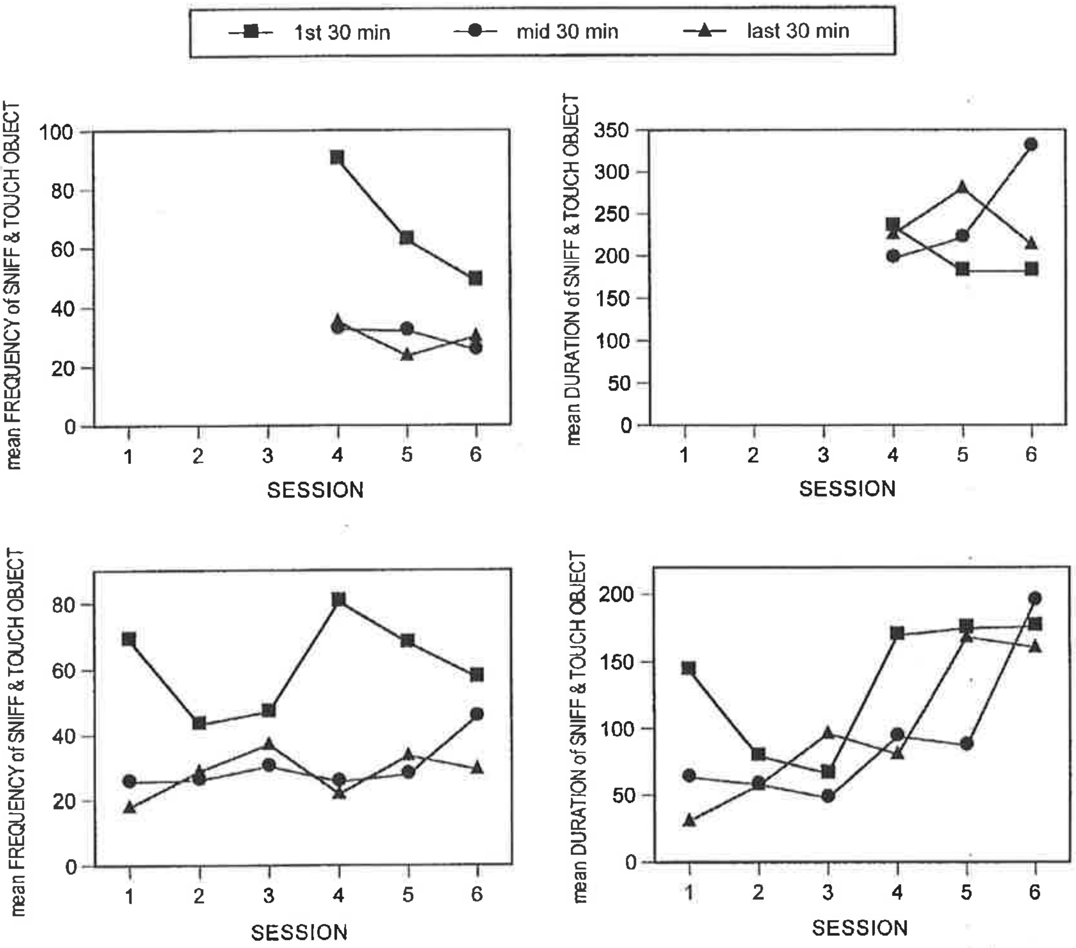


Figure 9.16 (II). Mean frequency (left) and duration (right) scores of ***sniff and touch object*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOS group, the frequency scores of ***sniff and touch object*** showed similar patterns (Figure 9.16:II) to those observed for the frequency scores of ***sniff object*** (Figure 9.16:I). The scores for the ***first 30 minutes*** of each session were markedly higher (more than double for session 1, 4 & 5) than those for the other two parts of session. The mean scores decreased over ***fixed-interval*** sessions, increased dramatically in the first ***extinction*** session, and then decreased steadily over ***extinction***. Interestingly, the values obtained in the ***extinction*** sessions were noticeably higher than their ***fixed-interval*** session counterparts. For the ***middle*** and ***last 30 minutes*** of each session, an overall increase in frequency scores was observed across the six sessions (with a decrease in the first ***extinction*** session). As with most frequency scores, the duration values obtained in the ***extinction*** sessions were noticeably higher than their ***fixed-interval*** session counterparts (with the exception of the ***last 30 minutes*** of session 4). Thus, there was an overall increase across the six sessions for all parts of session. For the ***first*** and ***middle 30 minutes*** of each session, an overall decrease in scores was observed over the first three sessions, whilst the scores for the last three sessions showed an overall increase. For the ***last 30 minutes*** of each session, an overall increase in mean scores occurred over both the ***fixed-interval*** and ***extinction*** sessions. For session 1 and 4, the scores for the ***first 30 minutes*** were markedly higher than for the other parts of session. Although the frequency values for this behavioural category did not differ markedly over the six sessions, for the ***middle*** and ***last 30 minutes*** of each session, the corresponding mean duration scores increased dramatically over the six sessions. (The mean frequency scores were all < 90 & the mean duration scores were all <200 seconds).

For the FIOE group, the frequency and duration scores of ***chew/bite object*** were virtually negligible (< 2) for the ***middle*** and ***last 30 minutes*** of each ***extinction*** session (Figure 9.16:III). The patterns for the frequency scores were almost identical to the duration scores (except session 6 for the ***first 30 minutes***). For the ***first 30 minutes*** of each session, there were also only few instances of this behaviour (low frequency scores), but the duration scores were high for the first and last of the ***extinction*** sessions. (The mean frequency scores were all < 12 & the mean duration scores were all < 140 seconds).

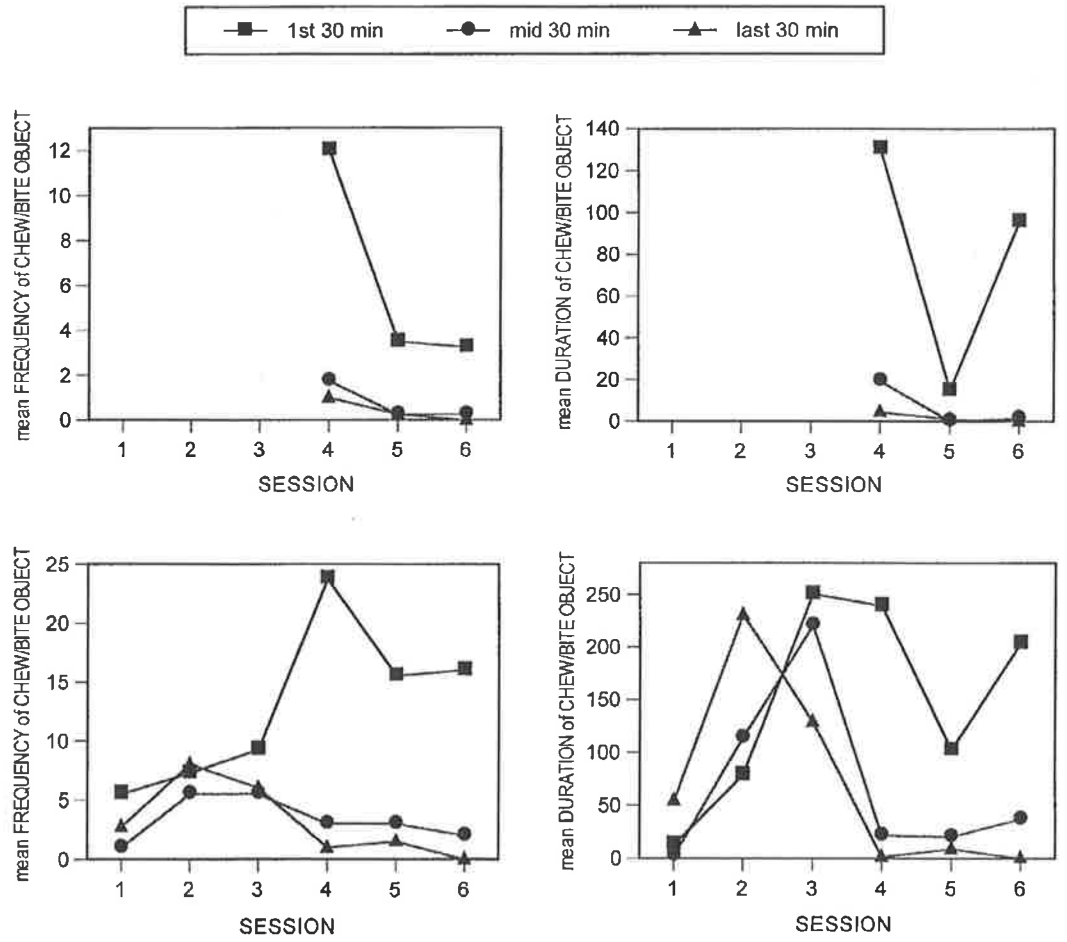


Figure 9.16 (III). Mean frequency (left) and duration (right) scores of ***chew/bite object*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes, middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOS group, the frequency scores of ***chew/bite object*** were low (<9) for the ***middle*** and ***last 30 minutes*** of each session, for all six sessions (Figure 9.16:III). The frequency scores for the ***first 30 minutes*** were equally low for the first three sessions. For all three parts of session, there was a slight overall increase in scores over the first three sessions. For the ***first 30 minutes*** of each session, the score more than doubled in session 4, before showing an overall decrease across ***extinction***. For the ***middle*** and ***last 30 minutes***, the frequency scores decreased in the first ***extinction*** sessions, and then continued to show an overall decrease across ***extinction***. For the ***first*** and ***middle 30 minutes*** of each session, mean duration scores increased sharply (by about 200 seconds) over the first three sessions, whilst there was an overall increase for the ***last 30 minutes*** (with a more than quadruple increase between session 1 & 2). This measure then plunged just as dramatically in session 4, for the ***middle 30 minutes***, before showing a slight overall increase over the three ***extinction*** sessions. For the ***first 30 minutes***, the score decreased slightly in the first ***extinction*** session, and then showed an overall decrease across ***extinction***. For the ***extinction*** sessions, the mean duration scores were low for the ***middle 30 minutes*** of each session, and almost negligible for the ***last 30 minutes*** of each session. By contrast, the values were still high for the ***first 30 minutes*** of each session, across the ***extinction*** sessions. (The mean frequency scores were all < 25 & the mean duration scores were all < 260 seconds).

Thus, ***chew/bite object*** was a feature of ***fixed-interval*** sessions, but almost absent from ***extinction*** sessions in both groups (except during the ***first 30 minutes*** of each session).

9.3.6.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

For the FIOE group, the frequency of ***propping*** was highest for the ***first 30 minutes*** of each session (Figure 9.17). The frequency and duration scores showed an overall increase across ***fixed-interval*** sessions for the ***first 30 minutes***, whereas an overall decrease occurred for the other parts of session. The frequency and duration then decreased in the first ***extinction*** session in the ***first*** and ***middle 30 minutes***, but increased in the ***last 30 minutes***. An overall increase in both measures was observed across ***extinction*** for all parts of session. Overall, there was a slight increase in frequency over the six sessions for the ***first*** and ***last 30 minutes***, and an increase in duration for all parts of session (All mean frequency scores were < 45 & all the mean duration scores were < 130 seconds).

For the FIOS group, the frequency scores of ***propping*** showed an interesting pattern (Figure 9.17). The scores for all parts of session were similar for every alternate session (*i.e.*, in session 2, 4 & 6). For the ***first 30 minutes*** of each session, the mean frequency and duration scores showed very little change over the first four sessions (slight increase in duration & slight decrease in frequency). There was an overall increase in frequency and duration across ***fixed-interval*** sessions for the ***last 30 minutes***, whereas these measures decreased for the ***middle 30 minutes***. The frequency and duration of ***propping*** decreased in the first ***extinction*** session for the ***middle*** and ***last 30 minutes***. Both measures showed an overall increase across ***extinction*** for all parts of session. (The mean frequency scores were all < 60 & the mean duration scores were < 180 seconds).

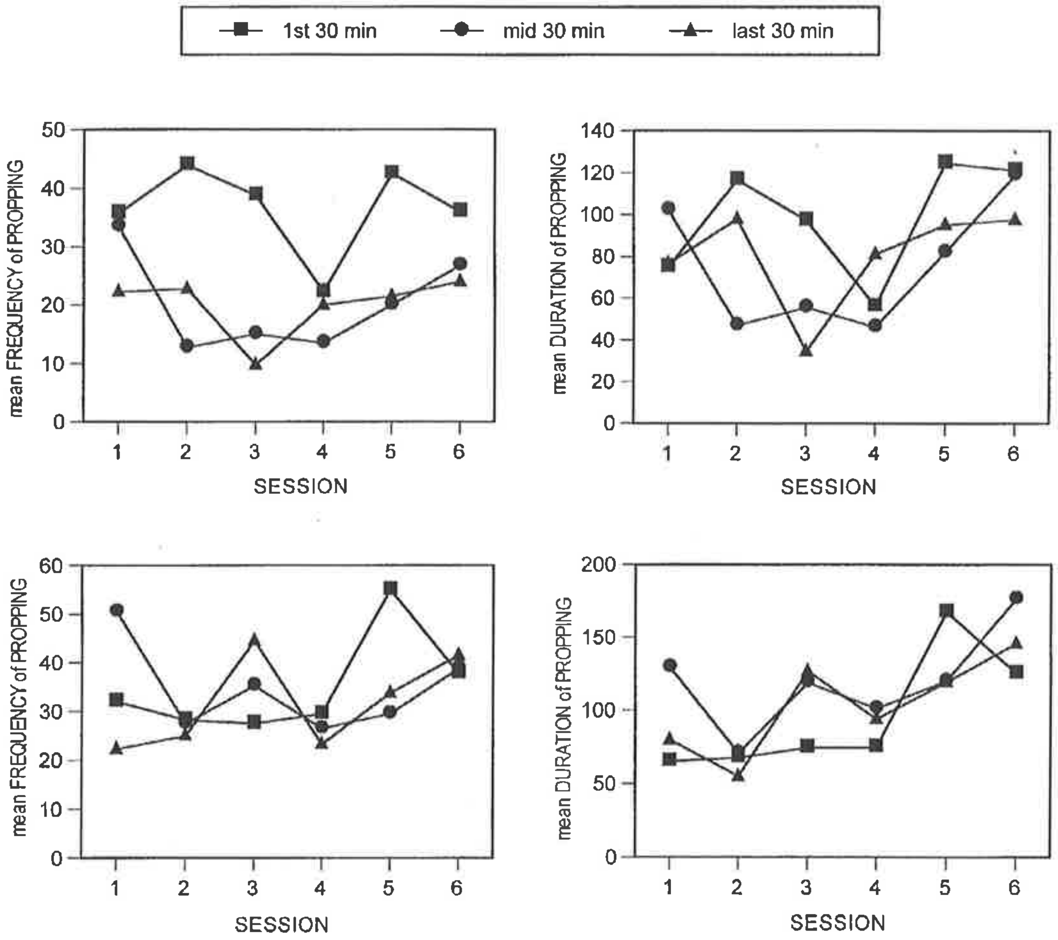


Figure 9.17. Mean frequency (left) and duration (right) scores of ***propping*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

9.3.6.4 BEHAVIOUR DIRECTED AT THE WATER BOTTLE

For the FIOE group, the frequency scores of ***sniff bottle*** were highest during the ***first 30 minutes*** of all sessions, except session 2 (Figure 9.18:I). The duration scores were all very low (<20 seconds). There was an overall increase in frequency and duration scores across ***fixed-interval*** sessions for all parts of session. These measures decreased in the first ***extinction*** session (session 4). The frequency scores showed an overall decrease across ***extinction*** for all parts of session. The duration scores, on the other hand, increased overall across ***extinction*** for the ***middle*** and ***last 30 minutes*** of every session. Overall, across the six sessions there was a decrease in frequency and duration of ***sniff bottle***, except duration for the ***middle 30 minutes***. (The mean frequency scores were all <40 & the duration scores were all <20 seconds).

For the FIOS group, the frequency scores of ***sniff bottle*** were highest in every session, for the ***first 30 minutes*** of each session (Figure 9.18:I). There was an overall decrease across the six sessions for all parts of session. The frequency and duration scores decreased over ***fixed-interval*** sessions, with the exception of duration for the ***last 30 minutes***. Both measures decreased in the first ***extinction*** session, except for frequency during the ***first 30 minutes***. Similarly, both measures decreased over ***extinction***, with the exception of duration in the ***middle 30 minutes*** of each session. (As with the FIOE group, the mean frequency scores were all < 40 & all duration scores were < 45 seconds -all but two, were < 20 seconds).

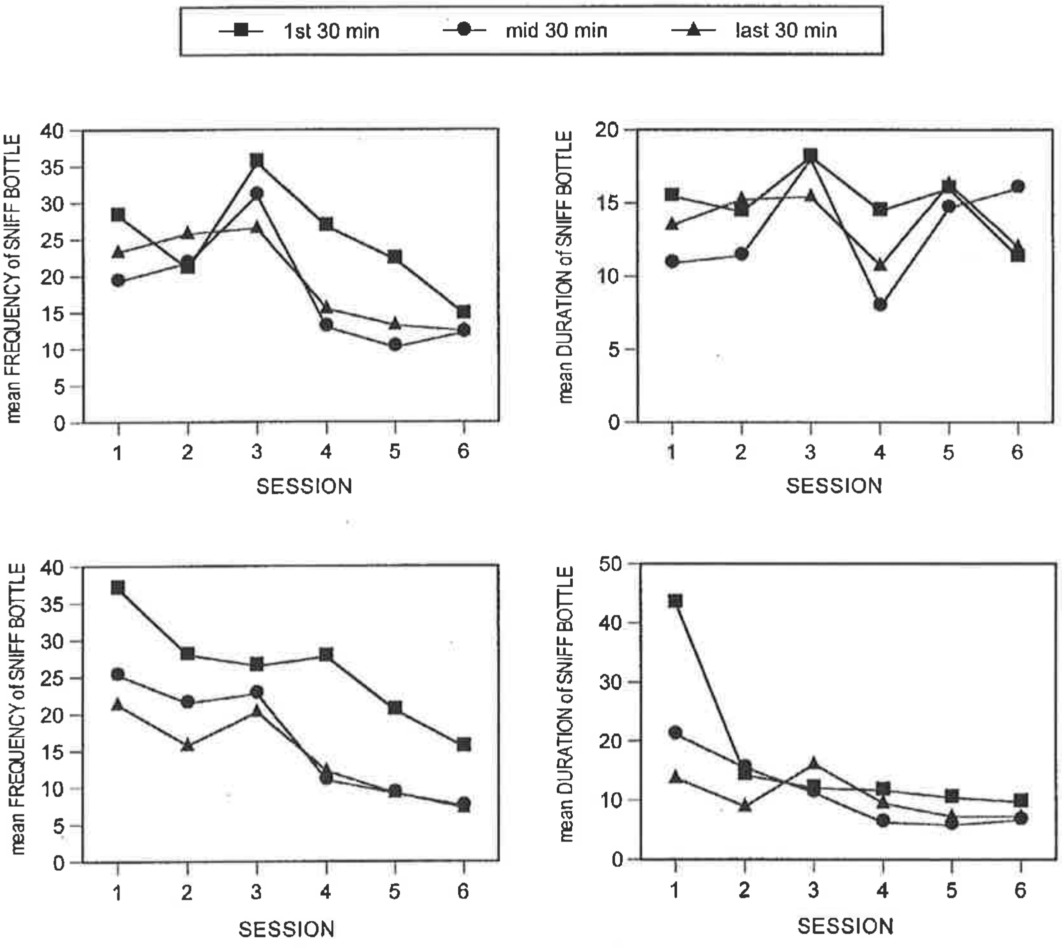


Figure 9.18 (I). Mean frequency (left) and duration (right) scores of ***sniff bottle*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOE group, the frequency scores of ***sniff and touch bottle*** were highest during the ***first 30 minutes*** of all sessions, except session 1 (Figure 9.18:II). The frequency scores showed an overall increase during the ***fixed-interval*** sessions, dropped noticeably in session 4, and then showed an overall decrease over the ***extinction*** sessions for all parts of session. The duration scores displayed greater differences over the ***fixed-interval*** sessions, than the ***extinction*** sessions, for all three parts of session. The values for the ***middle 30 minutes*** of each session were highest in four of the six sessions. There was an overall increase in duration across ***fixed-interval*** sessions and overall decrease over ***extinction*** for the ***middle*** and ***last 30 minutes*** of each session. Duration decreased in the first ***extinction*** session for all parts of session. Overall, frequency and duration of ***sniff and touch bottle*** decreased across the six sessions for all parts of session. (The mean frequency scores were all < 50 & the mean duration scores were all < 150 seconds).

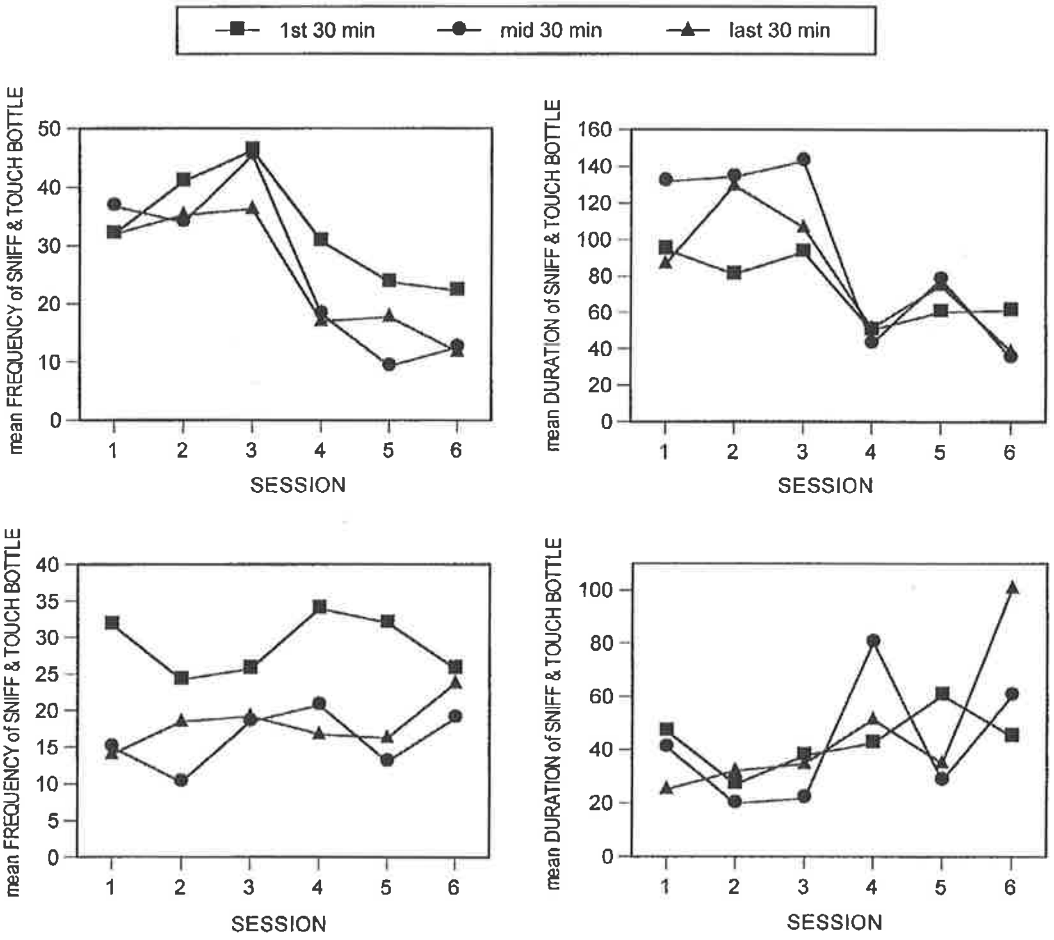


Figure 9.18 (II). Mean frequency (left) and duration (right) scores of ***sniff and touch bottle*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOS group, the frequency scores of ***sniff and touch bottle*** were highest in every session, for the ***first 30 minutes*** (Figure 9.18:II). Overall, there was an increase in frequency and duration across the six sessions for the ***middle*** and ***last 30 minutes***. Across ***fixed-interval*** sessions, there was an overall increase in frequency for the ***middle*** and ***last 30 minutes***, but an overall decrease in duration for the ***first*** and ***middle 30 minutes***. Both measures increased in the first ***extinction*** session, except frequency during the ***last 30 minutes***. Over ***extinction***, there was an overall decrease in frequency for the ***first*** and ***middle 30 minutes***, and an increase in duration for the ***first*** and ***last 30 minutes***. (The mean frequency scores were all < 35 & the mean duration scores were all < 105 seconds- with all but two <65 seconds).

For the FIOE group, the frequency scores of ***chew/bite bottle*** were very low for all three parts of session (<10). Thus, any patterns and changes may be considered quite negligible (Figure 9.18:III). The duration scores, by contrast, were particularly high on three occasions, namely, the ***middle 30 minutes*** of session 3 (>150 seconds), and the ***first 30 minutes*** of session 4 (>200 seconds) and session 6 (>300 seconds). Thus, whilst few instances of this behaviour were recorded, the mean duration scores were quite high in a number of cases. There was an overall increase in frequency and duration scores over ***fixed-interval*** sessions for all parts of session. The frequency and duration scores increased in the first ***extinction*** session for the ***first*** and ***last 30 minutes***. There was little change in either measure over extinction for the ***middle 30 minutes***. The frequency and duration increased overall during ***extinction*** for the ***first 30 minutes***, and decreased for the ***last 30 minutes***. For the ***first 30 minutes*** of each session, there was little difference in the duration scores of session 1, session 3 and session 5. In session 2, the score dropped to an almost negligible value. In session 4, the first of the ***extinction*** sessions, the mean score increased sharply (more than quadruple). By the last ***extinction*** session, the mean score had increased even more dramatically (more than five times the score in the previous session). Thus, during ***extinction*** there were few instances of ***chew/bite bottle***, but the duration scores could be high for the ***first 30 minutes*** of every session. (The mean duration scores were all < 350 seconds).

As with the FIOE group, the frequency scores of ***chew/bite bottle*** for the FIOS group, were low (<18). Again, any patterns and changes may be considered quite negligible (Figure 9.18:III). The duration scores, on the other hand, were high in a number of cases. Overall, the frequency scores decreased across the six sessions for the ***first*** and ***last 30 minutes*** of session, whereas the duration scores only decreased for the ***first 30 minutes***. The frequency scores increased over ***fixed-interval*** sessions for the ***first*** and ***middle 30 minutes***, and the duration scores decreased for the ***first*** and ***last 30 minutes***. Both measures increased in the first ***extinction*** session (session 4) for the ***first*** and ***middle 30 minutes***. Frequency and duration scores showed an overall decrease over ***extinction*** for the ***first*** and ***middle 30 minutes***. For the ***last 30 minutes***, a massive increase in duration was obtained in session 5, rising from zero to over 270 seconds. This score then decreased by more than half in the last session. Large increases in duration during ***extinction*** sessions also occurred for the other parts of session. (The mean duration scores were all < 300 seconds).

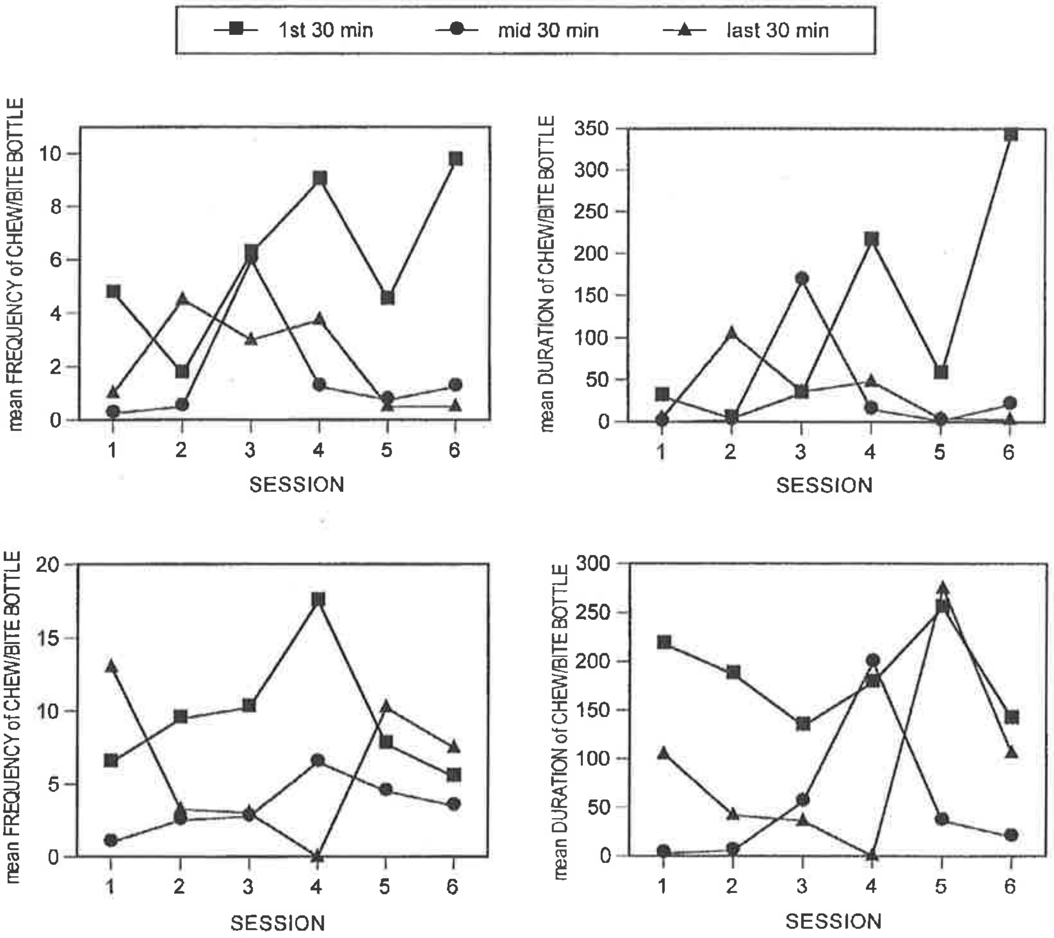


Figure 9.18 (III). Mean frequency (left) and duration (right) scores of ***chew/bite bottle*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOE group, the frequency scores of ***drinking*** were very low (<16). With the exception of the ***first 30 minutes*** of ***fixed-interval*** sessions, all values were less than eight (Figure 9.18:IV). Thus, any patterns and changes in frequency may be considered quite insignificant. The duration scores, however, were quite high in a number of cases (*e.g.*, the mean scores were > 110 seconds for the ***first 30 minutes***, during ***fixed-interval*** sessions). Overall, there was a quite marked decrease in frequency and duration of ***drinking*** across the six sessions, for all parts of session. Across ***fixed-interval*** sessions, there was an overall increase in frequency and duration for all parts of session (except frequency during the ***first 30 minutes***). Both measures dropped noticeably in the first ***extinction*** session for all parts of session. Over ***extinction***, there was an overall decrease in frequency and duration for all but the ***first 30 minutes*** of each session. The frequency and duration scores were zero or almost negligible for the ***middle*** and ***last 30 minutes*** of the ***extinction*** sessions (except duration in the ***middle 30 minutes*** of session 6).

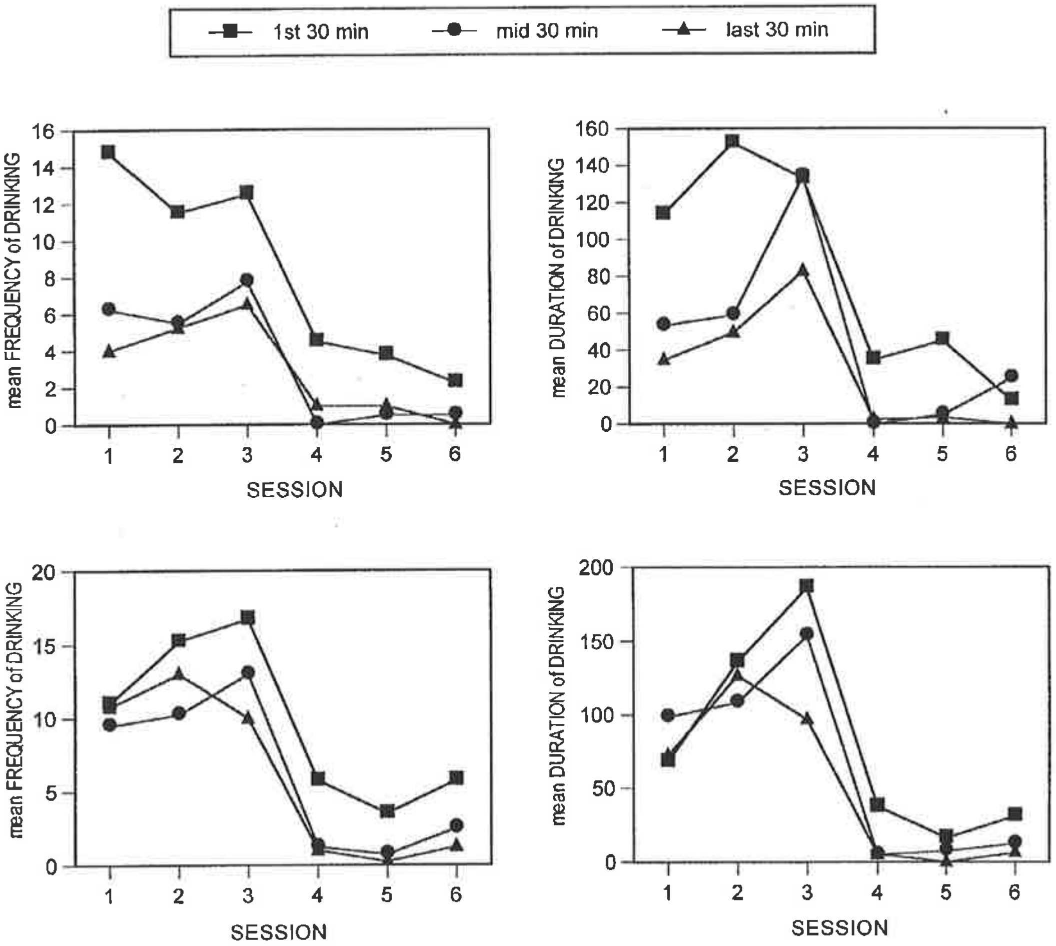


Figure 9.18 (IV). Mean frequency (left) and duration (right) scores of ***drinking*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

As with the FIOE group, for the FIOS group, the frequency scores of ***drinking*** were low (<18), whilst some of the duration scores were quite high (Figure 9.18:IV). With the exception of the ***first 30 minutes*** of session 2 and 3, all frequency values were less than 14. Thus, any patterns and changes may be quite insignificant. The highest mean frequency and duration scores for all six sessions were obtained during the ***first 30 minutes*** (with the exception of duration during session 1). Overall, there was a noticeable decrease in both measures over the six sessions. The frequency and duration scores increased across ***fixed-interval*** sessions for all but the frequency during the ***last 30 minutes*** of each session. Both measures decreased markedly in the first ***extinction*** session (session 4). There was a slight overall increase in frequency and duration over ***extinction*** for the ***middle*** and ***last 30 minutes*** of each session. During ***extinction***, the mean frequency scores were very low (<3 for the ***middle & last 30 minutes*** of each session, & <6 for the ***first 30 minutes*** of each session), and there was a very dramatic plunge in duration. Thus, high mean duration of ***drinking*** was a feature of ***fixed-interval*** sessions only. (The mean duration scores were all < 190 seconds).

9.3.6.5 OTHER BEHAVIOURAL CATEGORIES

For the FIOE group, the frequency scores of ***displacement*** were highest for the ***first 30 minutes*** of every session (Figure 9.19:I). Overall, there was a decrease in frequency scores across the six sessions for all parts of session, whereas there was an increase in duration scores for the ***first*** and ***middle 30 minutes*** of each session. The frequency scores decreased overall across ***fixed-interval*** and ***extinction*** sessions for all parts of session (& decreased in the first ***extinction*** session). The duration scores increased overall across ***fixed-interval*** sessions for all parts of session. This measure then decreased in the first ***extinction*** session and increased overall across ***extinction*** sessions for the ***first*** and ***middle 30 minutes***. A sharp increase to similar duration scores occurred in session 5 for the ***first*** and ***last 30 minutes*** (The mean frequency scores were all < 35 & mean duration scores were all < 505 seconds).

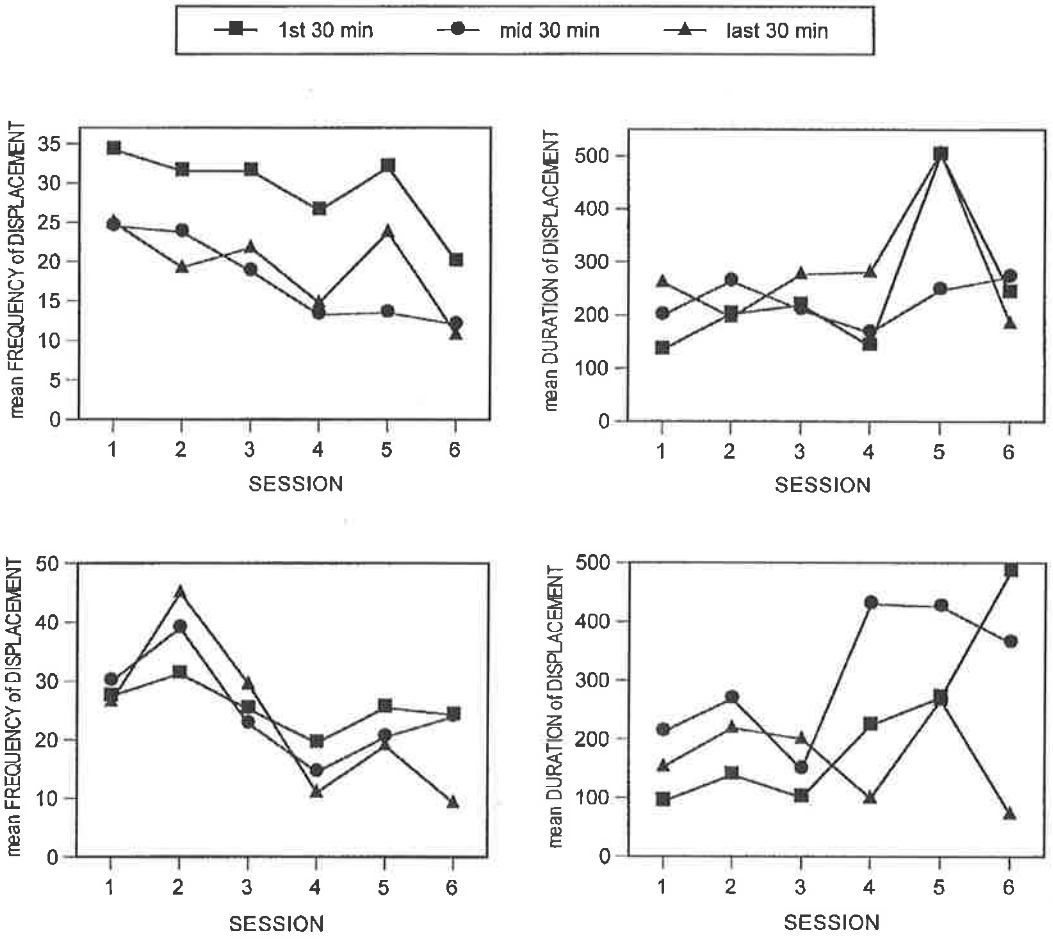


Figure 9.19 (I). Mean frequency (left) and duration (right) scores of ***displacement*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOS group, the mean frequency scores of ***displacement*** peaked in session 2, and the initial frequency (session 1) was very similar for all parts of session (Figure 9.19:I). There was an overall decrease in frequency across the six sessions for all parts of session. For the ***first*** and

middle 30 minutes of each session, there was a slight overall decrease in frequency across ***fixed-interval*** sessions and a slight overall increase over ***extinction***. All parts of session showed a decrease in the first ***extinction*** session. The duration scores showed a marked increase across the six sessions for the ***first*** and ***middle 30 minutes*** of each session, whereas this measure decreased during the ***last 30 minutes***. The increase over the six sessions was by almost 400 seconds for the ***first 30 minutes***. There was a small increase across ***fixed-interval*** sessions for the ***first*** and ***last 30 minutes***. The duration scores increased in the first ***extinction*** session for the ***first*** and ***middle 30 minutes***. Over ***extinction***, there was a marked increase in duration scores for the ***first 30 minutes***, whilst the scores decreased for the other parts of session. Thus, whilst the mean number of ***displacement*** bouts was generally lower during ***extinction*** than ***fixed-interval*** sessions, the duration of bouts was much higher during the ***first*** and ***middle 30 minutes*** of each session. (All the mean frequency scores were < 45 & the mean duration scores were all < 500 seconds).

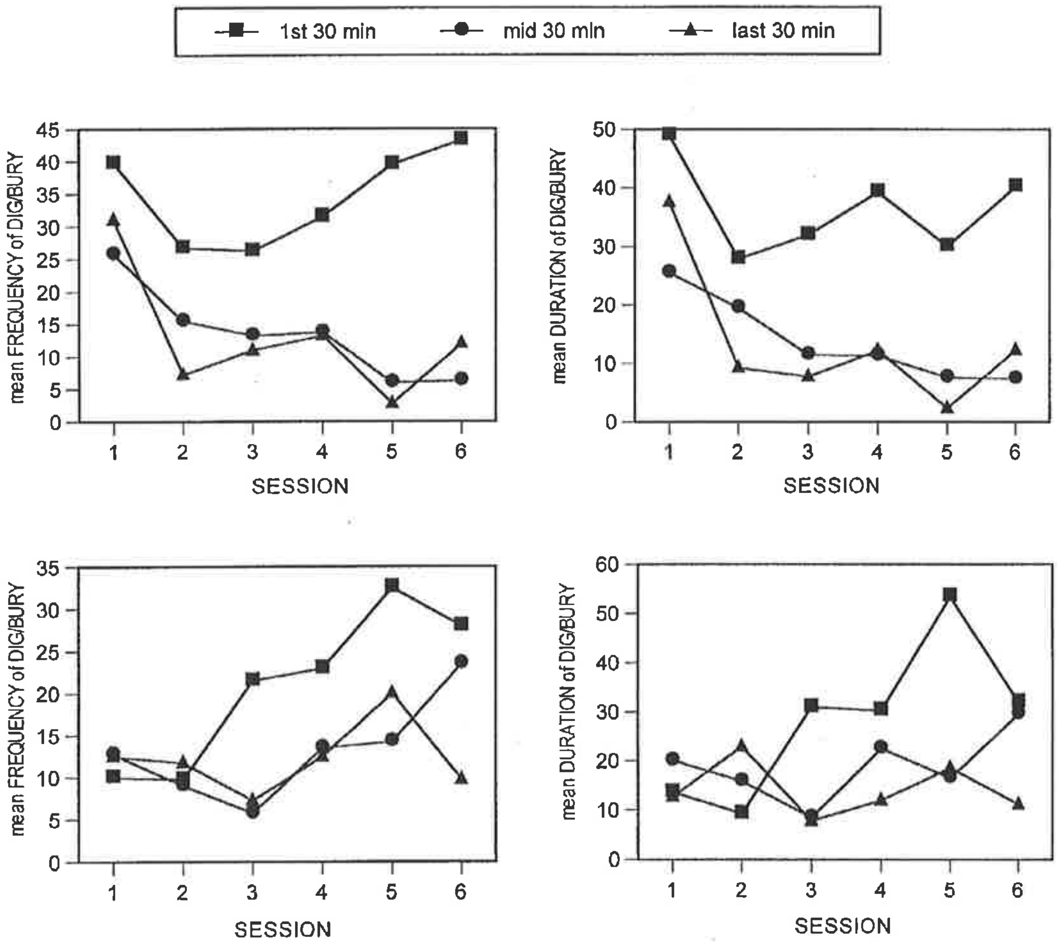


Figure 9.19 (II). Mean frequency (left) and duration (right) scores of ***digging/burying*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

For the FIOE group, the frequency and duration scores of ***digging/burying*** followed quite similar patterns of change across the six sessions, particularly for the ***middle*** and ***last 30 minutes*** of each session (Figure 9.19:II). In addition, the mean frequency scores were all quite similar to the corresponding duration score (& both were relatively low). The highest mean frequency and duration occurred during the ***first 30 minutes*** of every session. Overall, there was a decrease in frequency and duration across the six sessions, for all parts of session (except frequency during the ***first 30 minutes*** of each session). Across ***fixed-interval*** sessions, there was an overall decrease in both measures. Both measures increased slightly in the first ***extinction*** session (except duration for the ***middle 30 minutes***). The frequency scores decreased over ***extinction*** for the ***middle*** and ***last 30 minutes***, whilst the duration increased slightly overall for the ***first*** and ***last 30 minutes***. (The mean frequency scores were all <45 & all of thee mean duration scores were <50 seconds).

For the FIOS group, the frequency scores of ***digging/burying*** were similar for all parts of session, during the first two sessions (Figure 9.19:II). The frequency and duration scores were highest during the ***first 30 minutes*** of session in four of the six sessions. The scores for both measures were relatively low. Overall, both measures increased over the six sessions for the ***first*** and ***middle 30 minutes*** of each session, whereas they decreased during the ***last 30 minutes***. There was an overall decrease in frequency and duration across ***fixed-interval*** sessions for the ***middle*** and ***last 30 minutes***, and an increase in the first ***extinction*** session, for all parts of session (except duration in the ***first 30 minutes***). Over ***extinction***, there was an overall increase in both measures for the ***first*** and ***middle 30 minutes*** of each session. (All the mean frequency scores were < 35 & the mean duration scores were all < 55 seconds).

For the FIOE group, the frequency and duration scores of ***resting/sleeping*** were virtually non-existent for the ***first 30 minutes*** of every session (Figure 9.19:III). The mean scores were also low for the other two parts of session (<25). Thus, any patterns and changes may be considered quite insignificant. The frequency scores were highest in four of the six sessions for the ***last 30 minutes***. Overall, the frequency and duration scores increased over the six sessions (except frequency in the ***middle 30 minutes***). The frequency scores showed an overall decrease across ***fixed-interval*** and ***extinction*** sessions for the ***middle*** and ***last 30 minutes***, and the duration scores increased during the ***first*** and ***last 30 minutes***. Both measures increased in the first ***extinction*** session for the ***middle*** and ***last 30 minutes***. This increase was very striking for the ***middle 30 minutes*** (>500 seconds). Thus, there were relatively few bouts of ***resting/sleeping***, but during the ***extinction*** sessions, the mean duration of this behaviour was very high during the ***middle*** and ***last 30 minutes*** of each session. (All mean duration scores were < 700 seconds).

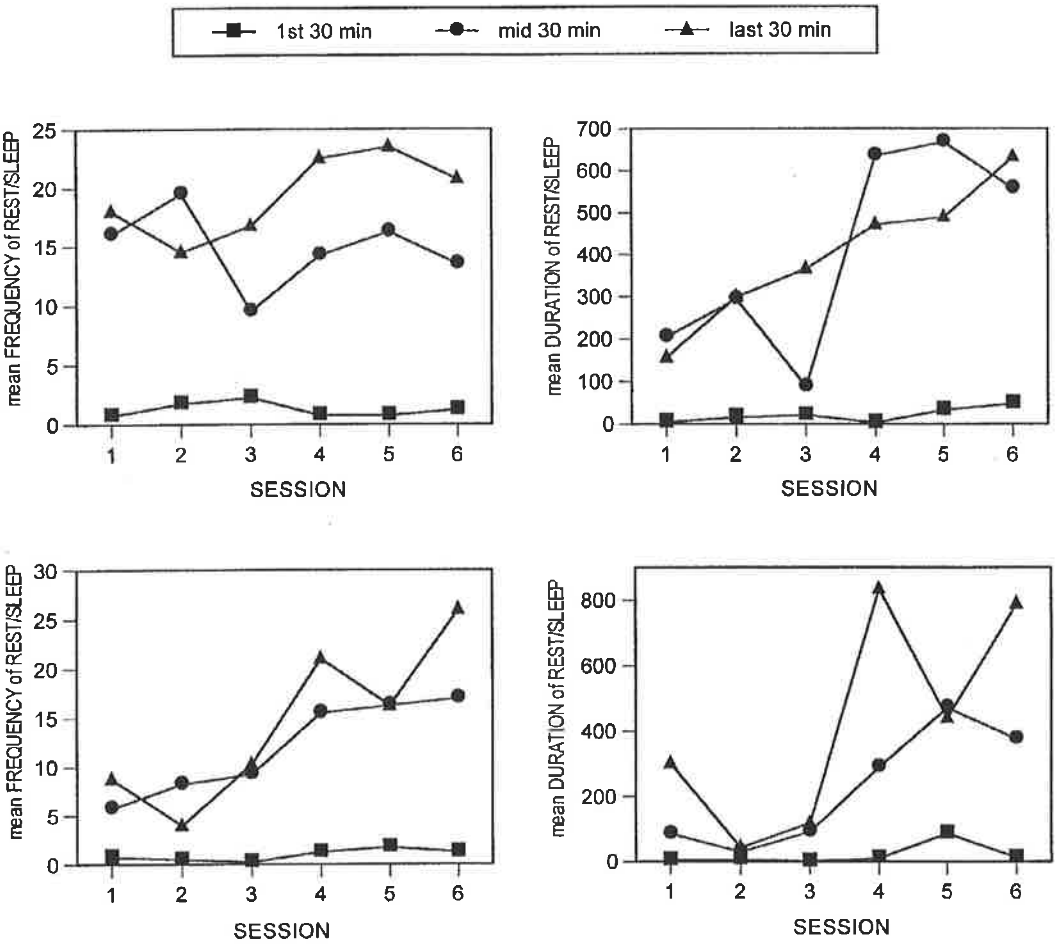


Figure 9.19 (III). Mean frequency (left) and duration (right) scores of ***resting/sleeping*** for the FIOE (top) and FIOS (bottom) groups in Experiment 3, for the ***first 30 minutes***, ***middle 30 minutes*** and ***last 30 minutes*** of each session

As with the FIOE group, for the FIOS group, the frequency and duration scores of ***resting/sleeping*** were virtually non-existent for the ***first 30 minutes*** of every session, with the exception of duration in session 5 (Figure 9.19:III). The mean frequency scores were also low for the other two parts of session (<27). Thus, any patterns and changes may be considered quite insignificant. However, the duration scores were very high in a number of cases (with two mean scores >750 seconds). Overall, there was an increase in both measures across the six sessions, for all parts of session. There was a slight overall increase in frequency across ***fixed-interval*** and ***extinction*** sessions for the ***middle*** and ***last 30 minutes***, and an increase in duration for the ***middle 30 minutes***. There was an increase in both measures in the first ***extinction*** session, for all parts of session. The frequency and duration scores were noticeably higher during ***extinction*** for the ***middle*** and ***last 30 minutes*** of each session. As with the FIOE group, there were relatively few bouts of ***resting/sleeping***, but during ***extinction***, the mean duration was very high during the ***middle*** and ***last 30 minutes*** of each session. (The mean duration scores were all < 850 seconds).

9.3.7 CHANGES IN BEHAVIOURS OVER SESSIONS, BETWEEN PART OF SESSION AND BETWEEN OBJECT CONDITIONS

The previous section presented the mean frequency and duration of the scored behaviours exhibited by the two groups of rats graphically. Since the sample sizes were small, the data have been primarily analysed by description. Bearing this in mind, the data are now analysed by means of statistical testing. As with Experiment 1 (section 6.3.7) and Experiment 2 (section 7.3.7), a multivariate analysis of variance (MANOVA) was performed for each of the frequency and duration measures, during the three ***fixed-interval*** sessions (section 9.3.7.1), the three ***extinction*** sessions (section 9.3.7.2), and over all six sessions (section 9.3.7.3). For each MANOVA there were three independent (or grouping) variables: object (objects first present during ***fixed-interval*** or ***extinction*** sessions), session and part of session (***first***, ***middle*** or ***last 30 minutes***). In each case there was one dependent variable: the frequency or duration measure of a particular behavioural category.

It should be noted that there were no objects present in one of the two groups (FIOE) during ***fixed-interval*** sessions. Therefore, the grouping variable ***object*** has an obvious effect on ***object-directed behaviours*** for the ***fixed-interval*** sessions. If the other independent variables (session or part of session) have a ***main effect*** on the frequency or duration of ***object-directed behaviours***, it is only relevant for the group with objects present during ***fixed-interval*** sessions (FIOS).

9.3.7.1 SCHEDULE SESSIONS

Main effect of *session*

As can be seen from Table 9.25, the differences between sessions were statistically significant for a number of measures. That is, the session number affected the frequency and duration of five behavioural categories. Visual inspection of Figure 9.20 (I) shows that there is a slight increase in the frequency of ***bar pressing***, and a marked increase in the duration of ***drinking*** over the three ***fixed-interval*** sessions. Slight overall decreases in frequency of ***digging/burying*** and ***sniff object*** were observed, whilst more noticeable decreases in duration of ***sniff object*** and ***bar-related behaviour*** took place over these same sessions.

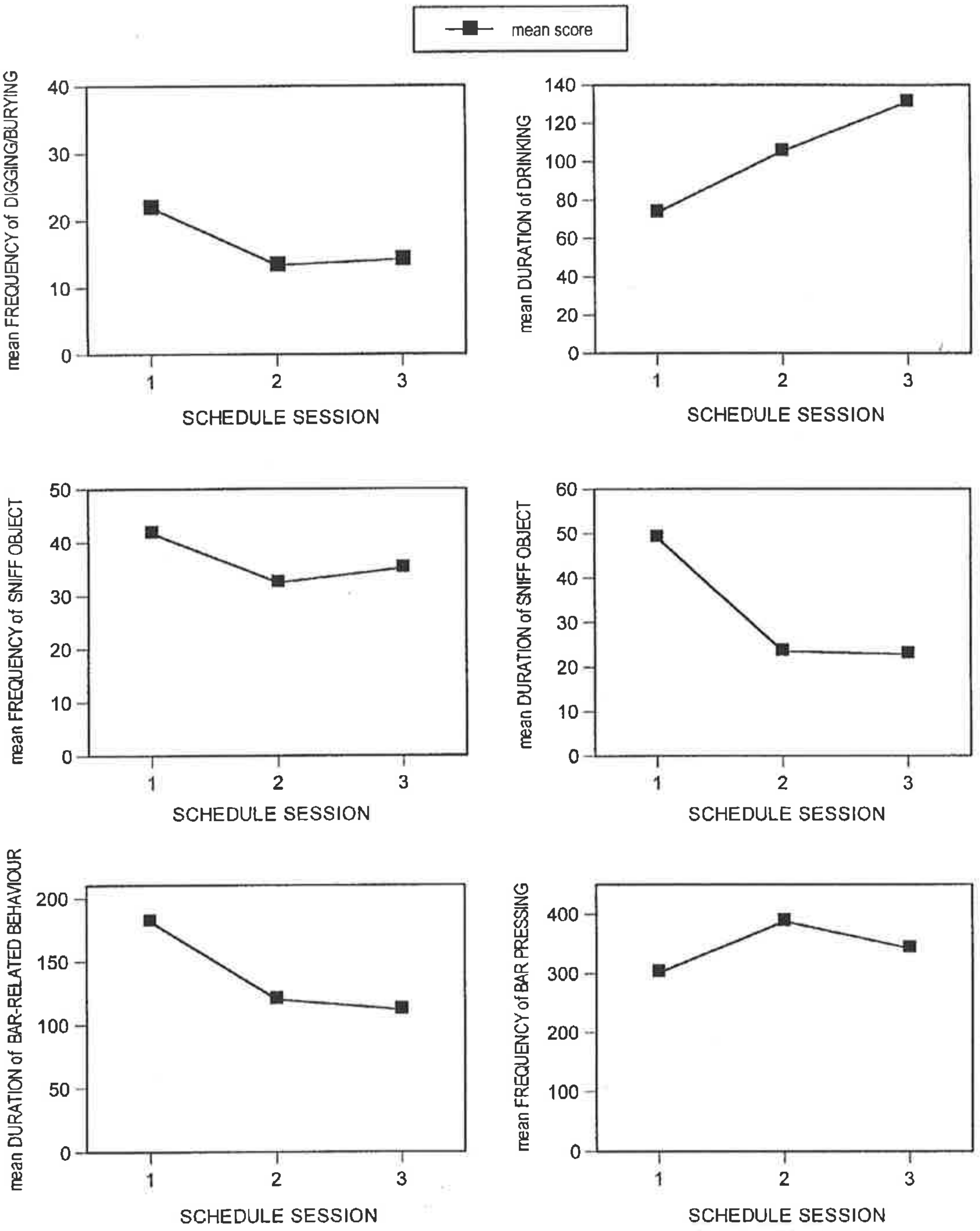


Figure 9.20 (I). Mean frequency and duration of behaviours for the "session" grouping variable during ***fixed-interval*** sessions (top- frequency of ***digging/burying*** & duration of ***drinking***, middle- frequency & duration of ***sniff object*** for the FIOS group, & bottom- duration of ***bar-related behaviour*** & frequency of ***bar pressing***)

Table 9.25

Experiment 3 significance levels obtained for measures of behavioural categories during the three ***fixed-interval*** sessions (***session*** main effect).

Variable	***F*(2,12)**	**Significance level (*p*)**
Frequency of ***digging/burying***	4.31	<.05
Duration of ***drinking***	6.73	<.05
Frequency of ***sniff object***	8.60	=.005
Duration of ***sniff object***	5.72	<.05
Duration of ***bar-related behaviour***	5.41	<.05
Frequency of ***bar pressing***	3.93	<.05

Note. Objects were only present in the FIOS group during ***fixed-interval*** sessions

Main effect of *part of session*

A statistically significant main effect of ***part of session*** was found for measures of seven behavioural categories during ***fixed-interval*** sessions (Table 9.26). Thus, the part of session (***first*, *middle*** or ***last 30 minutes***) affected a number of behaviours, excluding ***bar-related behaviour***, ***bar pressing***, ***chew/bite object***, ***propping***, ***sniff and touch bottle***, and ***chew/bite bottle***.

As shown in Figure 9.20 (II), the frequency and duration of ***resting/sleeping*** was almost negligible for the ***first 30 minutes*** of each session. Slight overall decreases in these measures were observed during the ***middle 30 minutes*** whilst slight overall increases over the three ***fixed-interval*** sessions took place during the ***last 30 minutes***. The mean frequency scores of ***digging/burying***, ***sniff bottle***, ***drinking***, ***sniff and touch object***, ***sniff object***, and duration of ***drinking*** and ***sniff object*** were highest in every session during the ***first 30 minutes*** (Figures 9.20: II & III). With the exception of ***drinking***, the scores for these same measures were very similar during the ***middle*** and ***last 30 minutes*** of each ***fixed-interval*** session.

For the ***first 30 minutes***, a slight overall decrease was observed over ***fixed-interval*** sessions for frequency of ***digging/burying***, ***sniff bottle*** and ***sniff and touch object*** (Figures 9.20: II & III). Marked decreases in the frequency and duration of ***sniff object*** occurred over these same sessions (Figure 9.20: III). Over sessions, there was a slight increase in frequency of ***drinking*** and duration of ***displacement***, and a noticeable increase in duration of ***drinking*** for the ***first 30 minutes*** (Figures 9.20: II & III).

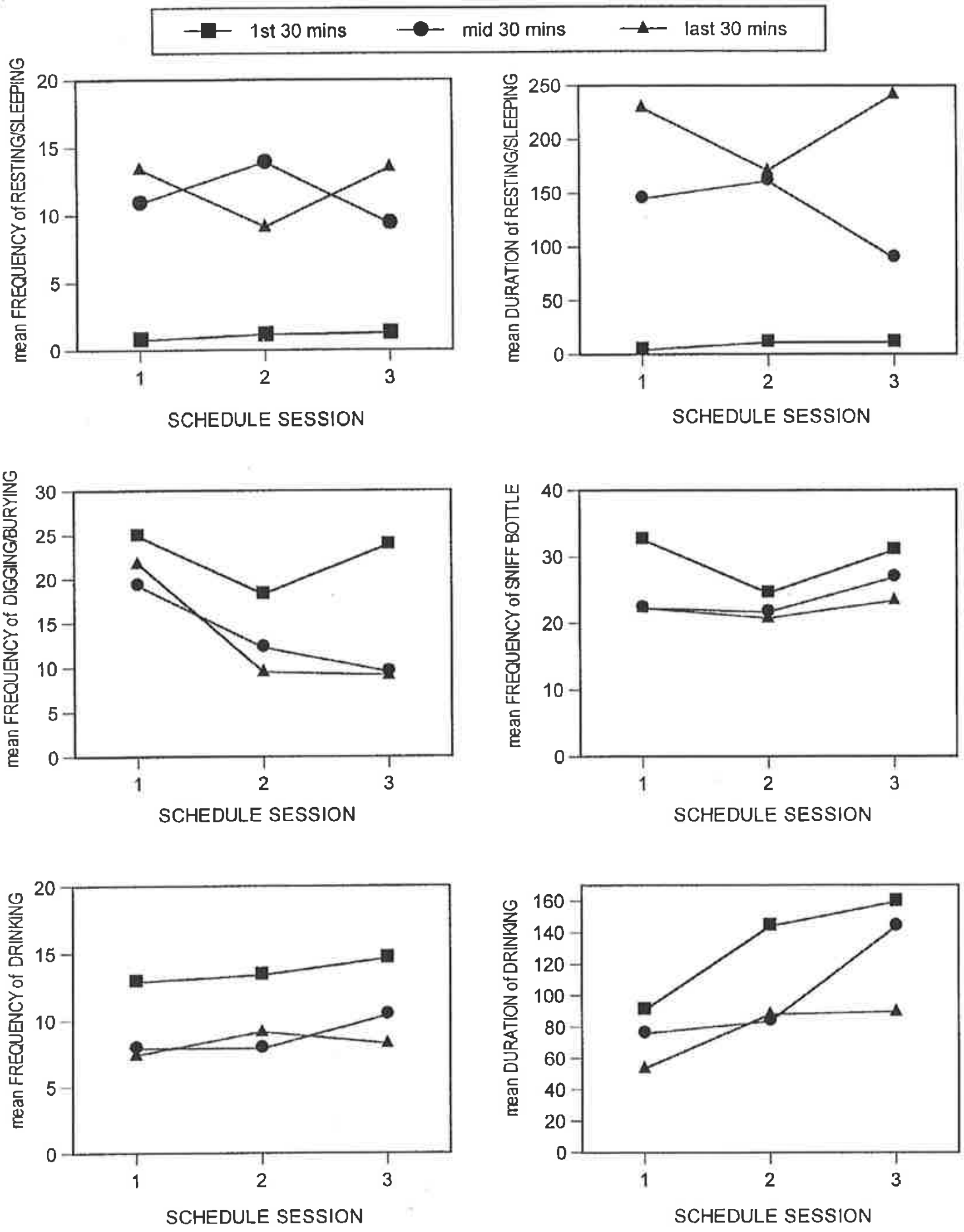


Figure 9.20 (II). Mean frequency and duration of behaviours for the "part of session" grouping variable during ***fixed-interval*** sessions (top- frequency & duration of ***resting/sleeping***, middle- frequency of ***digging/burying*** & ***sniff bottle***, & bottom- frequency & duration of ***drinking***)

Table 9.26

Experiment 3 significance levels obtained for measures of behavioural categories during the three ***fixed-interval*** sessions (***part of session*** effect).

Variable	***F*(2,12)**	**Significance level (*p*)**
Frequency of ***resting/sleeping***	5.41	<.05
Duration of ***resting/sleeping***	5.35	<.05
Frequency of ***digging/burying***	6.21	<.05
Frequency of ***sniff bottle***	8.89	<.005
Frequency of ***drinking***	7.08	<.01
Duration of ***drinking***	6.26	<.05
Duration of ***displacement***	9.10	<.005
Frequency of ***sniff and touch object***	10.84	<.005
Frequency of ***sniff object***	10.76	<.005
Duration of ***sniff object***	4.36	<.05

Note. Objects were only present in the FIOS group during ***fixed-interval*** sessions

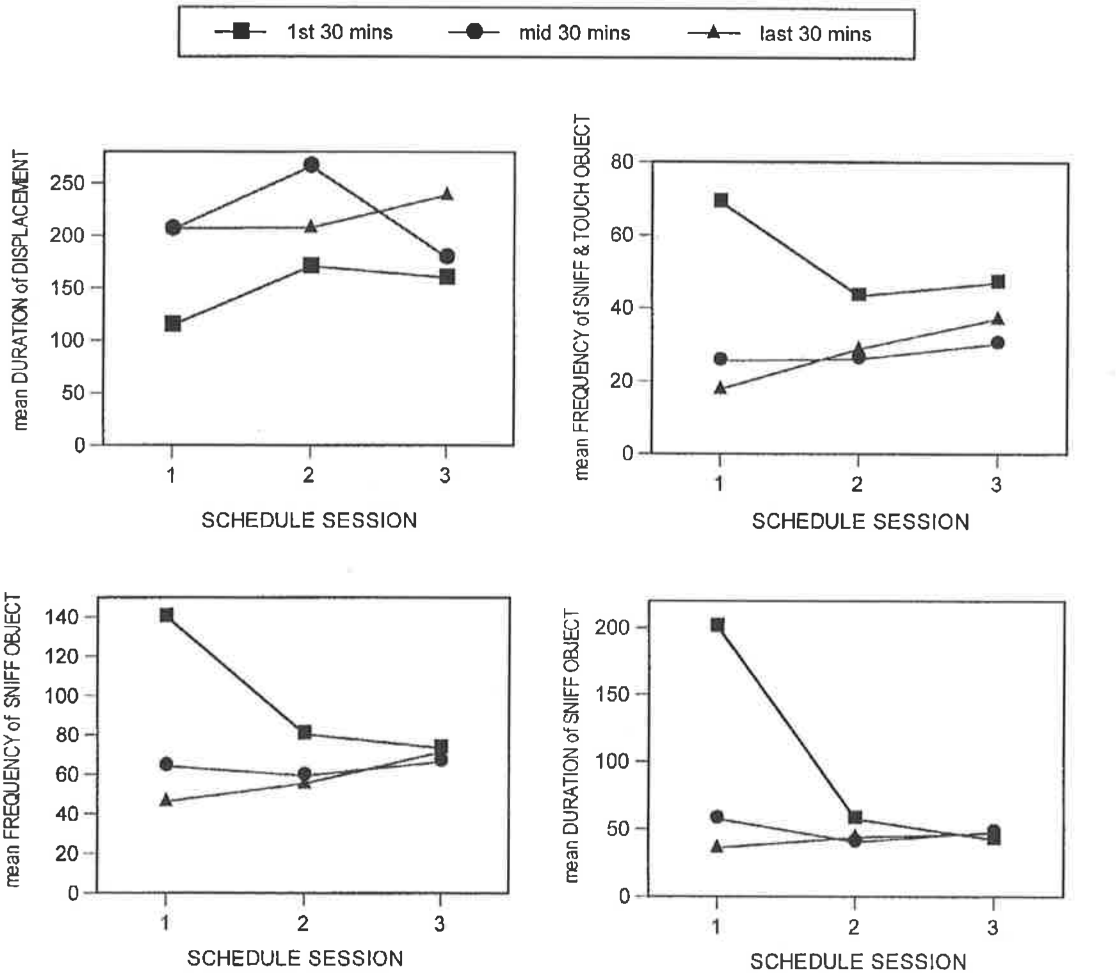


Figure 9.20 (III). Mean frequency and duration of behaviours for the "part of session" grouping variable during ***fixed-interval*** sessions (top- duration of ***displacement*** & frequency of ***sniff & touch object*** [for the FIOS group], & bottom- frequency & duration of ***sniff object*** for the FIOS group)

For the ***middle*** and ***last 30 minutes***, there was a slight increase over ***fixed-interval*** sessions for the frequency of ***sniff bottle***, ***drinking***, ***sniff and touch object*** and ***sniff object***, and a more marked increase for duration of ***drinking*** (Figures 9.20: II & III). By contrast, a decrease over sessions was observed for the ***middle*** and ***last 30 minutes*** for frequency of ***digging/burying*** (Figure 9.20: II). Duration of ***sniff object*** showed a slight decrease for the ***middle 30 minutes***, and a slight increase for the ***last 30 minutes*** over the ***fixed-interval*** sessions (Figure 9.20: III).

Object x part of session interaction effect

The MANOVA for the frequency of ***propping*** yielded a statistically significant ***object*** x ***part of session*** interaction [*F* (2,12)=4.38, *p*<.05]. This means that the frequency of ***propping*** was *jointly* affected by the object (objects present or absent) *and* part of session (***first***, ***middle*** or ***last 30 minutes***) grouping variables during ***fixed-interval*** sessions. As Figure 9.20 (IV) indicates, frequency of ***propping*** decreased over sessions for the FIOE group, but showed a slight overall increase for the FIOS group. Overall, a decrease was observed during the ***first*** (almost negligible) and ***middle 30 minutes***, whilst a slight increase in frequency of ***propping*** occurred over the three sessions for the ***last 30 minutes***.

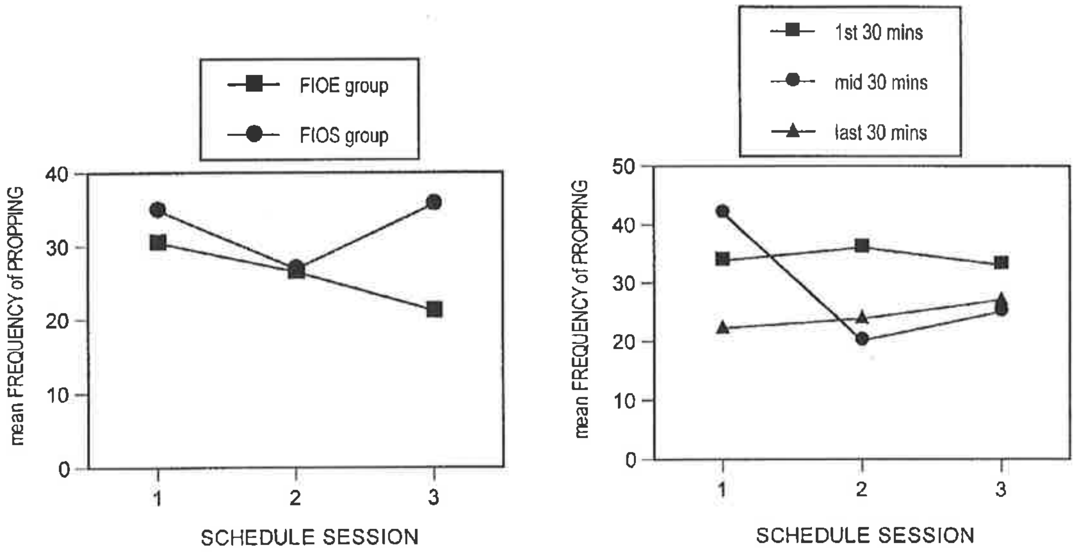


Figure 9.20 (IV). Mean frequency of ***propping*** was jointly affected by the "object" (left) and "part of session" (right) grouping variables during ***fixed-interval*** sessions

Object x session interaction effect

A statistically significant ***object*** x ***session*** interaction was found for the frequency of ***displacement*** [*F* (2,12)=4.72, *p*<.05]. In this instance, the frequency of ***displacement*** was *jointly* affected by object (objects present or absent) *and* session grouping variables during ***fixed-interval*** sessions. Visual inspection of Figure 9.20 (V) shows that there was a slight overall decrease in this measure over ***fixed-interval*** sessions. For the FIOE group there was a gradual (almost negligible) decrease in every session, whereas there was an increase in session 2 (overall slight decrease).

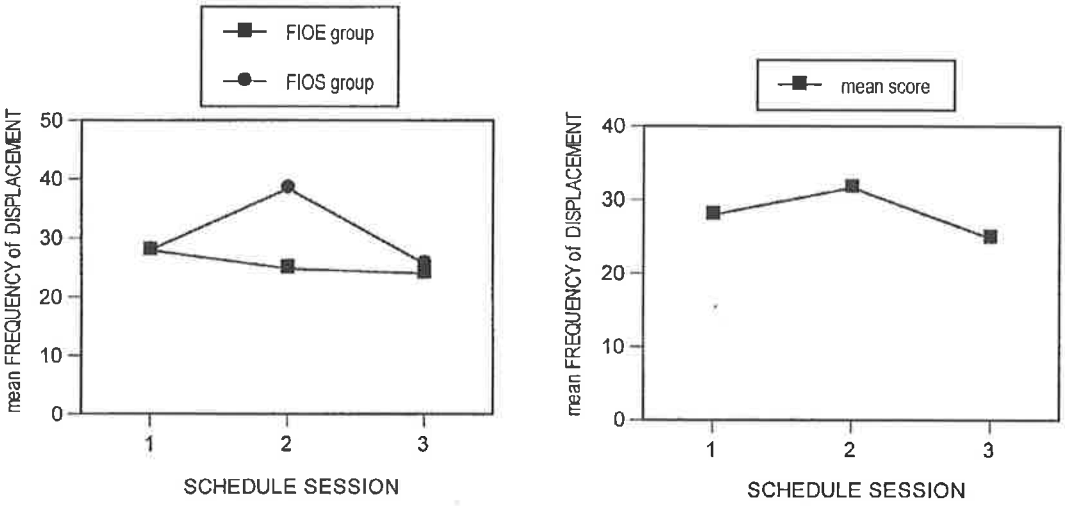


Figure 9.20 (V). Mean frequency of ***displacement*** was jointly affected by the "object" (left) and "session" (right) grouping variables during ***fixed-interval*** sessions

9.3.7.2 EXTINCTION SESSIONS

Main effect of *session*

The differences between ***extinction*** sessions were statistically significant for measures of two behavioural categories. That is, the session number affected the frequency of ***bar-related behaviour*** [F (2,12)=18.80, p<.0001], frequency of ***propping*** [F (2,12)=4.40, p<.05] and duration of ***propping*** [F (2,12)=6.77, p<.05]. As Figure 9.21 (I) indicates, the frequency of ***bar-related behaviour*** decreased steadily over sessions, whereas the frequency of ***propping*** increased.

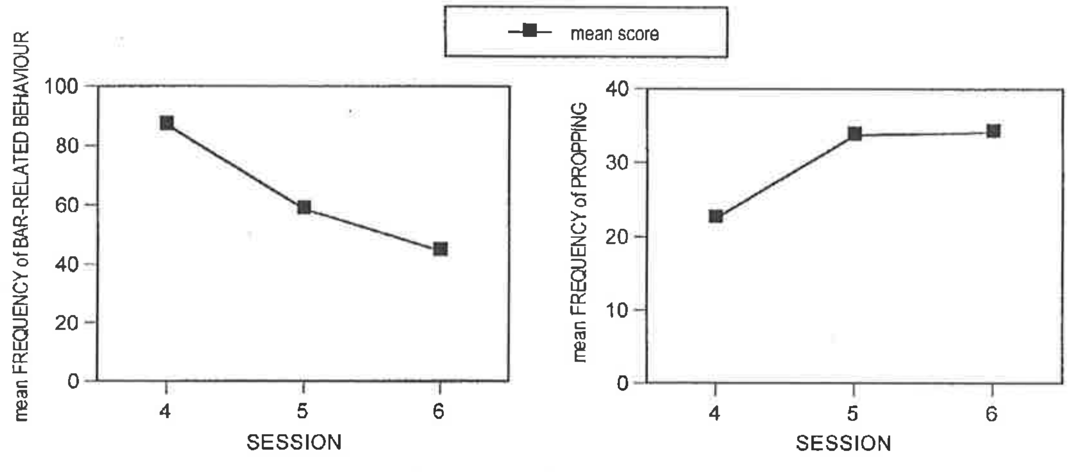


Figure 9.21 (I). The "session" grouping variable affected the mean frequency of ***bar-related behaviour*** (left) and ***propping*** (right) during ***extinction***

Main effect of *part of session*

A statistically significant main effect of ***part of session*** was found for measures of seven behavioural categories during ***extinction*** sessions (Table 9.27). That is, the part of session (***first***, ***middle*** or ***last 30 minutes***) affected a number of behaviours, excluding ***bar-related behaviour***, ***bar-pressing***, ***propping***, ***sniff object***, ***sniff and touch object***, and ***sniff bottle***.

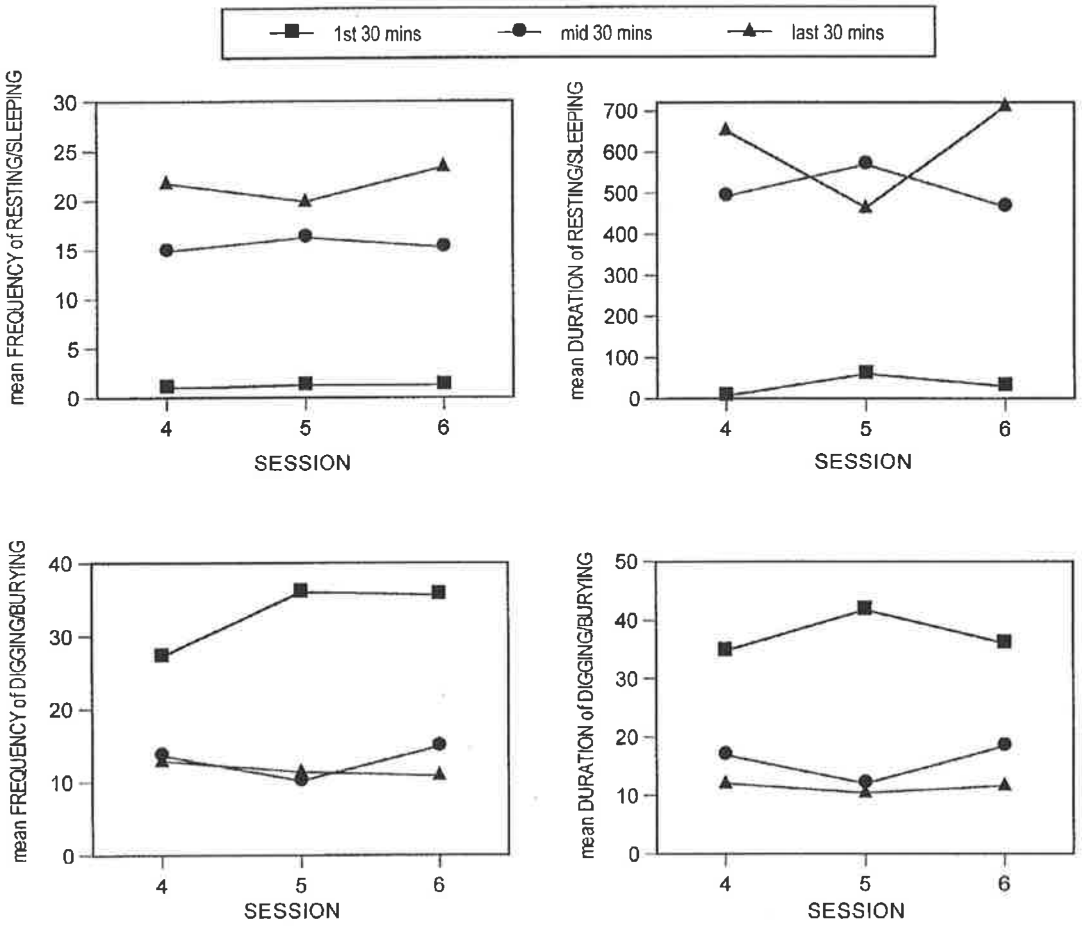


Figure 9.21 (II). Mean frequency (left) and duration (right) of behaviours for the "part of session" grouping variable during ***extinction*** (top- ***resting/sleeping***, & bottom- ***digging/burying***)

Figures 9.21 (II) and (III) show the effect of ***part of session*** on the various measures. The frequency and duration of ***resting/sleeping*** was almost negligible for the ***first 30 minutes*** of each ***extinction*** session (with a minimal increase over sessions). There was little overall change over sessions during the ***middle 30 minutes*** of each session whilst slight overall increases occurred during the ***last 30 minutes*** (Figure 9.21:II).

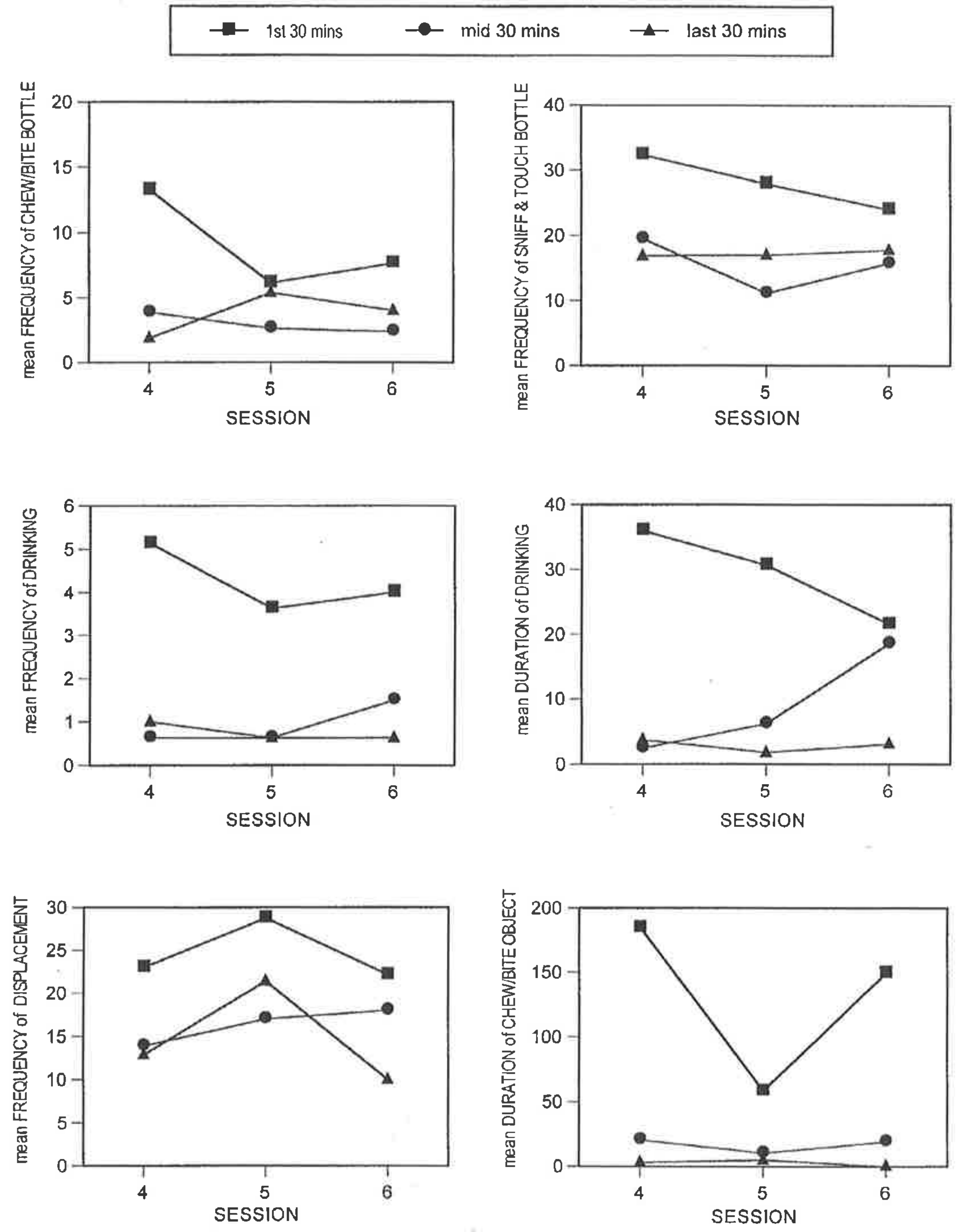


Figure 9.21 (III). Mean frequency (left) and duration (right) of behaviours for the "part of session" grouping variable during ***extinction*** (top- frequency of ***chew/bite bottle*** & ***sniff & touch bottle***, middle- frequency & duration of ***drinking***, & bottom- frequency of ***displacement*** & duration of ***chew/bite object***)

Table 9.27

Experiment 3 significance levels obtained for measures of behavioural categories during the three ***extinction*** sessions (***part of session*** effect).

Variable	*F*(2,12)	**Significance level (*p*)**
Frequency of ***resting/sleeping***	15.13	=.001
Duration of ***resting/sleeping***	15.29	=.001
Frequency of ***digging/burying***	17.61	<.0001
Duration of ***digging/burying***	9.05	<.005
Frequency of ***chew/bite bottle***	4.73	<.05
Frequency of ***sniff and touch bottle***	15.76	<.0001
Frequency of ***drinking***	13.47	=.001
Duration of ***drinking***	5.48	<.05
Frequency of ***displacement***	6.95	=.01
Duration of ***chew/bite object***	14.23	=.001

Note. Objects were only present in the FIOS group during ***fixed-interval*** sessions

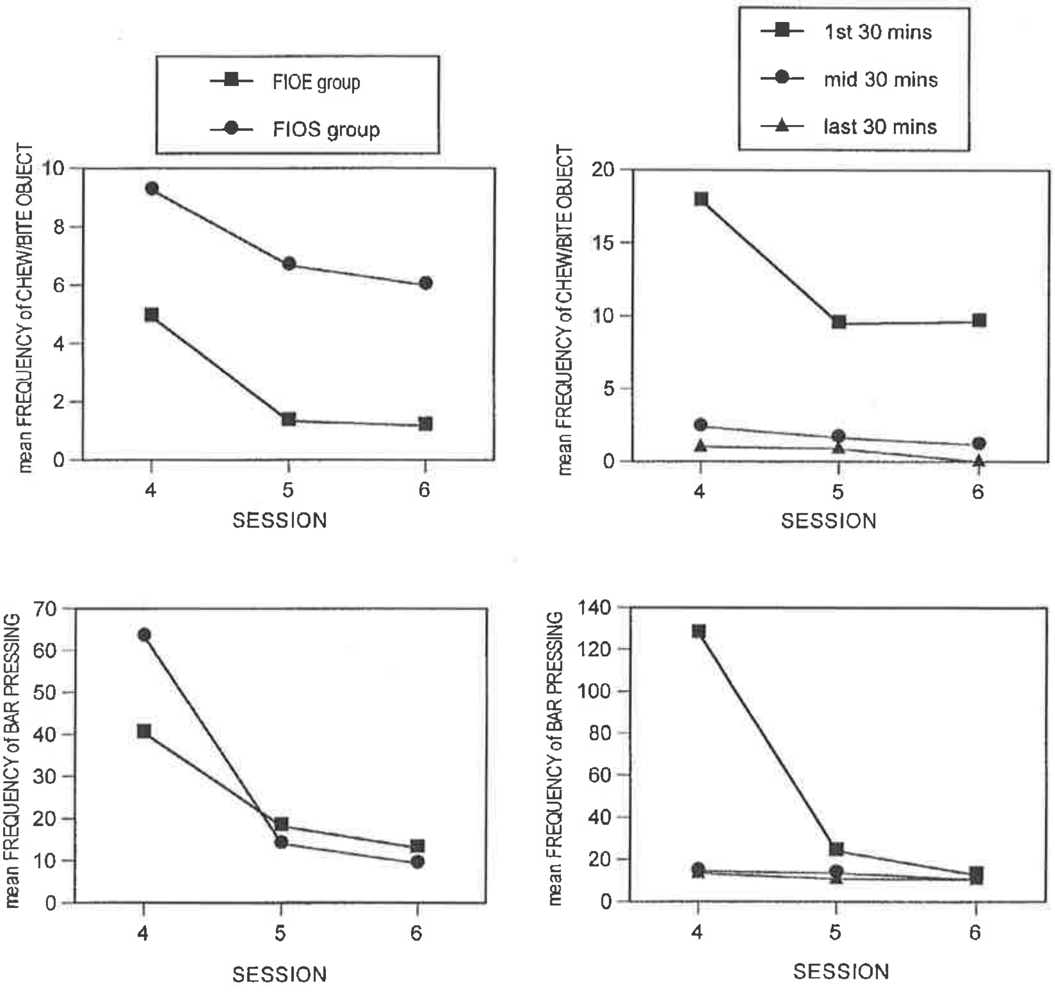
The highest mean scores for frequency and duration of ***digging/burying***, ***drinking***, and frequency of ***chew/bite bottle***, ***sniff and touch bottle***, ***displacement*** and duration of ***chew/bite object*** occurred during the ***first 30 minutes*** of each ***extinction*** session. For the ***first*** and ***middle 30 minutes***, there was a small overall increase in frequency and duration of ***digging/burying*** over sessions, whereas there was virtually no change for the ***last 30 minutes*** (Figure 9.21:II).

Over ***extinction***, the frequency and duration of ***drinking*** and the frequency of ***displacement*** decreased during the ***first*** and ***last 30 minutes***. By contrast, these measures increased during the ***middle 30 minutes*** (Figure 9.21:III). The frequency of ***chew/bite bottle*** and ***sniff and touch bottle*** decreased over sessions for the ***first*** and ***middle 30 minutes***, whereas the scores showed a minimal overall increase during the ***last 30 minutes*** (Figure 9.21:III). Over ***extinction***, duration of ***chew/bite object*** decreased overall during the ***first 30 minutes*** of each session (with a dramatic decrease in session 5). Little change occurred during the latter parts of session, with virtually no time spent engaged in this behaviour during the ***last 30 minutes*** of each session (Figure 9.21:III).

Object x part of session interaction effect

A statistically significant ***object*** x ***part of session*** interaction was found for the frequency of ***chew/bite object*** [*F* (2,12)=8.39, *p*=.005] and the frequency of ***bar pressing*** [*F* (2,12)=4.18, *p*<.05]. Thus, these two frequency measures were *jointly* affected by object (objects present or absent) *and* part of session (***first***, ***middle*** or ***last 30 minutes***) grouping variables during

extinction sessions. Figure 9.21 (IV) shows that for both groups the frequency of ***chew/bite object*** decreased over ***extinction***. However, more bouts of this behaviour occurred in the FIOS group. Although this measure decreased for all three parts of session, the number of bouts was higher during the ***first 30 minutes*** of each session, and the decrease was more noticeable for this part of session. In fact, there were very few bouts of ***chew/bite object*** during the latter parts of each session. Visual inspection of Figure 9.21 (IV) illustrates that a noticeable decrease in frequency of ***bar pressing*** over extinction occurred for both groups. This decrease was more dramatic for the FIOS group. This decrease in ***bar pressing*** was most noticeable during the ***first 30 minutes***, particularly in session 2. Only few ***bar presses*** took place during the ***middle*** and ***last 30 minutes***, and there was little change over the three ***extinction*** sessions.



<u>**Figure 9.21 (IV).**</u> Mean frequency of ***chew/bite object*** (top) and ***bar pressing*** (bottom) were jointly affected by the "object" (left) and "part of session" (right) grouping variables during ***extinction***

<u>***Object x session*** **interaction effect**</u>

The MANOVA for the frequency of ***drinking*** yielded a statistically significant ***object*** x ***session*** interaction [F (2,12)=4.75, p<.05]. This means that the frequency of ***drinking*** was *jointly* affected by the object (objects present or absent) *and* session grouping variables during

extinction sessions. Although there was a slight overall decrease in this measure over ***extinction***, frequency of ***drinking*** actually increased slightly for the FIOS group (Figure 9.21:V). However, it should be noted that there were very few bouts of ***drinking*** during ***extinction***.

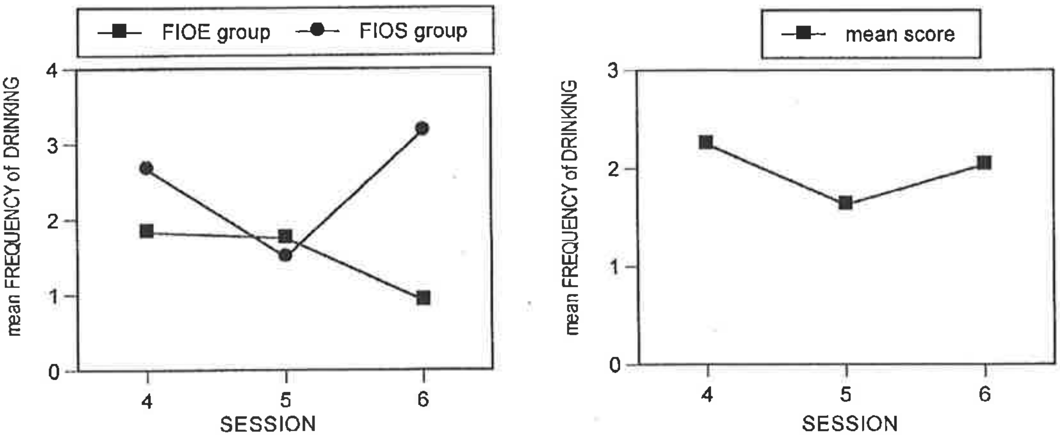


Figure 9.21 (V). Mean frequency of ***drinking*** was jointly affected by the "object" (left) and "session" (right) grouping variables during ***extinction***

Part of session x session **interaction effect**

As can be seen in Table 9.28, statistically significant ***part of session*** x ***session*** interactions were found for five frequency and one duration measure of behaviour. Thus, the frequency of the three ***object-directed behaviours***, ***sniff bottle*** and the frequency and duration of ***bar pressing*** were *jointly* affected by part of session (***first***, ***middle*** or ***last 30 minutes***) *and* session grouping variables during ***extinction***. As shown in Figures 9.21 (VI) and (VII), frequency and duration of ***bar pressing***, frequency of ***sniff bottle***, and the three frequency measures of ***object-directed behaviours*** decreased over ***extinction***. For all these measures, this decrease was most dramatic during the ***first 30 minutes*** of each session. Further, the mean scores were highest during this early part of each session. There was little change in these measures during the latter parts of session, and little difference in scores between the ***middle*** and ***last 30 minutes*** of each session.

Table 9.28
Experiment 3 significance levels obtained for measures of behavioural categories during the three ***extinction*** sessions (***part of session*** x ***session*** effect).

Variable	*F*(4,24)	**Significance level (*p*)**
Frequency of ***sniff bottle***	5.99	<.005
Frequency of ***chew/bite object***	3.75	<.05
Frequency of ***sniff and touch object***	9.07	<.0001
Frequency of ***sniff object***	5.83	<.005
Frequency of ***bar pressing***	29.47	<.0001
Duration of ***bar pressing***	27.15	<.0001

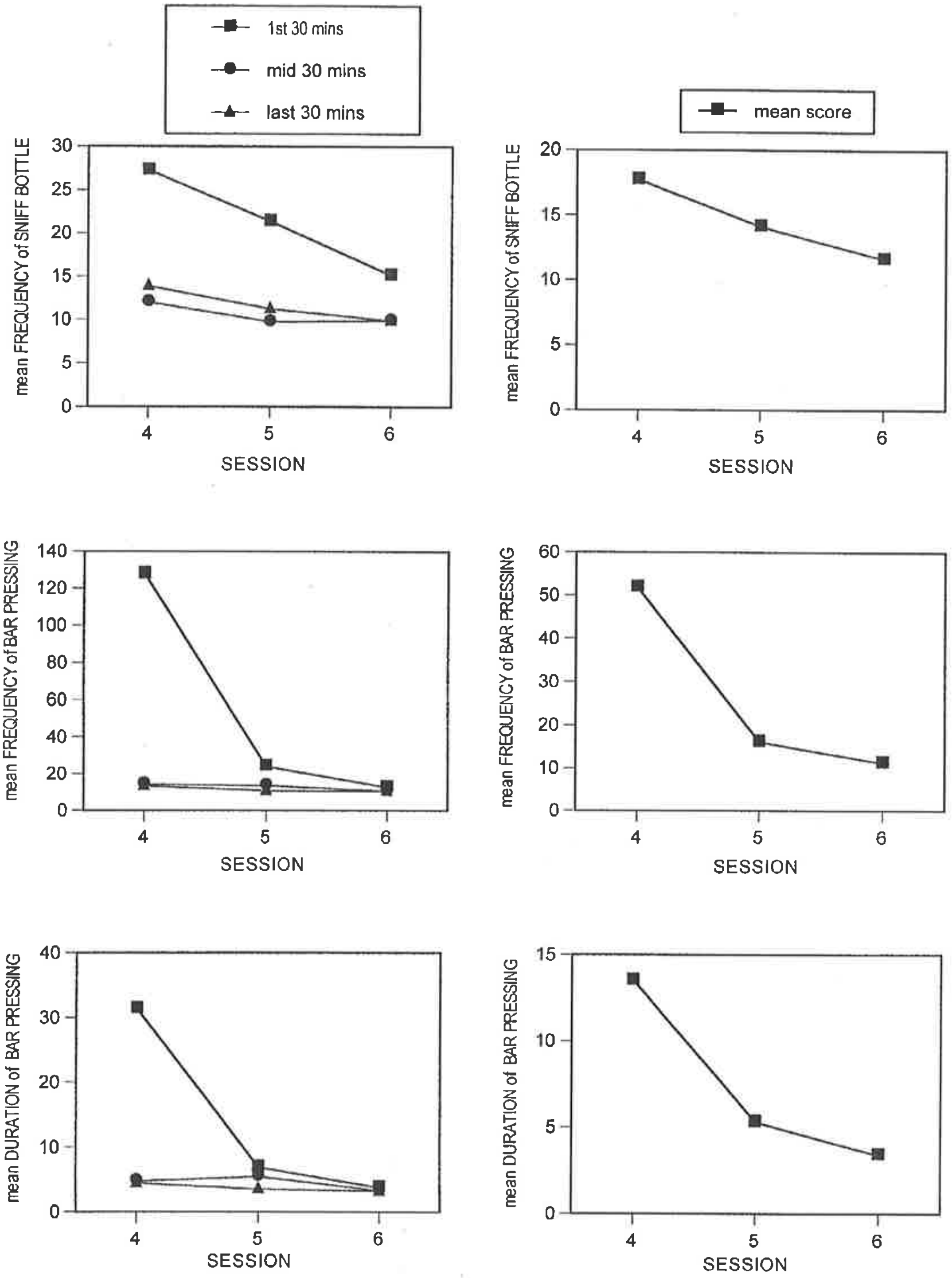
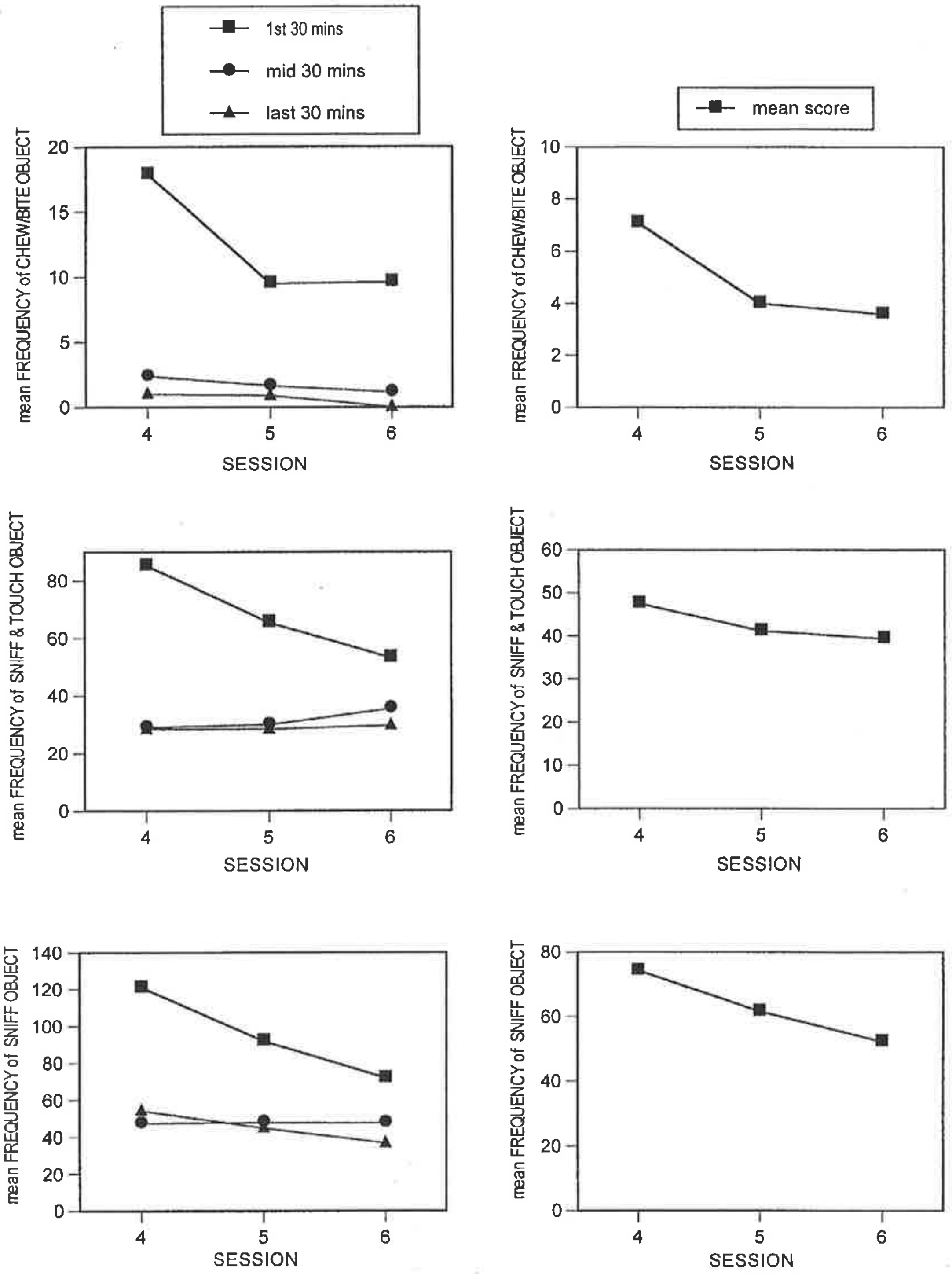


Figure 9.21 (VI). Mean frequency and duration of behaviours jointly affected by the "part of session" (left) and "session" (right) grouping variables during ***extinction*** (top- frequency of ***sniff bottle***, middle- frequency of ***bar pressing***, & bottom- duration of ***bar pressing***)



<u>Figure 9.21 (VII).</u> Mean frequency of behaviours jointly affected by the "part of session" (left) and "session" (right) grouping variables during ***extinction*** (top- ***chew/bite object***, middle- ***sniff & touch object***, & bottom- ***sniff object***)

9.3.7.3 ALL SIX SESSIONS

Main effect of *session*

The differences between sessions were statistically significant for a number of measures (Table 9.29). That is, the session number affected measures of six behavioural categories, namely the frequency and duration of ***drinking***, ***displacement***, ***bar-related behaviour*** and ***bar pressing***, as well as the frequency of ***sniff bottle*** and duration of ***propping***. Figures 9.22 (I) and (II) show the direction of these effects.

The frequency and duration of ***drinking*** increased steadily over ***fixed-interval*** sessions, dropped sharply in the first ***extinction*** session, and then showed little change over ***extinction*** (Figure 9.22:I). Overall there was a noticeable decrease over the six sessions. As shown in Figure 9.22 (I), frequency of ***displacement*** decreased over ***fixed-interval*** sessions, continued to drop in the first ***extinction*** session, and then increased slightly over ***extinction***. By contrast, duration of ***displacement*** increased slightly over ***fixed-interval*** sessions, and continued to increase in the first and subsequent ***extinction*** sessions. Overall, fewer bouts of ***displacement*** occurred over the six sessions, but more time was actually spent engaged in this behaviour (*i.e.*, fewer bouts, but of longer duration).

Table 9.29
Experiment 3 significance levels obtained for measures of behavioural categories during all six sessions (***session*** effect).

Variable	***F*(5,30)**	**Significance level (*p*)**
Frequency of ***sniff bottle***	9.14	<.0001
Frequency of ***drinking***	7.66	<.0001
Duration of ***drinking***	12.20	<.0001
Duration of ***propping***	3.22	<.05
Frequency of ***displacement***	5.94	=.001
Duration of ***displacement***	2.60	<.05
Frequency of ***bar-related behaviour***	15.58	<.0001
Duration of ***bar-related behaviour***	3.37	<.05
Frequency of ***bar pressing***	34.79	<.0001
Duration of ***bar pressing***	12.14	<.0001

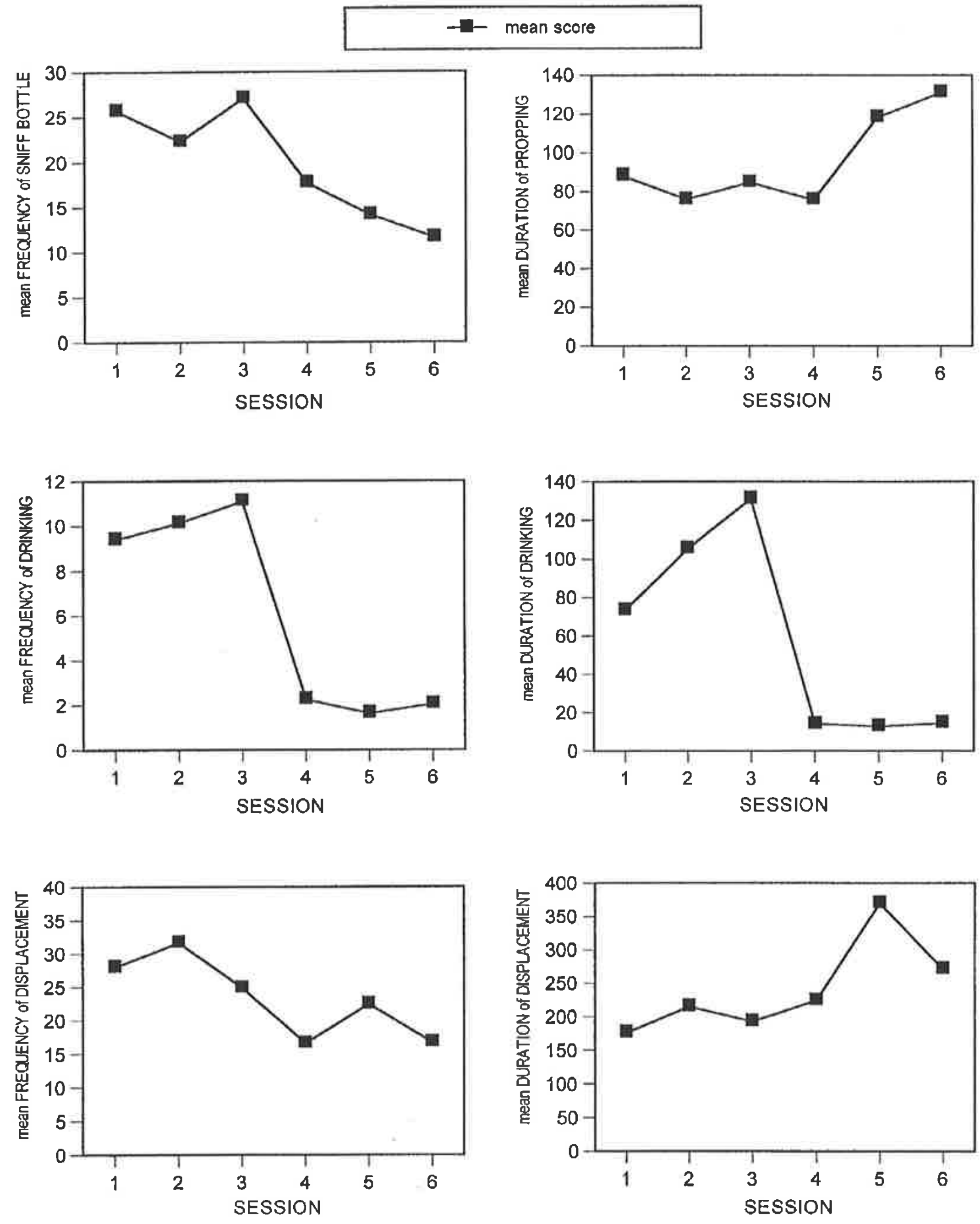


Figure 9.22 (I). Mean frequency and duration of behaviours for the "session" grouping variable over the six sessions (top- frequency of ***sniff bottle*** & duration of ***propping***, middle- frequency & duration of ***drinking***, & bottom- frequency & duration of ***displacement***)

Visual inspection of Figure 9.22 (I) shows that frequency of ***sniff bottle*** increased slightly over ***fixed-interval*** sessions, dropped in the first ***extinction*** session, and then continued to decrease over the remaining sessions. Overall, there was a decrease in this measure over the six sessions. Duration of ***propping*** decreased marginally over ***fixed-interval*** sessions, decreased slightly in the first ***extinction*** session, and then increased steadily over ***extinction***. Overall, there was a noticeable increase in the time spent ***propping*** over the six sessions.

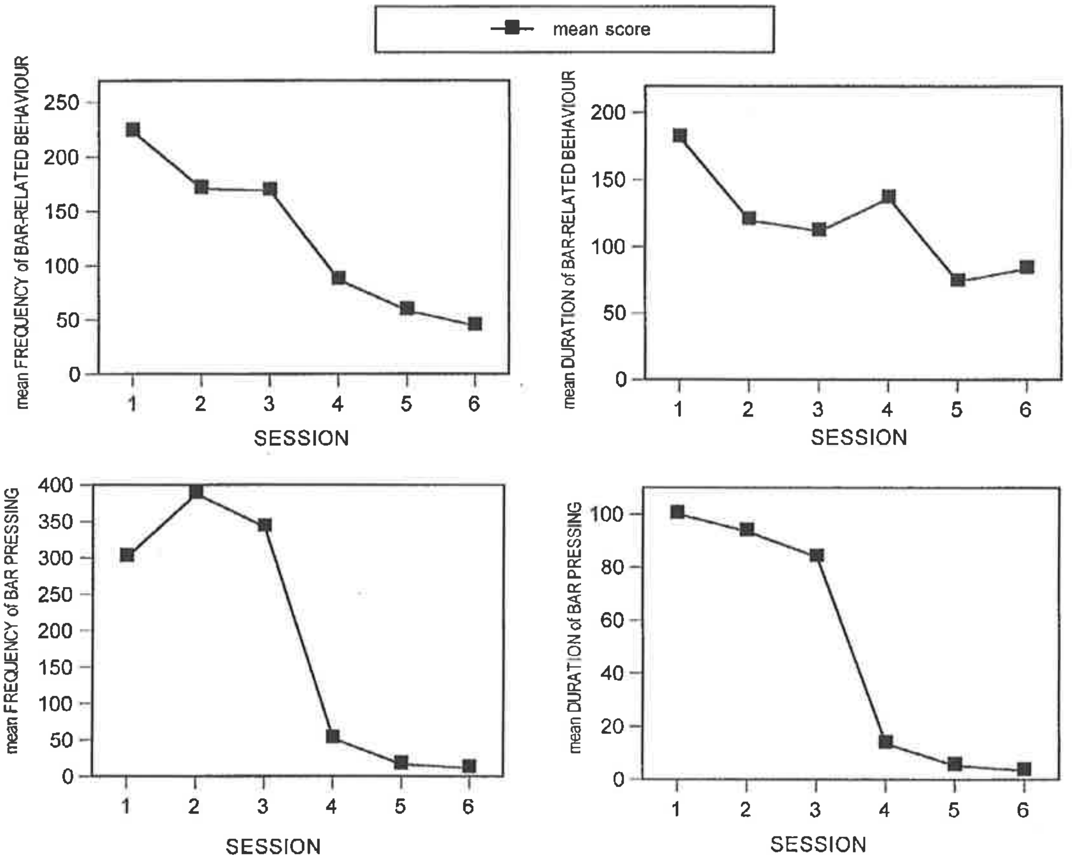


Figure 9.22 (II). Mean frequency (left) and duration (right) of behaviours for the "session" grouping variable over the six sessions (top- ***bar-related behaviour***, & bottom- ***bar pressing***)

As illustrated in Figure 9.22 (II), frequency and duration of ***bar pressing*** decreased over the six sessions. However, whilst both measures of this behaviour dropped sharply in the first ***extinction*** session, and then continued to decrease over ***extinction***, the frequency increased over ***fixed-interval*** sessions, whereas the duration decreased over these same sessions. That is, more ***bar presses*** occurred, but they were of a shorter duration during ***fixed-interval*** sessions. Frequency and duration of ***bar-related behaviour*** also showed an overall decrease over the six sessions. Both measures decreased over ***fixed-interval*** sessions, and decreased over ***extinction***. However, frequency of ***bar-related behaviour*** decreased quite sharply in the first ***extinction*** session, whereas duration increased. That is, there were fewer bouts of this behaviour, but the bouts were of a longer duration.

Main effect of *part of session*

A statistically significant main effect of ***part of session*** was found for measures of seven behavioural categories over the six sessions (Table 9.30). That is, the part of session (***first***, ***middle*** or ***last 30 minutes***) affected a number of behaviours, excluding ***bar pressing***, ***propping***, ***chew/bite bottle***, and the three ***object-directed behaviours***.

Although the pattern of change for frequency and duration of ***drinking*** over sessions is similar for all three parts of session, the mean scores are highest for the ***first 30 minutes*** of each session (Figure 9.22: IV). Very few bouts of this behaviour occurred during the ***middle*** and ***last 30 minutes*** of ***extinction***. All three parts of session show an overall increase in these measures over ***fixed-interval*** sessions, a sharp decrease in the first ***extinction*** session, and little change over subsequent ***extinction*** sessions.

The rats also directed more bouts of ***sniffing*** or ***sniffing and touching*** towards the bottle during the ***first 30 minutes*** of each session, although there was an overall decrease in these measures over the six sessions (Figure 9.22:IV). Frequency of ***sniff and touch bottle*** increased slightly over ***fixed-interval*** sessions, and dropped in the first ***extinction*** session for all three parts of session. This measure continued to decrease over ***extinction*** during the ***first*** and ***middle 30 minutes***, whereas it showed little change during the ***last 30 minutes***. Frequency of ***sniff bottle*** decreased slightly over ***fixed-interval*** sessions during the ***first 30 minutes***, whereas it showed a slight overall increase across these sessions for the latter parts of session. This measure dropped in the first ***extinction*** sessions, and continued to decrease over the remaining sessions for all three parts of session.

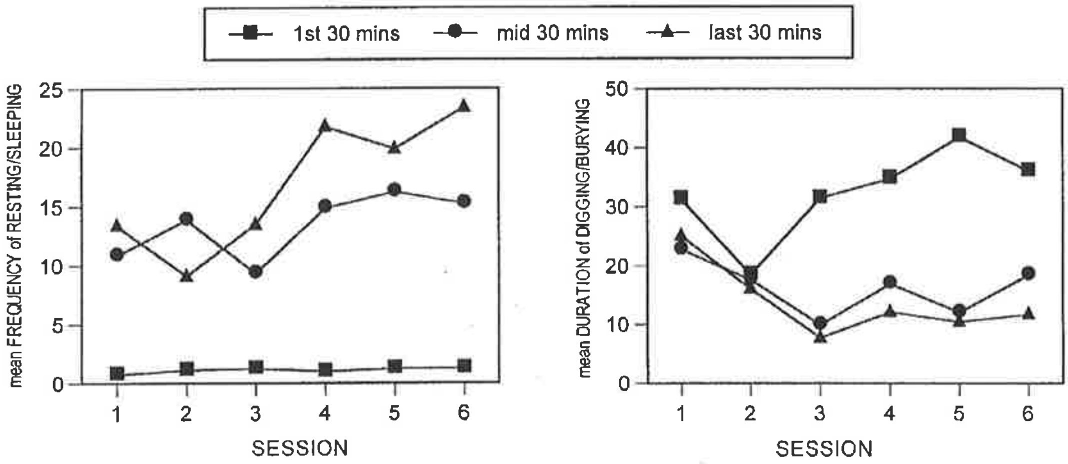


Figure 9.22 (III). The "part of session" grouping variable affected the mean frequency of ***resting/sleeping*** (left) and duration of ***digging/burying*** (right) over the six sessions

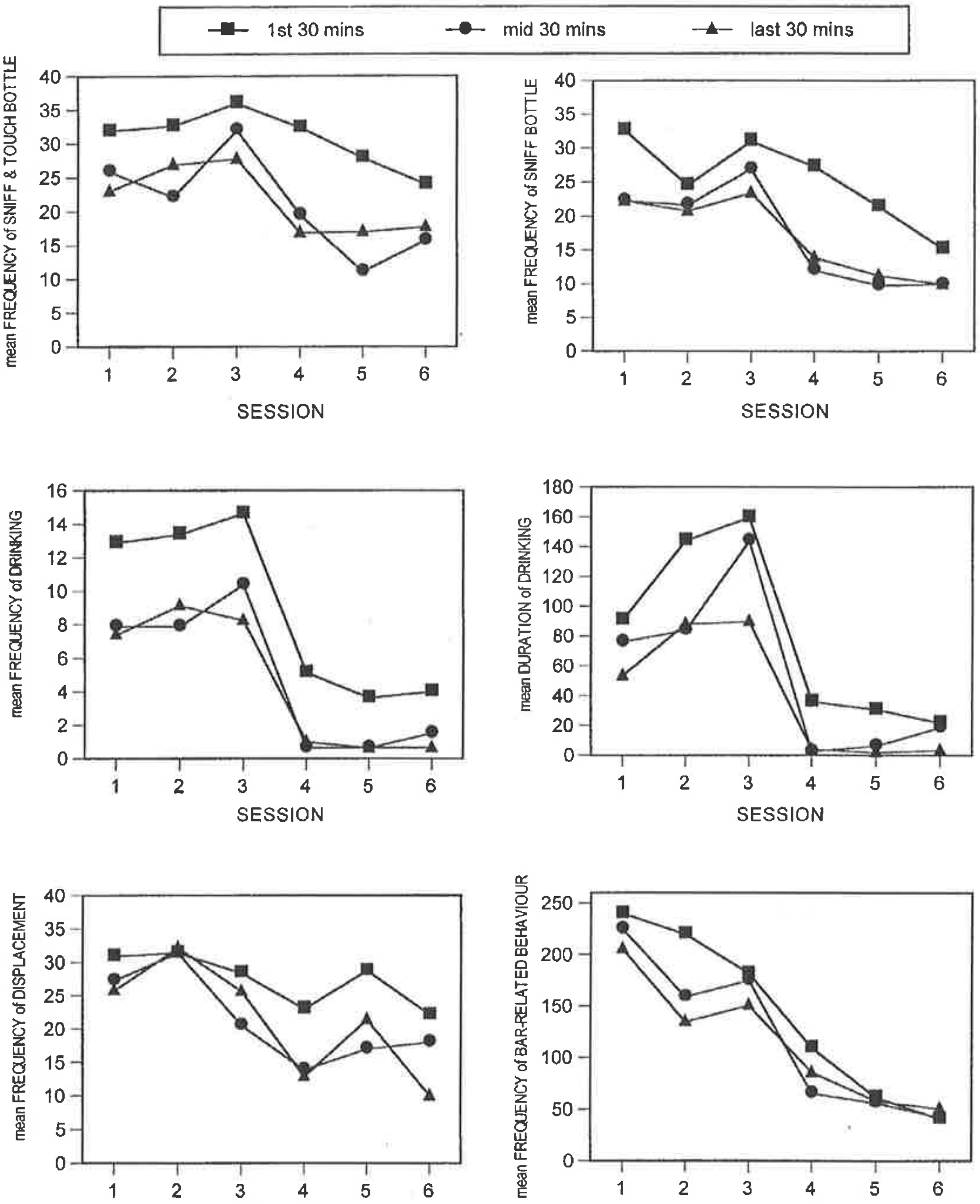


Figure 9.22 (IV). Mean frequency and duration of behaviours for the "part of session" grouping variable over the six sessions (top- frequency of ***sniff & touch bottle*** & ***sniff bottle***, middle- frequency & duration of ***drinking***, & bottom- frequency of ***displacement*** & ***bar-related behaviour***)

Figure 9.22 (III) indicates that frequency of ***resting/sleeping*** shows an overall increase across the six sessions for the ***middle*** and ***last 30 minutes***. For these latter parts of sessions, there is a slight overall decrease over ***fixed-interval*** sessions, an increase in the first ***extinction*** sessions, and further increases over the remaining sessions. However, during the ***first 30 minutes*** there were only very few bouts of ***resting/sleeping***, irrespective of session or schedule (***fixed-interval*** or ***extinction***).

For the frequency of ***displacement*** and ***bar-related behaviour***, as well as the duration of ***digging/burying***, the mean scores were usually highest for the ***first 30 minutes*** of each session (Figures 9.22: III & IV). Whilst the duration of ***digging/burying*** showed an overall increase over the six sessions for the ***first 30 minutes***, the measure during the latter parts of session decreased overall (Figure 9.22:III). This measure showed little change over ***fixed-interval*** sessions for the ***first 30 minutes*** (although it dropped in session 2), but decreased steadily during the latter parts of session. Duration of ***digging/burying*** then increased slightly in the first ***extinction*** session, and then showed little change over ***extinction*** for all three parts of session. Frequency of ***bar-related behaviour*** showed a similar pattern for all three parts of session (Figure 9.22:IV). It decreased over ***fixed-interval*** sessions, dropped noticeably during the first ***extinction*** session, and then continued to decrease over the remaining sessions. Frequency of ***displacement*** decreased slightly across ***fixed-interval*** sessions, decreased in the first ***extinction*** session, and then increased in the second ***extinction*** session for all three parts of session (Figure 9.22:IV). Overall, there was a slight decrease over ***extinction*** for the ***first*** and ***last 30 minutes***.

Table 9.30
Experiment 3 significance levels obtained for measures of behavioural categories during all six sessions (***part of session*** effect).

Variable	***F*(2,12)**	**Significance level (*p*)**
Frequency of ***resting/sleeping***	13.50	=.001
Duration of ***digging/burying***	8.87	<.005
Frequency of ***sniff and touch bottle***	15.41	<.0001
Frequency of ***sniff bottle***	24.91	<.0001
Frequency of ***drinking***	12.36	=.001
Duration of ***drinking***	7.19	<.01
Frequency of ***displacement***	6.95	=.01
Frequency of ***bar-related behaviour***	3.97	<.05

Note. Objects were only present in the FIOS group during ***fixed-interval*** sessions

Object x part of session interaction effect

A statistically significant ***object*** x ***part of session*** interaction was found for two frequency measures of behaviour. The frequency of ***digging/burying*** [*F* (2,12)=7.13, *p*<.01] and the frequency of ***chew/bite object*** [*F* (2,12)=10.50, *p*<.005] were *jointly* affected by object (objects first present during ***fixed-interval*** or ***extinction*** sessions) *and* part of session (***first***, ***middle*** or ***last 30 minutes***) grouping variables over the six sessions.

Figure 9.22 (V) shows that in five of the six sessions, the frequency of ***digging/burying*** was highest for the FIOE group. The difference between the groups was most obvious during the ***fixed-interval*** sessions. Frequency of ***digging/burying*** was highest if objects were absent during these sessions, and the measure decreased most noticeably in this group (FIOE) in the second session. Overall, this measure decreased over the six sessions in the FIOE group, whereas it increased for the FIOS group. Over ***fixed-interval*** sessions, there was little change for the FIOS group. The frequency of ***digging/burying*** increased in the first ***extinction*** session in both groups, and then showed a slight overall increase over the remaining sessions for both groups.

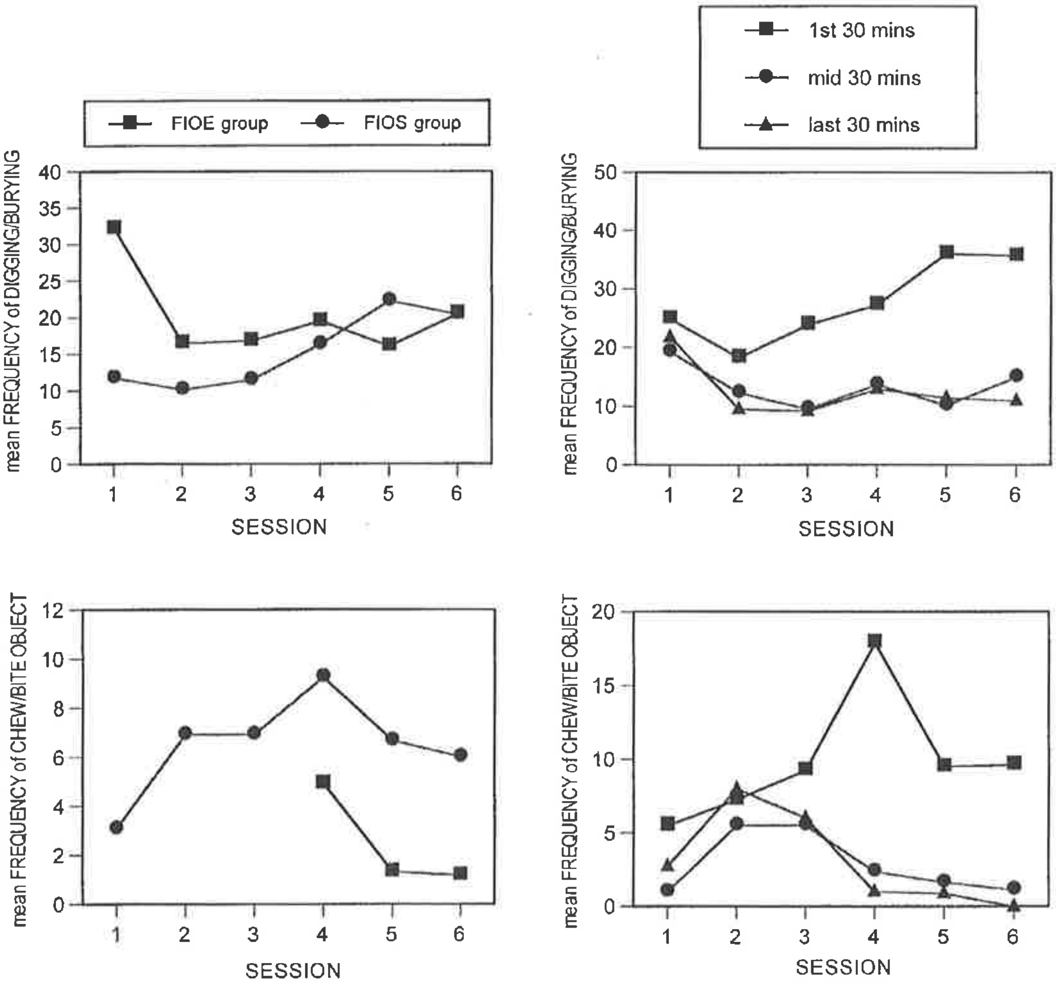


Figure 9.22 (V). Mean frequency of ***digging/burying*** (top) and duration of ***chew/bite object*** (bottom) were jointly affected by the "object" (left) and "part of session" (right) grouping variables over the six sessions

Visual inspection of Figure 9.22 (V) indicates that the frequency of ***digging/burying*** was highest during the ***first 30 minutes*** of every session. The mean scores were similar in every session during the ***middle*** and ***last 30 minutes***. During ***fixed-interval*** sessions, this measure decreased overall (more steadily during the latter parts of sessions), and there was an increase in the first ***extinction*** session for all parts of session. Frequency of ***digging/burying*** continued to increase over ***extinction*** during the ***first 30 minutes***, increased slightly during the ***middle 30 minutes***, and showed little change during the ***last 30 minutes***. Overall, there was an increase over the six sessions for the ***first 30 minutes***, whereas a decrease was noted for the latter parts of session.

For the FIOS group, the frequency of ***chew/bite object*** increased over ***fixed-interval*** sessions, and then increased again in the first ***extinction*** session (Figure 9.22:V). Both groups showed a decrease in this measure over ***extinction***, although the scores were highest for the FIOS group in every session. The frequency of ***chew/bite object*** was greatest in five of the six sessions during the ***first 30 minutes***. Overall, there was a slight increase over the six sessions for the ***first 30 minutes***, whereas there was a minimal decrease for the latter parts of session. Over ***fixed-interval*** sessions, there was a slight increase for all three parts of session. By contrast, there was a decrease for all parts of session over ***extinction*** (more marked for the ***first 30 minutes***). However, in the first ***extinction*** session, frequency of ***chew/bite object*** increased during the ***first 30 minutes***, but decreased during the latter parts of session.

Object x session **interaction effect**

As can be seen in Table 9.31, statistically significant ***object*** x ***session*** interactions were found for two frequency and three duration measures of behaviour. Both measures of ***digging/burying*** and ***sniff and touch bottle***, and the duration of ***sniff and touch object*** were *jointly* affected by the object (objects first present during ***fixed-interval*** or ***extinction*** sessions) *and* session grouping variables over the six sessions.

As shown in Figure 9.22 (VI), the frequency and duration of ***digging/burying*** decreased over ***fixed-interval*** sessions, increased in the first ***extinction*** session, and then increased almost imperceptibly over the remaining sessions. Overall, there was a small decrease over the six sessions for both measures. The decrease over ***fixed-interval*** sessions was most noticeable for the FIOE group, which also showed the highest scores in each of these sessions. Frequency of ***digging/burying*** was almost the same for both groups in session 6, and duration was similar in session 4. Although both measures showed similar patterns across ***extinction*** for both groups, they differed in session 5. In that session, frequency and duration of ***digging/burying*** increased for the FIOS group, but decreased in the FIOE group.

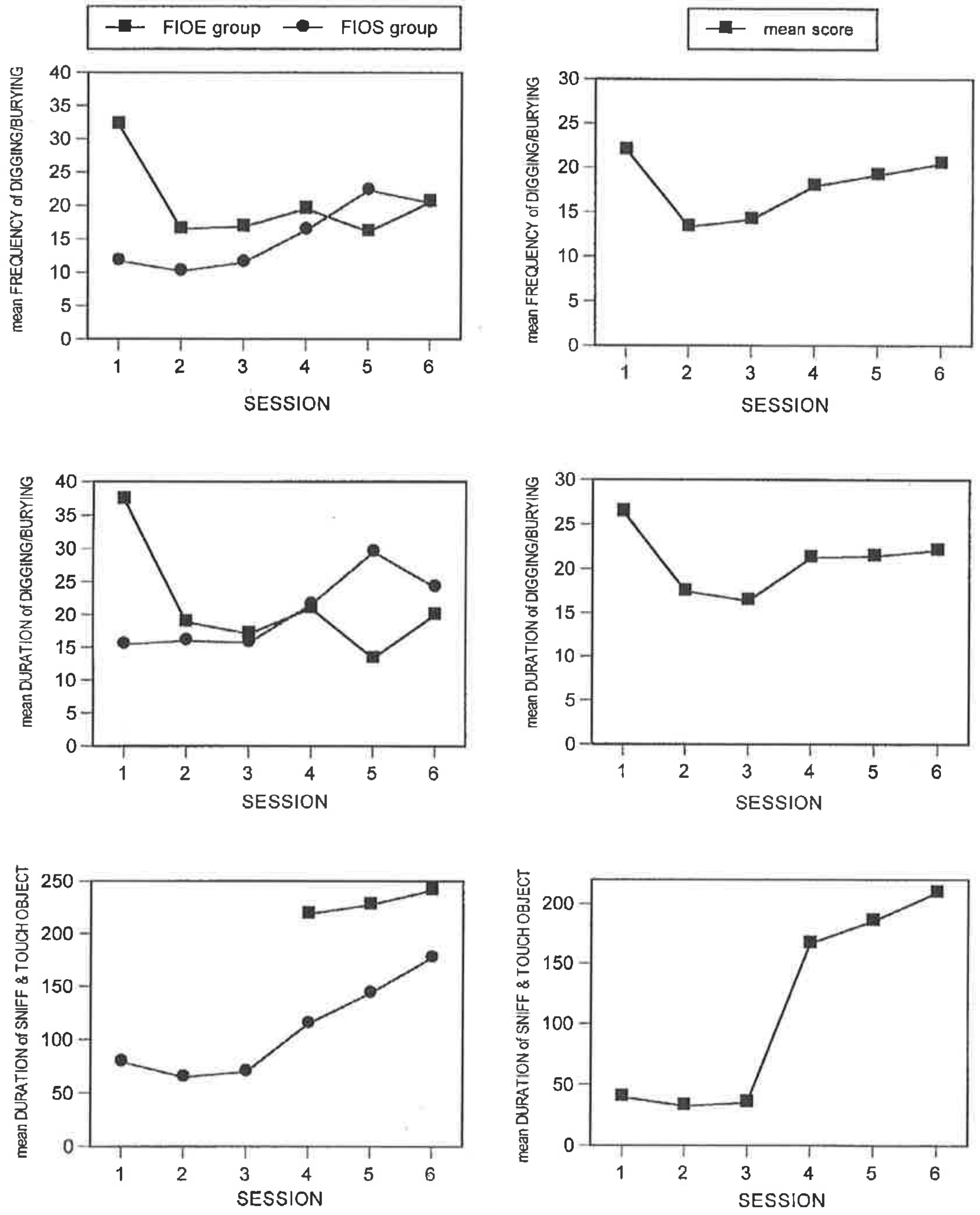


Figure 9.22 (VI). Mean frequency and duration of behaviours jointly affected by the "object" (left) and "session" (right) grouping variables over the six sessions (top- frequency of ***digging/burying***, middle- duration of ***digging/burying***, & bottom- duration of ***sniff & touch object***)

Duration of ***sniff and touch object*** decreased very slightly over ***fixed-interval*** sessions, increased sharply in the first ***extinction*** session, and then continued to rise (Figure 9.22:VI). Although both groups displayed similar patterns over ***extinction***, the time spent engaged in ***sniff and touch object*** was markedly higher for the FIOE group in every session.

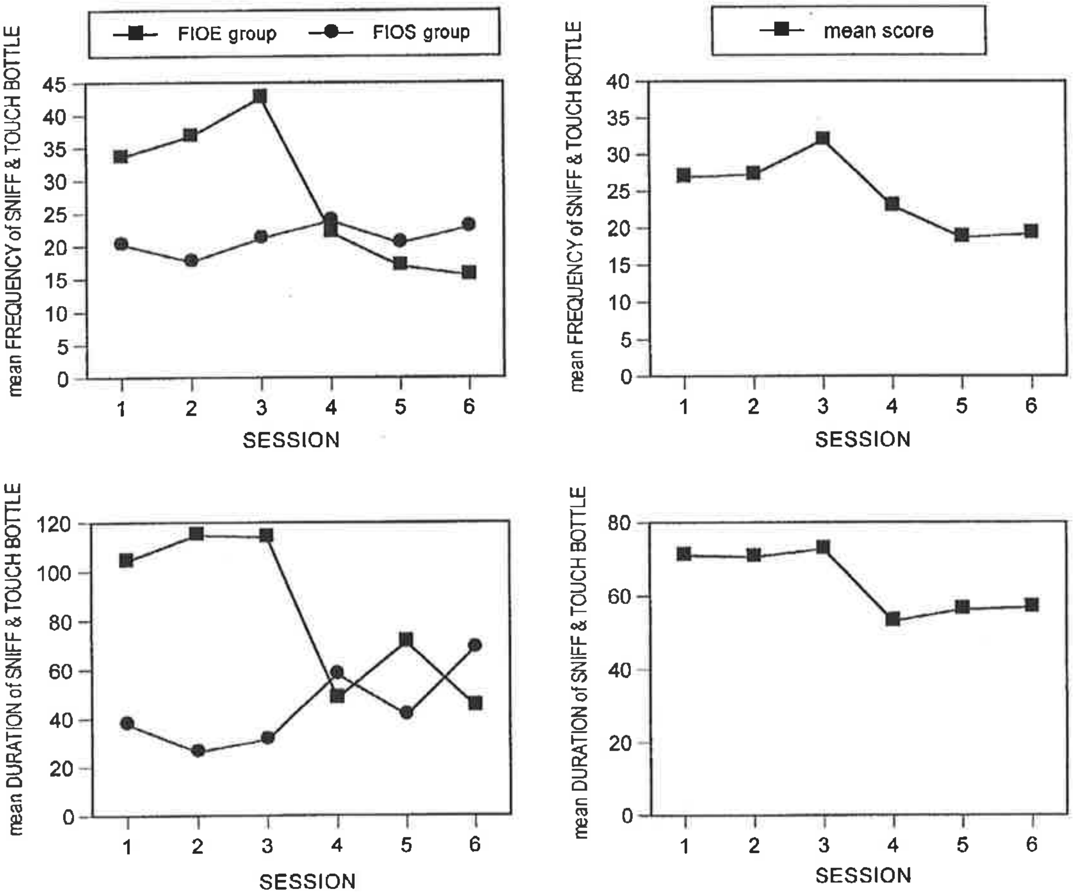


Figure 9.22 (VII). Mean frequency (top) and duration (bottom) of ***sniff and touch bottle*** were jointly affected by the "object" (left) and "session" (right) grouping variables over the six sessions

Visual inspection of Figure 9.22 (VII) indicates that frequency and duration of ***sniff and touch bottle*** increased slightly over the three ***fixed-interval*** sessions, and then decreased in the first ***extinction*** session. However, over ***extinction*** there was a slight decrease in frequency of ***sniff and touch bottle***, whereas the duration measure showed a small increase. The mean scores for both measures were noticeably higher in every ***fixed-interval*** session for the FIOE group. That is, when objects were absent during these sessions, frequency and duration (especially) scores of ***sniff and touch bottle*** were much higher. Over ***extinction***, both groups showed a slight decrease in the frequency measure, with slightly higher scores in every session for the FIOS group. With respect to the duration measure, the most noticeable difference between the two groups during ***extinction*** was in session 5, when the FIOE group score increased quite noticeably, whilst the FIOS score showed the opposite effect.

Table 9.31
Experiment 3 significance levels obtained for measures of behavioural categories during all six sessions (***object*** x ***session*** effect).

Variable	*F*(5,30)	Significance level (*p*)
Frequency of ***digging/burying***	2.97	<.05
Duration of ***digging/burying***	2.74	<.05
Frequency of ***sniff and touch bottle***	6.57	<.0001
Duration of ***sniff and touch bottle***	5.27	=.001
Duration of ***sniff and touch object***	6.04	=.001

Part of session x session **interaction effect**

MANOVAs of three measures of behaviour yielded statistically significant ***part of session*** x ***session*** interactions. Thus, the frequency of ***chew/bite object*** [*F* (10,60)=9.21, *p*<.0001], duration of ***chew/bite object*** [*F* (10,60)=2.99, *p*<.005] and the duration of ***resting/sleeping*** [*F* (10,60)=2.26, *p*<.05] were *jointly* affected by part of session (***first***, ***middle*** or ***last 30 minutes***) *and* session grouping variables over all sessions.

As shown in Figure 9.22 (VIII), the frequency of ***chew/bite object*** increased very slightly over ***fixed-interval*** sessions, increased in the first ***extinction*** session, and then decreased during ***extinction***. This pattern was typical for all parts of session, except during the first ***extinction*** session for the latter parts of session, that displayed a slight decrease. In five of the six sessions, the mean scores were highest during the ***first 30 minutes***.

The duration of ***chew/bite object*** increased markedly over the three ***fixed-interval*** sessions, decreased just as sharply during the first two ***extinction*** sessions, and then increased again during the last session (Figure 9.22:VIII). This pattern was typical of the ***first 30 minutes***, although the increases and decreases were greater (higher scores). For the ***middle 30 minutes***, there was a massive drop in the first ***extinction*** session and then little change over the remaining sessions. For the ***last 30 minutes***, the scores began to decrease noticeably from session 2 to 4, and remained almost negligible during ***extinction***. From session 3 onwards, the mean scores were highest during the ***first 30 minutes*** of every session.

Visual inspection of Figure 9.22 (VIII) indicates that the duration of ***resting/sleeping*** decreased slightly over the three ***fixed-interval*** sessions, increased sharply in the first ***extinction*** sessions, and showed a slight overall increase across ***extinction***. However, this pattern was only typical for the latter parts of session. Very little time was spent engaged in ***resting/sleeping*** during the ***first 30 minutes*** of any session. During ***extinction***, substantial amounts of the ***middle*** and ***last 30 minutes*** of each session were spent ***resting/sleeping***.

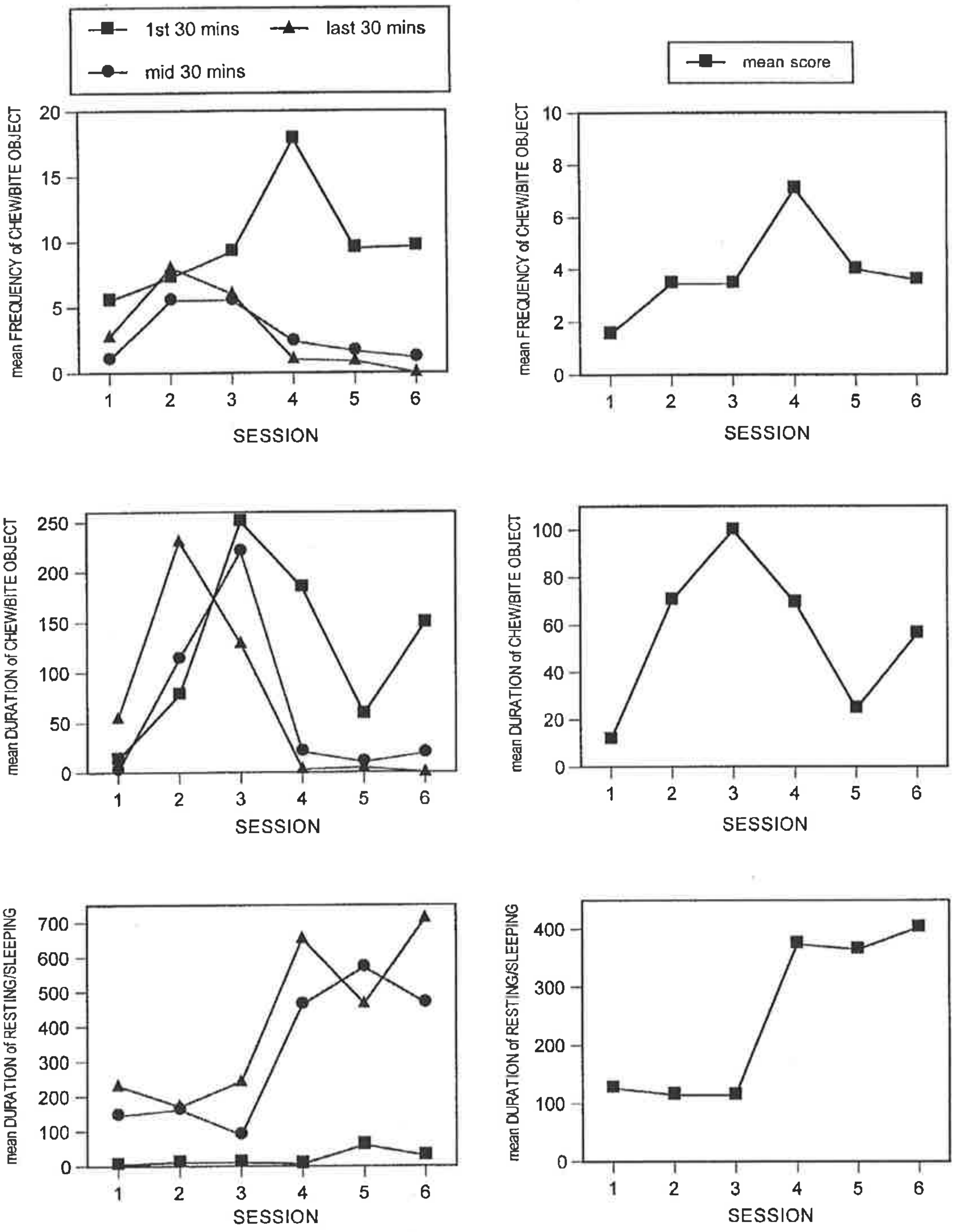


Figure 9.22 (VIII). Mean frequency and duration of behaviours jointly affected by the "part of session" (left) and "session" (right) grouping variables over the six sessions (top- frequency of ***chew/bite object***, middle- duration of ***chew/bite object***, & bottom- duration of ***resting/sleeping***)

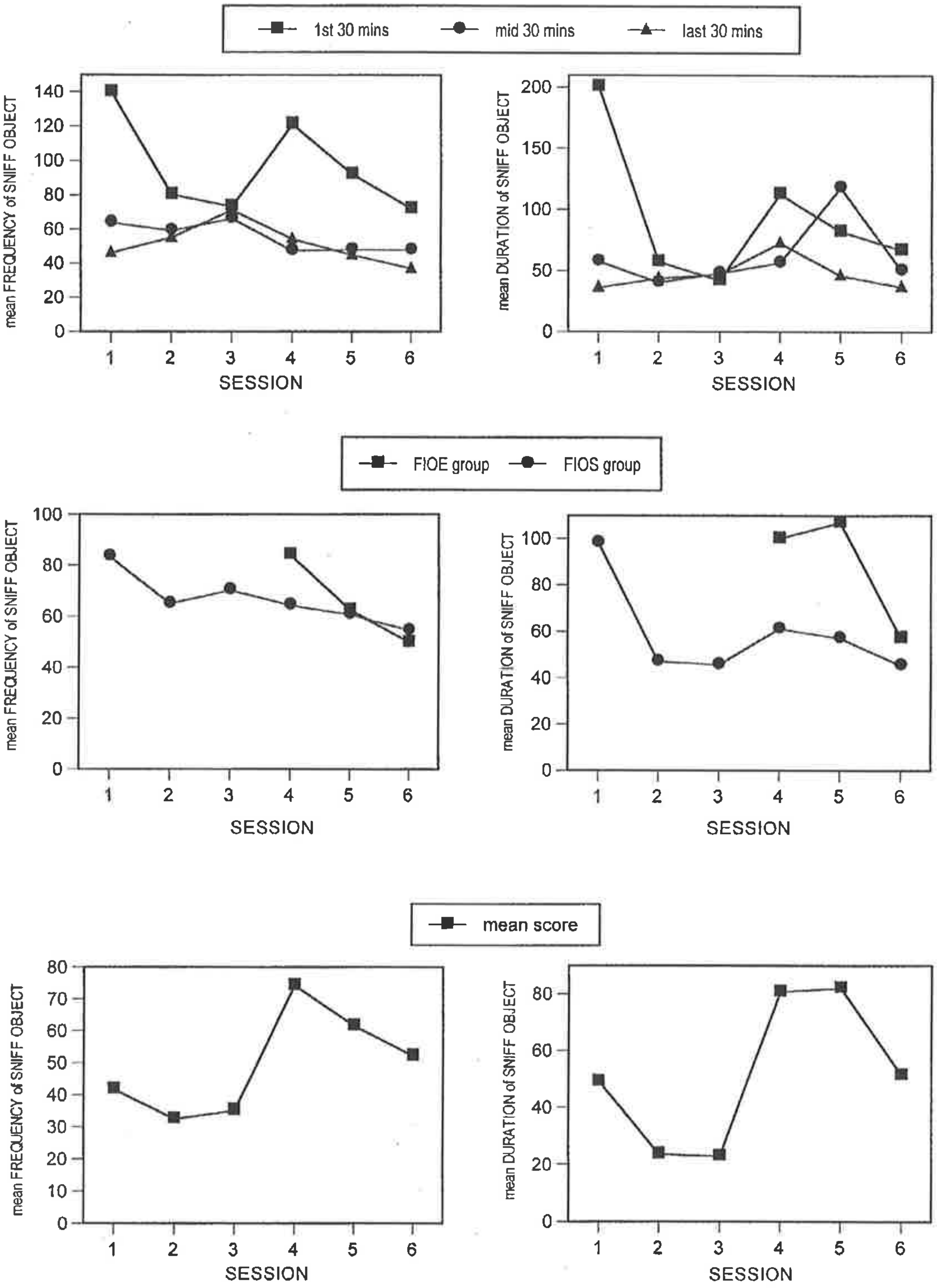


Figure 9.22 (IX). Mean frequency (left) and duration (right) of ***sniff object*** was affected by all three grouping variables over the six sessions (top- "part of session" grouping variable, middle- "object" grouping variable, & bottom- "session" grouping variable)

***Object x part of session x session* interaction effect**

A statistically significant ***object*** x ***part of session*** x ***session*** interaction was found for the frequency of ***sniff and touch object*** [*F* (10,60)=3.41, *p*<.001], frequency of ***sniff object*** [*F* (10,60)=6.81, *p*<.0001] and duration of ***sniff object*** [*F* (10,60)=2.59, *p*<.05]. In this instance, these measures of two ***object-directed behaviours*** were affected by all three grouping variables over the six sessions.

Figure 9.22 (IX) shows that the frequency and duration of ***sniff object*** decreased over ***fixed-interval*** sessions, increased markedly in the first ***extinction*** session, and then decreased over the remaining ***extinction*** sessions. However, the marked increase in the first ***extinction*** session occurred as a result of the FIOE group scores, which were much higher than the FIOS group scores. In fact, for the FIOS group there was actually a slight decrease in the first ***extinction*** session. The FIOE rats spent more time engaged in ***sniff object*** in every ***extinction*** session.

Visual inspection of Figure 9.22 (IX) also shows that that there was a sharp decrease in frequency and duration of ***sniff object*** over ***fixed-interval*** sessions for the ***first 30 minutes***. However, during the ***middle 30 minutes*** there was very little change, whilst during the ***last 30 minutes*** there was a slight increase over these three sessions. The frequency scores were highest during the ***first 30 minutes*** of every session. The noticeable increase in both measures during the first ***extinction*** session was only observed during the ***first 30 minutes***. A steady decrease in frequency and duration of ***sniff object*** over ***extinction*** was observed during the ***first 30 minutes*** and to a lesser extent during the ***last 30 minutes***. By contrast, there was little change over these sessions for the ***middle 30 minutes*** (although there was an increase in duration of ***sniff object*** in session 5).

The frequency of ***sniff and touch object*** demonstrated little change over ***fixed-interval*** sessions, increased sharply in the first ***extinction*** session, and then decreased steadily over ***extinction*** (Figure 9.22: X). The sharp increase in the first ***extinction*** session occurred as a result of the high mean score for the FIOE group. For this group, the frequency scores then steadily decreased over ***extinction***, whereas the scores increased slightly for the FIOS group. The highest frequency of ***sniff and touch object*** scores were obtained during the ***first 30 minutes*** of every session. The pattern observed over the six sessions was different for the latter parts of session. During the ***middle*** and ***last 30 minutes***, frequency of ***sniff and touch object*** increased slightly over ***fixed-interval*** sessions, decreased slightly during the first ***extinction*** session, and then increased very slightly over the remaining sessions.

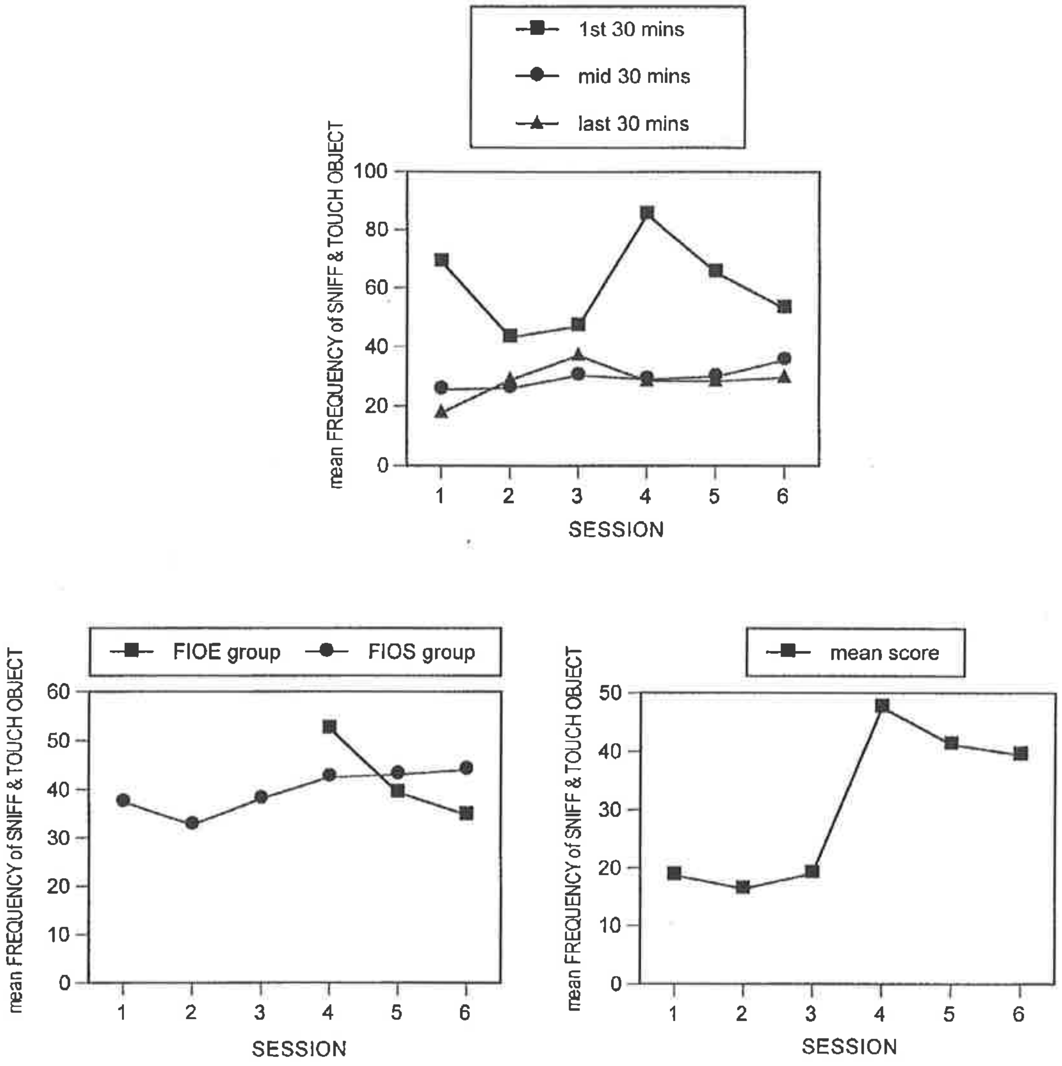


Figure 9.22 (X). Mean frequency of ***sniff and touch object*** was affected by all three grouping variables over the six sessions (top- "part of session" grouping variable, bottom left- "object" grouping variable, & bottom right- "session" grouping variable)

9.3.7.4 TOTAL NUMBER OF LICKS AND BAR PRESSES FOR EACH SESSION, AND OTHER NOTABLE BEHAVIOURS

Total number of *licks* and *bar presses*

For the purposes of this study, ***drinking*** was included in the event-recording programme. This behaviour could be readily observed on the videotape by the experimenter, and an accurate frequency and duration measure could be obtained. However, it should be noted that only the ***first***, ***middle*** and ***last 30 minutes*** of six sessions were used for event recording. The computer recorded the total number of ***licks***, ***bar presses*** and ***reinforcements received*** by each rat in each session, and the amount of water used was measured manually. Thus a complete record of these measures is available, but the accuracy of the ***number of licks*** and ***water used*** measures may be questionable.

If the bottle itself is present in the experimental box, event recording provides an accurate measure of ***drinking*** (in terms of number of bouts & duration of bouts). A number of rats in this study ***attacked the bottle*** throughout the experimental session, which resulted in the partial or complete destruction of the outer plastic housing (Table 9.33 & 9.34). At the very least, most rats directed some ***chewing and biting*** towards the outer plastic housing of the bottle (see Figure 9.7). This resulted in some water spillage or leakage in a number of cases thus rendering the ***water used*** measure unreliable.

For at least three rats (Rats 1, 7 & 10), the licks were not all registered in some sessions. These rats chewed through the wire leading to the lick counter, or pulled it out or snapped it at some stage during a number of sessions. Rat 7 did not trigger the counter in at least one session, since he merely flicked the tongue into the opening of the bottle. To trigger the counter, the rats needed to have at least one paw on the metal grid placed under the bottle to complete the circuit. In addition, the biting and chewing of the bottle housing and manipulation of the bottle tube with the paws may have triggered the lick counter on occasion. As a result, the ***licks*** measure may also be somewhat spurious. This should be born in mind when inspecting Figures 9.23 (I) and (II).

For both groups, a total of between 1000 and 4000 ***bar presses*** (in one case >5000) were made during each FI60-s session (Figure 9.23:I & II). By comparison, the number of ***bar presses*** was very low in every other session (***CRF** & **extinction***). A similar peak in the total number of ***licks*** (between 1000 & 6000 in most cases) was observed in the FI60-s sessions for two of the four rats in the FIOS group. However, as mentioned above, the two rats with low ***lick*** scores were the ones that did not always trigger the lick counter. A peak in the total number of ***licks*** (between 500 & 3000 in most cases) was also observed in the FI60-s sessions in a number of cases in the FIOE group. Thus, the highest total number of ***bar presses*** and ***licks*** appeared to occur during FI60-s sessions.

Table 9.32
Total number of ***licks***, ***bar presses*** and ***reinforcements*** per session for the two groups.

PHASE OF EXPERIMENT	SESSION	MEASURE (MEAN)	FIOS GROUP	FIOE GROUP
Mass reinforcement	1	Licks Reinforcements	378.75 210	595.5 210
Mass reinforcement	2	Licks Reinforcements	496.5 210	815.25 210
Continuous reinforcement	3	Licks Bar-presses Reinforcements	88.5 264 284.5	312.75 244.75 264.5
Extinction	4	Licks Bar-presses Reinforcements	134.5 268.25 0	133.25 176.5 0
FI60	5	Licks Bar-presses Reinforcements	419.5 3299 188	653.5 2605.25 177.75
FI60	6	Licks Bar-presses Reinforcements	1619.75 2723.5 198	1110 1990.5 184.75
FI60	7	Licks Bar-presses Reinforcements	1443.25 2265.5 197.5	1020.5 1738.75 187
FI60 (Experimental Session 1)	8	Licks Bar-presses Reinforcements	2069.5 2311.75 174.75	1600.75 1607.5 186
FI60 (Experimental Session 2)	9	Licks Bar-presses Reinforcements	2118.75 2833.5 201.25	2135 2387 190.5
FI60 (Experimental Session 3)	10	Licks Bar-presses Reinforcements	2379.25 2655 167.25	2331.75 2267.25 188.75
Extinction (Experimental Session 4)	11	Licks Bar-presses Reinforcements	227.5 268.5 0	297.25 209.5 0
Extinction (Experimental Session 5)	12	Licks Bar-presses Reinforcements	68 70.25 0	246 99.25 0
Extinction (Experimental Session 6)	13	Licks Bar-presses Reinforcements	242.5 49 0	252.75 66.25 0
Extinction	14	Licks Bar-presses Reinforcements	130.5 35 0	394 75.75 0
Extinction	15	Licks Bar-presses Reinforcements	34.25 33.25 0	53.5 73.5 0
Extinction	16	Licks Bar-presses Reinforcements	74.75 30 0	199.5 73.5 0
Extinction	17	Licks Bar-presses Reinforcements	111.75 79.25 0	194 176.25 0

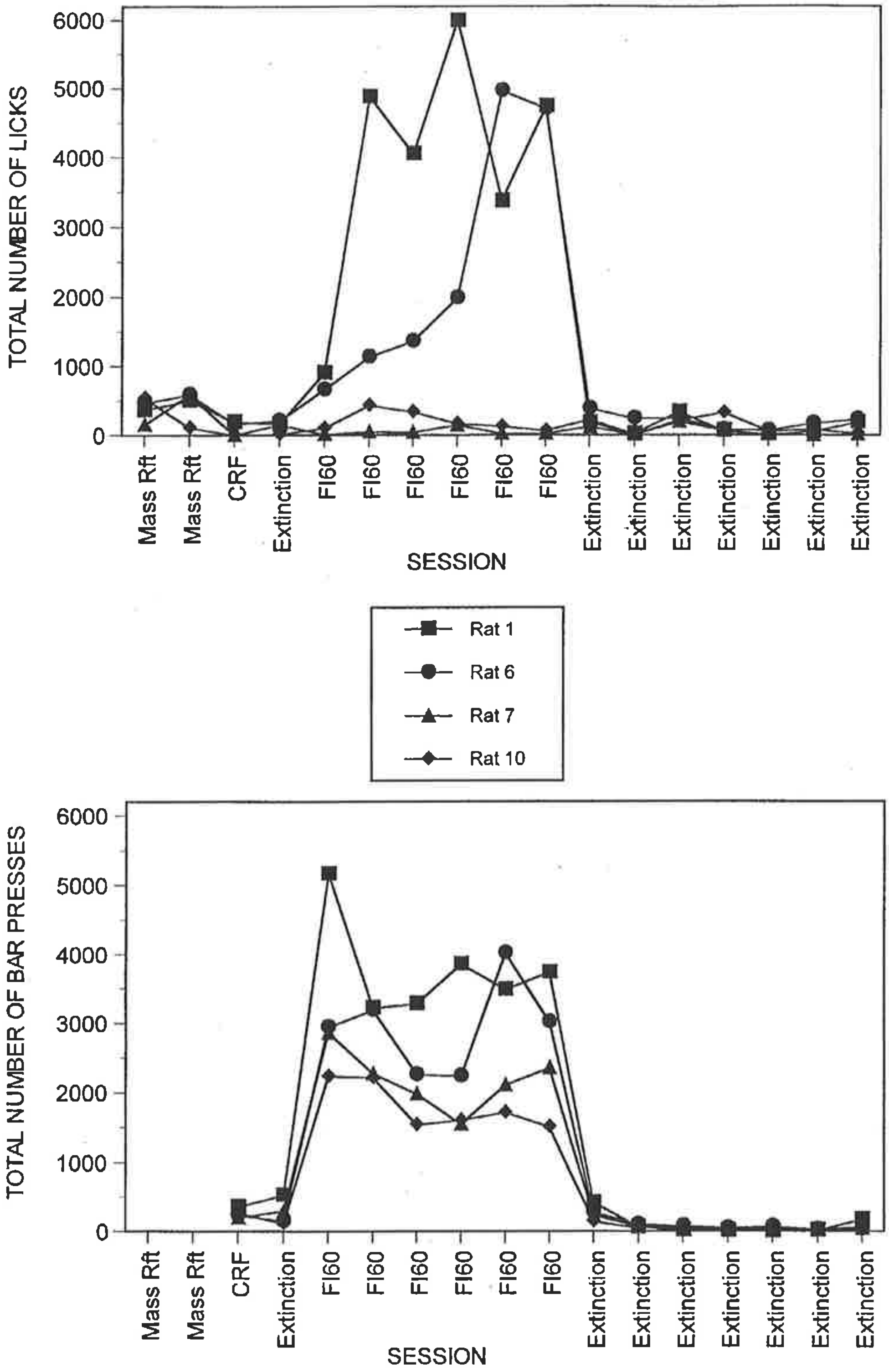


Figure 9.23 (I). Total number of ***licks*** (top) and ***bar presses*** (bottom) for individual rats in the FIOS group

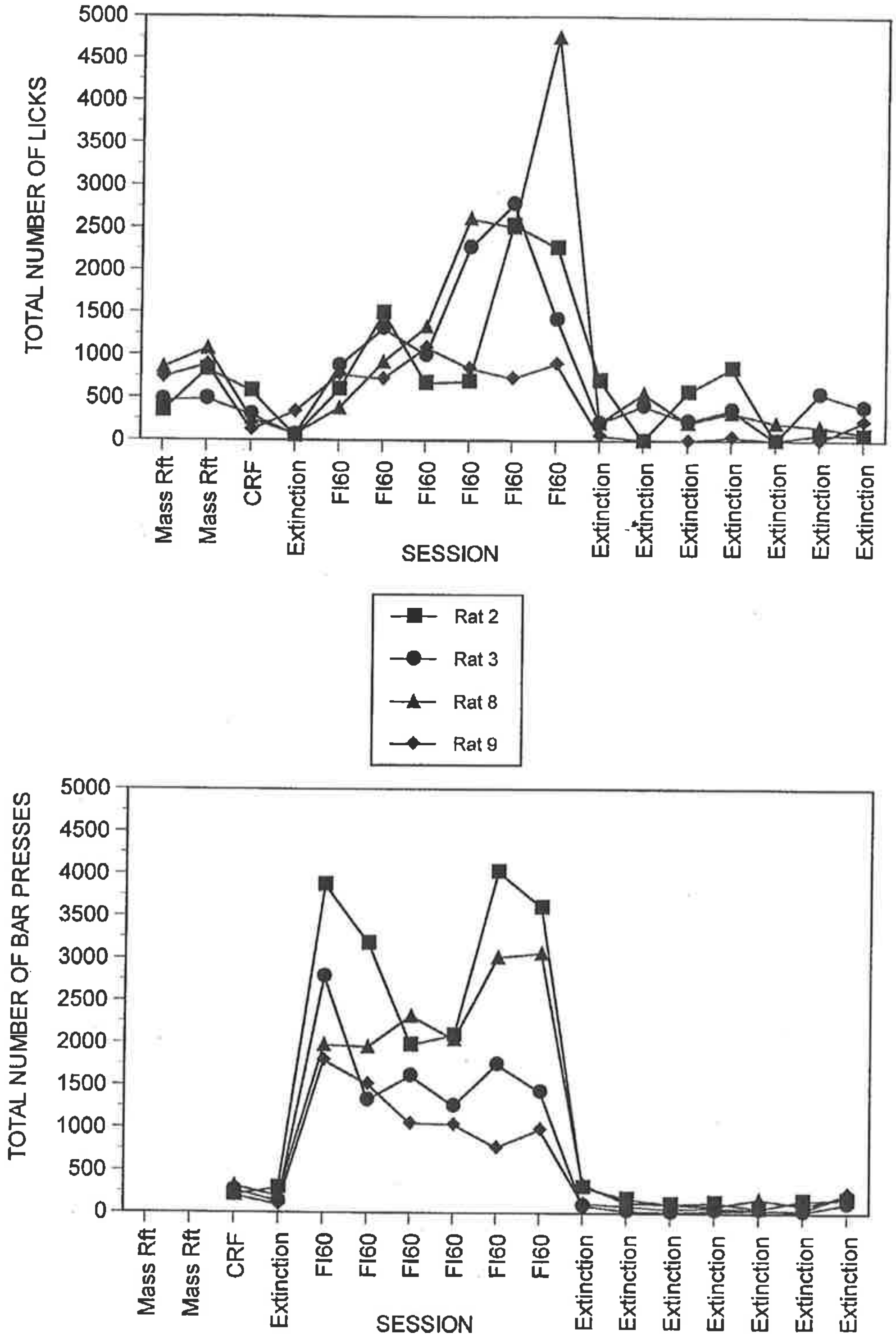


Figure 9.23 (II). Total number of ***licks*** (top) and ***bar presses*** (bottom) for individual rats in the FIOE group

Other notable behaviours

Instances of notable behaviours for each rat during the six experimental sessions are reported in Table 9.33 (FIOS group) and 9.34 (FIOE group). Specific details about notable behaviours (frequency & duration) during the other observation sessions (***mass reinforcement***, ***CRF***, FI60-s & ***extinction*** sessions) can be found in Appendix C.

Table 9.33

Instances of ***attacking the water bottle***, ***sawdust pushing*** or other notable behaviours by each rat in the FIOS group for each session in Experiment 3 (during the three parts of session scored).

SESSION NUMBER	**FIOS Rat 1**	**FIOS Rat 6**	**FIOS Rat 7**	**FIOS Rat 10**
SESSION 1 (FI60-s)	• "attack" bottle • push lid with snout	• "attack" bottle • water leak out • sawdust mound at back wall • 5 x coprophagia	• sawdust mound by bottle & back wall	• 4 x coprophagia
SESSION 2 (FI60-s)	• "attack" bottle • water leak out • push lid with snout	• "attack" bottle • 7 x coprophagia	• sawdust mound by bottle & back wall • 1 x coprophagia	• chew up windmill object • 5 x coprophagia
SESSION 3 (FI60-s)	• "attack" bottle • push lid with snout & push nose through gap- during ***middle 30 minutes*** (8x, 15s) & ***last 30 minutes*** (8x, 19.9s)	• "attack" bottle • 5 x coprophagia	• sawdust mound by bottle	• chew up windmill object • 7 x coprophagia • push lid with snout- during ***last 30 minutes*** (1x, 0.1s)
SESSION 4 (Extinction)	• "attack" bottle • sawdust mound over object • push lid with snout- during ***middle 30 minutes*** (4x, 6.1s) & ***last 30 minutes*** (8x, 19s) • 4 x coprophagia	• "attack" bottle • 3 x coprophagia	• sawdust mound by bottle & front corner • 3 x coprophagia	• chew up springs on scrap metal object • 6 x coprophagia
SESSION 5 (Extinction)	• "attack" bottle • chew up wire • push lid with snout & try to climb out- during ***first 30 minutes*** (33x, 62.7s)	• "attack" bottle • 1 x coprophagia	• sawdust mound by bottle • 1 x coprophagia	• chew up springs on scrap metal object • 7 x coprophagia
SESSION 6 (Extinction)	• "attack" bottle • chew up wire • push lid with snout & try to climb out- during ***last 30 minutes*** (13x, 20.1s) • 2 x coprophagia	• "attack" bottle • sawdust mound by bottle • 3 x coprophagia	• sawdust mound by bottle & back wall • chew up wire • 1 x coprophagia	• sawdust mound by objects • 6 x coprophagia

Event recording provided frequency and duration measures of ***chew/bite bottle***. However, this category does not indicate which rats really appeared to ***attack the bottle*** in a very aggressive way that resulted in severe damage to the outer plastic housing of the bottle (in some cases, complete destruction). That is, these rats were not just directing ***exploratory behaviour towards the bottle*** but they literally chewed the housing to pieces. As can be seen from Table 9.33 and Table 9.34, there were two rats in the FIOS group and two rats in the FIOE group that ***attacked*** the bottle in all experimental sessions (except Rat 2 in session 1 & 2). In some cases, this activity resulted in water obviously leaking out of the bottle. In session 17, when a loose bottle was present on the floor of the experimental box, all but one rat were ***aggressive towards the loose bottle*** (& three ***attacked*** both bottles). Rat 1 was so ***aggressive towards the bottles*** that this activity resulted in him ripping out a nail (front paw).

One rat in the FIOS group (Rat 10) was also very ***aggressive towards the stimulus objects*** that could be readily chewed or destroyed. Of the group A objects, he chewed up and destroyed the fan part of the ***windmill*** object. With the group B objects, he directed his chewing behaviour at the springs on the ***scrap metal*** object. Two of the FIOS group rats (Rat 1 & 7) chewed up and destroyed the wire that connected the bottle to the lick counter in some of the ***extinction*** sessions.

All rats engaged in bouts of ***coprophagia*** (typically between 1 & 10 bouts) during some (or all) experimental sessions. In some cases, the rats had barely finished defecating before turning around, picking up the fecal "pellet" and consuming it. One rat in the FIOE group (Rat 9) developed some unusual behavioural patterns linked to his bouts of ***coprophagia***. Sometimes he defecated and then picked up the fecal pellet, carried it to the metal grid area under the bottle and consumed it. Some of the fecal pellets were dropped and fell through the grid, which resulted in a build up of feces under the grid in some sessions. On other occasions, he engaged in flurries of ***burying behaviour***, then defecated, turned around and buried the fecal pellet with sawdust using the paws and/or snout. Later he uncovered the fecal pellets and consumed them. It was noted that during FI60-s sessions, Rat 9 sometimes carried fecal pellets to the grid and engaged in ***coprophagia*** for two or three PRPs in succession.

Burying behaviour (or ***sawdust pushing***) was included as a category for event recording, but the direction of this behaviour was not scored. However, in a number of cases quite large mounds of sawdust were created by this behaviour, and these are referred to in Table 9.33 and Table 9.34. Most of these mounds developed near the bottle or back wall areas.

Table 9.34

Instances of ***attacking the water bottle***, ***sawdust pushing*** or other notable behaviours by each rat in the FIOE group for each session in Experiment 3 (during the three parts of session scored.

SESSION NUMBER	**FIOE Rat 2**	**FIOE Rat 3**	**FIOE Rat 8**	**FIOE Rat 9**
SESSION 1 (FI60-s)	• 2 x coprophagia • push lid with snout- during ***middle 30 minutes*** (1x, 1.3s)	• "attack" bottle • 4 x coprophagia • push lid with snout- during ***first 30 minutes*** (1x, 1.6s) & ***last 30 minutes*** (2x, 2s)	• sawdust mound by bottle & back wall • 5 x coprophagia	• faeces build up under bottle • carries faecal pellets to grid & engages in coprophagia or drops them • buries faecal pellets with sawdust & later digs them up & engages in coprophagia
SESSION 2 (FI60-s)	• sawdust mound by bottle • 3 x coprophagia	• "attack" bottle • water leak out • 4 x coprophagia • push lid with snout- during ***first 30 minutes*** (2x, 2.7s)	• sawdust mound by bottle • 3 x coprophagia	• faeces build up under bottle • carries faecal pellets to grid & engages in coprophagia or drops them • buries faecal pellets with sawdust & later digs them up & engages in coprophagia
SESSION 3 (FI60-s)	• "attack" bottle • 6 x coprophagia	• "attack" bottle • 5 x coprophagia	• sawdust mound by bottle & back wall • 10 x coprophagia • push lid with snout- during ***middle 30 minutes*** (2x, 0.1s)	• faeces build up under bottle • carries faecal pellets to grid & engages in coprophagia or drops them • buries faecal pellets with sawdust & later digs them up & engages in coprophagia • sawdust mound by bottle
SESSION 4 (Extinction)	• "attack" bottle	• "attack" bottle • all water leak out • 4 x coprophagia	• 6 x coprophagia	• sometimes buries faecal pellets with sawdust & later digs them up & engages in coprophagia • 7 x coprophagia
SESSION 5 (Extinction)	• "attack" bottle • 2 x coprophagia	• "attack" bottle • 9 x coprophagia	• 2 x coprophagia	• carries faecal pellets to grid & engages in coprophagia • buries faecal pellets with sawdust & later digs them up & engages in coprophagia
SESSION 6 (Extinction)	• "attack" bottle • 4 x coprophagia	• "attack" bottle • 6 x coprophagia	• 2 x coprophagia	• carries faecal pellets to grid & engages in coprophagia • buries faecal pellets with sawdust & later digs them up & engages in coprophagia

An ***escape-directed exploratory behaviour*** was observed in some rats, during some of the sessions. By ***propping*** against the wall and stretching their heads up, these rats were able to ***push at the lid with their snouts***. In the FIOE group (Table 9.34), three rats engaged in this behaviour, but the bouts were few (one or two), and length of bouts was very small (<3 seconds). This behaviour was only observed in the FIOE group during the ***fixed-interval*** sessions, in the absence of objects. Once objects were present during ***extinction***, this behaviour was no longer observed. In the FIOS group (Table 9.33), two rats engaged in ***push at lid with snout*** during session 3 (***fixed-interval*** session). Thus it only appeared in this group of rats during ***fixed-***

interval sessions (<10 bouts per rat), once the objects had begun to "lose novelty" or once the food source was depleted (up to 33 bouts in one part of session). During ***extinction***, it was only observed in one rat (Rat 1). This rat was persistent and used enough force to move the lid enough to create a gap through which he pushed his nose or tried to climb out of the apparatus (Table 9.33). During the ***first 30 minutes*** of session 5 and the ***last 30 minutes*** of session 6, he succeeded in climbing out of the gap and onto the lid of the apparatus, on several occasions. Each time he had left the box, he climbed around on top of the lid and explored this surface thoroughly. He climbed back into the box of his own accord each time, and never climbed down onto the floor in the experimental room. That is, he never physically explored beyond the apparatus, although visually he was able to monitor the surroundings outside the box.

9.3.7.5 BEHAVIOURAL CATEGORIES ENGAGED IN FOR MORE THAN 10% OF TOTAL SESSION TIME

As mentioned in section 8.6, a specific behaviour might be considered to be ***excessive*** if it occurs for more than 10% of total (session) time. The mean total of each duration measure for the three ***fixed-interval*** and three ***extinction*** sessions was taken (from Tables 9.7 - 9.12), and then divided by the total duration for the three ***fixed-interval*** sessions (5400 seconds), or three ***extinction*** sessions (5400 seconds). This then provided a percentage of total session time spent engaged in each behavioural category. Then it is possible to determine which behavioural categories were engaged in fore more than 10% of total session time. For differences between individual sessions, the reader may refer to section 9.3.5.

Neither group engaged in ***drinking*** for more than 10% of total ***fixed-interval*** or ***extinction*** session time, for any part of session (Table 9.35 & 9.36). It was not possible to compare this result with the groups in Experiment 1, since no water bottle was present for those groups. Both groups spent less than 10% of total ***fixed-interval*** or ***extinction*** session time (all parts of session) engaged in ***digging/burying*** (Table 9.35 & 9.36). The FIOS and FIOE group rats in Experiment 1 also spent less than 10% of their time ***digging/burying***. Both groups in Experiment 3 also spent less than 10% of their session time (all parts of session) in ***propping***, whereas both groups in Experiment 1 engaged in ***excessive*** (>10%) amounts of this behaviour during both ***fixed-interval*** and ***extinction*** sessions.

Both groups spent more than 10% of session time (all parts of session) engaged in ***behaviours directed at the bar and food-trough area*** during ***fixed-interval*** sessions (Table 9.35 & 9.36). In Experiment 1, however, the two groups spent more than 20% of their session time engaged in these activities. During ***extinction***, less than 10% of session time (all parts of session) was spent in ***behaviours directed at the bar and food-trough area*** (except for the FIOE group during the ***last 30 minutes***). Again, both groups in Experiment 1 spent more than 10% of their time engaged in these behaviours during ***extinction***.

Table 9.35
The percentage (>10%) of total session time spent engaged in the various behavioural categories, for the FIOS group (separately for the 3 parts of session & as a mean for the 3 parts of session). The percentage obtained by the FIOS group in Experiment 1 is provided for comparison (final column). A dash (-) indicates that the percentage was less than 10%.

Behaviour	**FIOS** 1st 30 mins	**FIOS** mid 30 mins	**FIOS** last 30 mins	**Mean for 3 parts of session**	**FIOS Expt.1**
Behaviours directed at the bar & food-trough area (*bar pressing; bar-related behaviour*) - schedule	14.59%	10.87%	-	11.28%	21.8%
- extinction	-	-	-	-	17.1%
Behaviours directed at the stimulus objects (*sniff object; sniff & touch object; chew/bite object*) - schedule	17.24%	12.06%	13.42%	14.25%	13.4%
- extinction	23.13%	11.35%	10.52%	15%	11.2%
Behaviours directed at the water bottle (*sniff bottle; sniff & touch bottle; chew/bite bottle*) - schedule	13.34%	-	-	-	No Bottle present
- extinction	13.99%	-	10.96%	11.05%	
"Aggressive" behaviours (*chew/bite object; chew/bite bottle*) - schedule	16.3%	-	11.04%	11.59%	No Bottle present (*chew/bite* object <10%)
- extinction	20.74%	-	-	11.39%	
Drinking - schedule	-	-	-	-	No Bottle present
- extinction	-	-	-	-	
Propping - schedule	-	-	-	-	10.1%
- extinction	-	-	-	-	13.8%
Displacement - schedule	-	11.67%	10.6%	-	-
- extinction	18.15%	22.58%	-	16.28%	-
Digging/burying - schedule	-	-	-	-	-
- extinction	-	-	-	-	-
Resting/sleeping - schedule	-	-	-	-	Not scored
- extinction	-	21.07%	38.23%	20.42%	

The FIOS group spent more than 10% of total ***fixed-interval*** session time (all parts of session) engaged in ***behaviours directed at the stimulus objects*** (objects were absent for the FIOE group). Overall, the levels were slightly higher than for the same group in Experiment 1 (Table 9.35). During ***extinction***, both groups spent more time overall engaged in these ***exploratory behaviours***. In fact, during the ***first 30 minutes***, more than 20% of total time was spent ***exploring the stimulus objects***. On average, both Experiment 3 groups of rats spent more time engaged in ***behaviours directed at the stimulus objects*** than their Experiment 1 counterparts during ***extinction***.

The FIOS group spent more than 10% of the ***first 30 minutes*** of ***fixed-interval*** time engaged in ***bottle-directed behaviours*** (Table 9.35), whilst the FIOE group engaged in these behaviours for more than 10% of the ***middle 30 minutes*** of ***fixed-interval*** session time (Table 9.36). During ***extinction***, slightly higher levels were observed. The FIOS group spent more than 10% of time engaged in ***behaviours directed at the water bottle*** during the ***first*** and ***last 30 minutes*** of ***extinction***. More than 10% of the ***first 30 minutes*** of ***extinction*** time was spent engaged in these activities by the FIOE group. (No water bottle was present during Experiment 1).

If objects were absent during ***fixed-interval*** sessions (FIOE group), then more than 10% of all parts of session were spent engaged in ***displacement*** (Table 9.36). The FIOS group spent less than 10% of the ***first 30 minutes*** of ***fixed-interval*** sessions in ***displacement*** activities (Table 9.35). However, in the latter parts of session, more than 10% of total time was also spent engaged this ***conflict-related behaviour***. Overall, both groups spent more time engaged in this behaviour during ***extinction***. For the FIOE group, less than 20% (>10%) of total session time (all parts of session) was spent in ***displacement***. For the FIOS group, ***displacement*** peaked during the ***middle 30 minutes*** of ***extinction***, when more than 20% of total time was spent in these activities. This figure then dropped to less than 10% during the ***last 30 minutes*** of ***extinction***. By contrast, neither group in Experiment 1 devoted more than 10% of ***fixed-interval*** or ***extinction*** session time to ***displacement***.

The presence of objects during ***fixed-interval*** sessions clearly reduced the amount of time spent ***resting/sleeping***. The FIOS group spent less than 10% of total session time engaged in this behaviour (Table 9.35), whereas more than 10% of the ***middle*** and ***last 30 minutes*** of these sessions were spent ***resting/sleeping*** in the FIOE group (Table 9.36). During ***extinction***, these values increased markedly for both groups for the ***middle*** and ***last 30 minutes***. Less than 10% of the ***first 30 minutes*** was spent ***inactive***. For the latter parts of session, both groups spent more than 20% of session time engaged in ***resting/sleeping***, and in one part of session this jumped to more than 30% of session time. This behaviour was not scored in Experiment 1.

Table 9.36
The percentage (>10%) of total session time spent engaged in the various behavioural categories, for the FIOE group (separately for the 3 parts of session & as a mean for the 3 parts of session). The percentage obtained by the FIOE group in Experiment 1 is provided for comparison (final column). A dash (-) indicates that the percentage was less than 10%.

Behaviour	**FIOE** 1st 30 mins	**FIOE** mid 30 mins	**FIOE** last 30 mins	**Mean for 3 parts of session**	**FIOE Expt.1**
Behaviours directed at the bar & food-trough area (*bar pressing; bar-related behaviour*)					
- schedule	14.99%	14.37%	13.59%	14.31%	25.2%
- extinction	-	-	10.66%	-	14.9%
Behaviours directed at the stimulus objects (*sniff object; sniff & touch object; chew/bite object*)					
- schedule	No objects	No objects	No objects	No objects	No objects
- extinction	21.8%	19.63%	16.39%	19.27%	14.9%
Behaviours directed at the water bottle (*sniff bottle; sniff & touch bottle; chew/bite bottle*)					
- schedule	-	11.47%	-	-	No Bottle present
- extinction	15.33%	-	-	-	
"Aggressive" behaviours (*chew/bite object; chew/bite bottle*)					
- schedule	-	-	-	-	-
- extinction	15.84%	-	-	-	- no bottle present
*note: no objects present during *fixed-interval* sessions, so score is only for *chew/bite bottle*					
Drinking					
- schedule	-	-	-	-	No Bottle present
- extinction	-	-	-	-	
Propping					
- schedule	-	-	-	-	13.9%
- extinction	-	-	-	-	12.2%
Displacement					
- schedule	10.3%	12.47%	13.59%	12.12%	-
- extinction	16.44%	12.72%	18%	15.72%	-
Digging/burying					
- schedule	-	-	-	-	-
- extinction	-	-	-	-	-
Resting/sleeping					
- schedule	-	10.86%	15.23%	-	Not scored
- extinction	-	34.46%	29.5%	21.84%	

Since only the FIOS group had objects present during ***fixed-interval*** sessions, the combined ***aggressive behaviour*** category is only relevant to this group during those sessions. (The FIOE group spent less than 10% of total session time engaged in ***chew/bite object***). The FIOS group spent more than 10% of session time ***chewing/biting*** the water bottle and objects during the ***first*** and ***last 30 minutes*** of ***fixed-interval*** sessions (Table 9.35). During ***extinction***, more than 20% of the ***first 30 minutes*** was spent engaged in these ***aggressive behaviours***, whilst the figure decreased to less than 10% of session time for the latter parts of session. The FIOE group spent more than 15% of the ***first 30 minutes*** of ***extinction*** engaged in these behaviours (Table 9.36). No bottle was present during Experiment 1, and the ***chew/bite object*** levels never exceeded 10% of total session time.

9.3.7.6 TIME AND "EFFORT" SPENT OBTAINING REINFORCEMENTS

As mentioned in section 8.10, there is no "right" or "wrong" amount of time that should be spent by each rat at the ***bar and food-trough area*** of the box, or number of ***bar presses*** performed. However, an ***optimal foraging strategy*** would be one in which the least amount of energy is exerted, for the maximum amount of food. That is, many pellets or reinforcers for few ***bar presses***.

Both Experiment 1 and Experiment 3 ran rats on a ***fixed-interval*** schedule, although the session lengths were very different. For Experiment 1, the sessions were half an hour long, whereas during Experiment 3, sessions were 3.5 hours long. Both Experiments had stimulus objects present during these sessions for one of the ***fixed-interval*** groups (FIOS groups). The main difference between the two Experiments was the presence of a concurrent water source during Experiment 3. Despite the differences, it is interesting to compare the results for the mean number of ***bar presses*** per reinforcement (Table 9.37), to determine whether the presence of stimulus objects or a concurrent water source affects the amount of energy exerted per reinforcement. That is, this section seeks to discover which experimental conditions encourage ***optimal foraging*** during ***fixed-interval*** sessions.

Although the ratio was not exactly 1:1, the total mean ***bar presses*** were not very different from the total mean ***licks*** during the three ***fixed-interval*** sessions for the two groups in Experiment 3. Table 9.37 indicates that the mean frequency of ***bar presses*** per reinforcement was lowest for the two groups in Experiment 3. Thus, the presence of the water bottle increased the rats' ability to forage in the most ***optimal*** fashion. These rats were able to exert far less energy per reinforcement than their Experiment 1 counterparts. For the FIOS rats- Experiment 1 rats exerted at least twice as much energy per reinforcement, than Experiment 3 rats. For the FIOE rats- Experiment 1 rats exerted more than three times as much energy per reinforcement, than FIOE Experiment 3 rats.

Table 9.37
The total mean frequency of ***bar presses*** and ***reinforcers*** during the three ***fixed-interval*** sessions, for the FIOS and FIOE groups in Experiments 1 & 3. The mean frequency of ***bar presses*** per reinforcement is also provided for these four groups. The total mean frequency of ***licks*** during the ***fixed-interval*** sessions is given for the two groups in Experiment 3.

GROUP	Total mean frequency of ***bar presses*** during ***fixed-interval*** sessions	Total mean frequency of reinforcements received during ***fixed-interval*** sessions	Mean frequency of ***bar presses*** per reinforcement	Total mean frequency of ***licks*** during ***fixed-interval*** sessions
FIOS group-Experiment 3 **(3.5 hour session)**	7800.25	543.25	14.36	6567.5
FIOS group-Experiment 1 **(0.5 hour session)**	2494.25	89	28.03	No Bottle Present
FIOE group-Experiment 3 **(3.5 hour session)**	6261.75	565.25	11.08	6067.5
FIOE group-Experiment 1 **(0.5 hour session)**	3427.25	88.5	38.73	No Bottle Present

If the session was half an hour long, the presence of stimulus objects greatly reduced the number of ***bar presses*** per reinforcement. That is, less energy was spent ***bar pressing*** per reinforcement when objects were present. By contrast, if the session was 3.5 hours long, the reverse was true. That is, slightly more energy was spent ***bar pressing*** per reinforcement when objects were present. Overall, the most ***optimal foraging*** condition during ***fixed-interval*** sessions was when a water bottle was concurrently available, and stimulus objects were absent.

9.3.7.7 INDEPENDENT JUDGING

As with Experiment 1 and 2, the reliability of the experimenter's behavioural measurements and the behavioural criteria were tested via independent judging of an animal chosen at random. Again, two procedures were followed in order to analyse the data obtained from the three independent judges.

Firstly, two inter-correlation matrices were constructed, namely: one for the frequency of behavioural events, and one for the duration of these events. The inter-correlation matrices were used to determine the degree of correlation between the three independent judges and the experimenter. The probability values pertaining to the frequency of behavioural events were statistically significant for all judges:

	JUDGE 4 (Experimenter)	
JUDGE 1	$r=.879$	$p<.01$
JUDGE 2	$r=.794$	$p<.05$
JUDGE 3	$r=.982$	$p<.001$

The probability values were also statistically significant for all judges with respect to the duration measures of behavioural events:

	JUDGE 4 (Experimenter)	
JUDGE 1	$r=.734$	$p<.05$
JUDGE 2	$r=.712$	$p<.05$
JUDGE 3	$r=.889$	$p<.01$

The second stage of statistical analysis involved the application of Kendall's *W* coefficient of concordance to the data. This programme was designed to measure the agreement amongst the judges. A high degree of agreement was found to exist between the judges for the frequency and duration measures of all behavioural categories:

$W=$ .854 $p<.001$.

9.4 DISCUSSION FOR EXPERIMENT 3

9.4.1 THE PRESENCE OF EXPLORATORY AND OTHER BEHAVIOURS DURING THE POST-REINFORCEMENT PAUSES

9.4.1.1 HYPOTHESIS THIRTEEN: PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Hypothesis 13 predicted that a large proportion of ***drinking*** (Falk, 1971) and each of the other scored behaviours would take place during the PRPs for rats run on the ***fixed-interval*** schedule, since these schedules are characterised by the existence of regular PRPs (see Hypothesis 1).

Hypothesis 13 was supported, with respect to both the frequency and duration measures of all behavioural categories. More than a quarter of each frequency measure (& up to 97.44%) and over a third of each duration measure (& up to 99.89%) occurred during the PRPs for both groups.

More than 70% of all ***drinking*** (frequency & duration) took place during the PRPs for both groups. In fact, during the ***middle 30 minutes***, almost all ***drinking*** (>90%) occurred during the PRPs. Thus, ***drinking*** did tend to occur after consumption of the food pellet, but this behaviour was not always restricted to the PRPs. Gilbert's (1974) studies also found that polydipsia was not restricted to the period immediately following pellet delivery on a fixed-interval schedule of reinforcement. However, when water was continuously available, the rats in his studies engaged in more licks during the first half of each interval. Interestingly, more than 60% of all ***chew/bite bottle*** (frequency & duration) occurred during PRPs, and the values were also at their peak during the ***middle 30 minutes***. Therefore, when ***drinking*** was most likely to occur during PRPs, the ***aggressive bottle-directed behaviour*** was also restricted to the PRPs. In addition, more than half of frequency and duration of ***sniff bottle*** and ***sniff and touch bottle*** occurred during the PRPs. Clearly, rats were attracted towards the water source during the PRPs. However, the ***behaviours directed towards the bottle*** varied greatly in topography (from ***exploration*** in the form of ***sniffing and touching*** to ***aggression*** in the form of ***chewing/biting*** to ***drinking***).

The other ***aggressive behaviour***, namely ***chew/bite object***, also tended to be restricted to the PRPs, particularly during the ***middle*** and ***last 30 minutes***. Other ***object-directed behaviours*** were also prominent during the PRPs. Although less than 50% (but >40%) of these measures took place during the PRPs in the ***first 30 minutes***, by the middle of the session, more than 80% of all

exploratory behaviour directed towards the objects took place during the PRPs. Thus, rats in the FIOS group were also attracted towards the stimulus objects during the PRPs. As with the ***bottle-directed behaviours***, the topography of ***behaviours directed towards the objects*** varied greatly (from ***exploration*** in the form of ***sniffing and touching*** to ***aggression*** in the form of ***chewing/biting***).

The lowest overall percentages were obtained for ***bar-related behaviour***. Less than 40% of the frequency measures and less than 51% of the duration measures took place during the PRPs. If the stimuli present during PRPs are negative predictors of food, and tend to suppress operant responding (Dinsmoor, Lee & Brown, 1986), then one would expect less time to be spent around the food-trough and bar area. However, obviously the rats did still engage in ***bar-related*** activities during the PRPs.

More than a third (<50%) of frequency and duration of ***propping*** and more than half of frequency and duration of ***digging/burying*** took place during the PRPs in the ***first 30 minutes*** of ***fixed-interval*** sessions. During the ***last 30 minutes***, more than two thirds of these measures occurred during PRPs. Although behaviour was ***directed towards the peripheral areas*** of the box during any period of zero instrumental responding throughout the session, towards the end of sessions most of this behaviour took place during the PRPs. As the ***fixed-interval*** session progressed, rats began to direct more of their ***behaviour towards the outer perimeters*** when food was least likely to be obtained. Both ***propping*** and ***digging/burying*** may represent ***escape-directed behaviours***, or attempts to explore beyond the confines of the box. It is not surprising, that they would engage in these behaviours when food was (predictably) not available at the known food source.

Large proportions of frequency and duration of ***displacement*** also took place during PRPs (>50%). Again, as the ***fixed-interval*** session progressed, more bouts of this behaviour took place during PRPs, and most of the time spent engaged in this behaviour occurred during these predictable periods of non-reinforcement.

Along with the findings of Experiment 1 (Hypothesis 1), it is clear that given the chance to engage in a variety of behaviours, rats showed heightened activity during periods of zero instrumental responding. They engaged in ***behaviours directed at a water source***, ***stimulus objects***, and ***outer perimeters*** of the experimental box (& so on). However, rats also engaged in ***resting/sleeping*** during these periods. During the ***middle*** and ***last 30 minutes***, more than 80% of this ***inactivity*** took place during the PRPs for both groups. Thus, the PRPs included periods of both ***activity*** and ***inactivity***.

The aversive nature of the stimuli present during the PRPs (negative predictors of food) may be reflected in the presence of the ***aggressive behaviours*** (***chew/bite bottle*** & ***chew/bite object***). However, adaptive ***exploratory behaviours*** were also a feature of PRPs. The predictability of the ***fixed-interval*** schedule and PRPs may be reflected in the presence of ***resting/sleeping***. It should be noted that the actual amount of time spent engaged in ***resting/sleeping*** during ***fixed-interval*** sessions was quite low (see section 9.3.5.6). If this ***inactivity*** was observed, it tended to take place during PRPs. Thus, a full range of behaviours took place during PRPs of the FI60-s schedule.

9.4.1.2 HYPOTHESIS FOURTEEN: EFFECT OF NOVEL STIMULUS OBJECTS ON PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs OF FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Some support was found for the prediction that the presence or absence of objects during ***fixed-interval*** sessions would have an effect on the proportion of non object-related behaviours that occurred during PRPs. That is, there was ***partial support for Hypothesis 14***. The presence or absence of objects had an effect on the proportion of frequency and duration of <u>some</u> of the non object-directed behaviours that occurred during PRPs.

During the ***first 30 minutes***, when objects were <u>absent</u> (FIOE group), the proportions were <u>lower</u> (>10% difference) for frequency of ***drinking*** and ***resting/sleeping***, and <u>lower</u> (>6% difference) for duration of ***drinking***, ***propping*** and ***resting/sleeping*** (almost 35% lower). For this same group, the proportion was <u>higher</u> (about 6.5%) for the duration of ***chew/bite bottle***. Thus, a greater proportion of ***drinking*** and ***resting/sleeping*** and time spent ***propping*** took place during PRPs when there were objects to explore. Similarly, the presence of objects seemed to reduce the proportion of time spent engaged in ***chew/bite bottle*** during PRPs. That is, the ***aggression*** displayed by the FIOE rats was only ***directed towards the water source*** during PRPs, whereas the FIOS rats were also able to direct ***aggression towards the stimulus objects***.

For the ***middle 30 minutes***, when objects were <u>absent</u> (FIOE group), the proportions were <u>higher</u> (between 5% & 20%) for the frequency and duration of ***drinking***, ***chew/bite bottle***, ***sniff and touch bottle***, and frequency of ***sniff bottle***. That is, if there were no objects to explore, higher proportions of ***behaviour directed towards the bottle*** took place during PRPs (except duration of ***sniff bottle***). In the absence of objects, the proportions were also <u>higher</u> for the duration of

propping. That is, proportionately more time (<10%) was spent ***propping*** during PRPs when there were no objects to investigate.

During the ***last 30 minutes***, when objects were absent (FIOE group), the proportions were lower (by up to 16%) for frequency and duration of ***digging/burying***, frequency of ***propping***, and duration of ***drinking***, ***chew/bite bottle*** and ***sniff bottle***. Thus, if there were no objects to explore, there was proportionately less time spent ***drinking*** or ***sniffing*** and ***chewing/biting the bottle*** or ***digging/burying*** during PRPs. There were also proportionately fewer bouts of ***digging/burying*** and ***propping*** during PRPs. In the absence of objects, the proportions were higher (by about 6%) for duration of ***sniff and touch bottle*** and ***bar-related behaviour***. That is, during the latter part of session, proportionately more time was spent ***investigating the water source*** (via ***sniffing & touching***) and area around the known food source, if there were no objects to explore.

Overall, the presence or absence of objects appeared to have little effect upon the proportion of behaviours that occurred during PRPs. Thus, the ***fixed-interval*** schedule itself (& part of session), rather than the presence of objects (potential alternative sources of stimulation or food), appeared to affect the proportion of behaviours taking place during PRPs. However, presence of objects did have an effect upon proportion of potentially aberrant ***chew/bite bottle*** (***aggression***), ***drinking*** (***polydipsia***) and ***propping*** (***escape-directed behaviour***) that occurred during PRPs in every part of session (although the effects varied depending upon the part of session).

9.4.1.3 HYPOTHESIS FIFTEEN: WITHIN-SESSION CHANGES IN PROPORTION OF BEHAVIOURS OCCURRING DURING PRPs (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Hypothesis 15 predicted that within-session changes in the proportions of behaviours occurring during PRPs might occur. Furthermore, it was expected that higher percentages of total frequency and duration might be observed as the session continues, since PRPs might stabilise over the 3.5-hour session. That is, higher percentages were expected to occur during the ***last 30 minutes*** than during the ***first 30 minutes***.

Hypothesis 15 was supported, with respect to all of the frequency measures for both groups. It was also supported, with respect to the duration measures (with two exceptions). The exceptions were for duration of ***drinking*** in the FIOS group (which was almost the same during the ***first & last 30 minutes***), and duration of ***chew/bite bottle*** in the FIOE group.

Thus, if objects were present during ***fixed-interval*** sessions, the percentage of total time spent ***drinking*** during PRPs stabilised quickly. Right from the ***first 30 minutes*** onwards, FIOS group rats confined most of their ***drinking*** time to the PRPs. For both groups, the most ***stable*** PRP ***drinking*** performances occurred during the ***middle 30 minutes***, when almost all of their ***drinking*** took place during PRPs. Interestingly, in the absence of objects (FIOE group), percentage of total time spent ***chewing/biting the bottle*** also peaked during the ***middle 30 minutes***. The high percentages for both behaviours suggest that ***drinking*** and ***aggression towards the source of water*** appear to be linked or triggered by the stimuli that are associated with non-food reinforcement. After reaching its peak during the earlier parts of session, the percentage of total duration of ***chew/bite bottle*** occurring during PRPs (for the FIOE group) decreased slightly during the ***last 30 minutes***.

More bouts of each of the scored behaviours (percentage of total frequency) took place during the PRPs as the ***fixed-interval*** sessions progressed. Similarly, more time was spent engaged in each of the behavioural categories (percentage of duration) during PRPs over the 3.5-hour long sessions, apart from the exceptions already mentioned. One would certainly expect that the rats would become more accustomed to the schedule requirements over time. That is, the predictability of the ***fixed-interval*** schedule would result in more stable and predictable PRPs, or periods of non-operant responding. Notably, the percentage of frequency of ***resting/sleeping*** and ***object-directed behaviours*** (for the FIOS group) occurring during the PRPs increased substantially over the session. Thus, rats were most likely to engage in bouts of ***exploratory behaviour directed at stimulus objects*** (sources of stimulation & potential food), as well as periods of ***inactivity*** during the stable and predictable PRPs.

9.4.2 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE DURING THE PRPs, OVER SCHEDULE SESSIONS, BETWEEN PART OF SESSION, AND BETWEEN GROUPS

Visual inspection of Figures 9.8 - 9.12:III (inclusive) indicates that when objects were present during ***fixed-interval*** sessions, in most cases, the frequency and duration of ***bar-related behaviour*** and ***resting/sleeping*** occurring during PRPs was lower. That is, with objects to explore, these rats spent less PRP time ***inactive*** or engaged in behaviour centered at the only known food source. They engaged in these activities during other periods of non-operant responding.

There were relatively few bouts of ***sniff bottle***, ***chew/bite bottle*** and ***drinking*** during the PRPs in either group. Thus most of the ***behaviours directed towards the water source*** took place outside the PRPs (except ***exploratory sniffing & touching***). This is certainly contrary to the findings of Falk (1971), with respect to ***polydipsia***, which occurred almost exclusively during the PRPs. However, as shown in section 9.3.7.5, less than 10% of total session time was spent engaged in ***drinking***, so this behaviour was clearly not ***excessive***, and could not be classified as ***polydipsia***. If objects were present, less cases of ***sniff and touch bottle*** occurred and less time was spent in this behaviour and more bouts of ***drinking*** and ***displacement*** occurred and more time was spent in those activities during the PRPs. For these rats, these activities took place during other periods of non-operant responding.

9.4.3 CHANGES IN BEHAVIOURS DURING PRPs OVER SCHEDULE SESSIONS, BETWEEN PART OF SESSION, AND BETWEEN OBJECT CONDITIONS

Visual inspection of the Figures mentioned in the previous section identified general patterns or trends during the PRPs, whereas this section discusses the statistically significant differences that were found.

(a) Changes over ***fixed-interval*** sessions

Over the three ***fixed-interval*** sessions only the duration of ***drinking*** showed a statistically significant difference. The time spent ***drinking*** during the PRPs tended to increase over sessions. A greater proportion of this behaviour took place during the PRPs over time. Thus, although ***drinking*** was not ***excessive***, perhaps given more time, this behaviour may have tended to occur during PRPs, like the ***polydipsia*** of rats in Falk's (1971) study.

(b) Differences between parts of session

The differences between the parts of session (***first***, ***middle*** or ***last 30 minutes***) were not statistically significant for any measure of behaviour. That is, the part of session had no apparent effect upon the frequency or duration of behaviours occurring during the PRPs. This suggests that the stability or predictability of the PRP did not vary over the 3.5 hour long session (no within-session changes).

(c) Differences between object conditions

No measure of behaviour showed statistically significant differences between the object conditions. Thus the presence or absence of objects during these sessions had no apparent effect upon the frequency or duration of behaviours occurring during the PRPs.

(d) Interaction effects

Object by part of session by session **interaction effect**

An ***object by part of session by session*** interaction was found for the duration of ***sniff and touch object*** (Figure 9.9). This measure was affected by all three grouping variables during schedule sessions. It should be noted that objects were only present in the FIOS group, so there was obviously an effect of object. There was a slight increase in time spent ***sniffing and touching objects*** during the PRPs over sessions, but this increase was actually restricted to the ***last 30 minutes***. Thus, over sessions, the time spent ***exploring the objects*** tended to be restricted to the PRPs during the latter part of session. That is, when the food source was temporarily and predictably depleted, rats were most likely to direct ***exploration*** in the form of ***sniffing and touching*** towards the objects.

9.4.4 THE MOST FREQUENTLY OCCURRING BEHAVIOURS, AND ONES OF LONGEST DURATION IN SCHEDULE AND EXTINCTION SESSIONS

9.4.4.1 HYPOTHESIS SIXTEEN: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Hypothesis 16 predicted that the absence of objects would allow rats in the FIOE group to devote more time and effort to other non-object directed behaviours (reflected in higher frequency & duration scores). Furthermore, it was expected that the absence of "distracting" objects would allow the FIOE rats to engage in more ***bar pressing*** and ***drinking*** (frequency & duration).

Hypothesis 16 was supported, with respect to the frequency and duration measures for most of the non object-directed behaviours during all three parts of session (***first***, ***middle*** & ***last 30 minutes***). Without objects to "distract" them during ***fixed-interval*** sessions, the FIOE rats were able to engage in more non-object behaviours. However, during the ***first 30 minutes***, the frequency and duration of ***chew/bite bottle*** was markedly lower and the ***sniff bottle*** measures were also lower. During the ***middle 30 minutes***, the frequency and duration of ***propping*** was markedly lower, whilst the frequency of ***displacement*** and duration of ***sniff bottle*** was also lower. During the ***last 30 minutes***, the frequency and duration of ***chew/bite bottle*** was markedly lower. In addition, the frequency and duration of ***propping*** and frequency of ***displacement*** was also lower.

Thus, the presence of objects tended to result in increased ***aggression*** directed towards the water source (***chew/bite bottle***) during the ***first*** and ***last 30 minutes***. Rats that were able to explore objects, also tended to direct more ***exploratory behaviour*** in the form of ***sniffing*** towards the water source during the earlier parts of session.

During the ***middle*** and ***last 30 minutes***, more time and effort was directed towards the ***peripheral areas of the box*** (***propping***) if objects were present. That is, the presence of objects appeared to increase ***escape-directed behaviour*** or the attempts to explore beyond the confines of the box. The chance to explore stimulus objects may have elicited other ***exploratory responses***, which were ***directed towards the peripheral areas*** once it was clear that the objects did not provide an alternative source of food during the ***first 30 minutes*** (or habituation took place). The frequency of ***displacement*** was also higher during the latter parts of session, if objects were present. Thus, there were more bouts of this behaviour (but the time spent engaged in ***displacement*** was not greater). That is, there were more bouts of shorter duration if objects were present, but habituation towards the objects may have occurred (*i.e.*, during the latter parts of session).

Hypothesis 16 was <u>not</u> supported, with respect to measures of ***bar pressing*** and ***drinking***. Without objects present to "distract" them during ***fixed-interval*** sessions, the FIOE group actually engaged in <u>less</u> ***bar pressing*** and ***drinking.*** During the ***first 30 minutes***, these measures were lower for this group (with the exception of duration of ***drinking***, which was slightly higher). During the ***middle 30 minutes***, the frequency and duration of ***bar pressing*** and ***drinking*** was lower (noticeably so for ***drinking***), and markedly so for the ***last 30 minutes***. Thus, the opportunity to ***explore stimulus objects*** did not "distract" rats or prevent them from engaging in ***bar pressing*** or ***drinking***. If the objects elicited exploration, but the rats discovered no alternative sources of food, then they may have directed more effort towards obtaining food from the only known food source. One might argue that the extra activity in the form of ***bar pressing*** and ***object-directed exploration*** resulted in more ***drinking*** due to increased thirst (particularly since ***drinking*** did not appear to be ***schedule-induced***).

9.4.4.2 HYPOTHESIS SEVENTEEN: EFFECT OF NOVEL STIMULUS OBJECTS ON FREQUENCY AND DURATION OF BEHAVIOURS DURING EXTINCTION (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Hypothesis 17 predicted that <u>higher</u> frequency and duration of ***object-directed behaviours*** would be observed in the FIOE group during ***extinction***, since this was their first encounter with objects. ***There was some support for Hypothesis 17***. The main exception was frequency and duration of ***chew/bite object***, which was lower for the FIOE group (markedly so during the earlier parts of session). Thus, when objects were first encountered during ***extinction*** there was less ***aggression*** or ***chewing/biting of objects***, than if objects were first encountered during ***fixed-interval*** sessions. Thus the topography of the ***behaviour directed towards the objects*** during ***extinction*** was different depending upon when objects were first encountered.

As expected, during the ***first*** and ***last 30 minutes***, the measures of ***sniff object*** and ***sniff and touch object*** were indeed higher for the FIOE group (frequency of ***sniff & touch object*** was slightly less during the ***first 30 minutes***). For the ***middle 30 minutes***, the frequency of all three ***object-directed behaviours*** was actually lower for the FIOE group (*i.e.*, Hypothesis 17 was not supported). By contrast, duration of ***sniff and touch object*** was much higher in this group, as was duration of ***sniff object*** (as predicted). Thus, there were fewer bouts but of longer duration for ***sniff object*** and ***sniff and touch object*** if objects were first encountered during ***extinction***.

No firm expectations were held for the other non-object behaviours. During the ***first 30 minutes***, the FIOE frequency scores were lower for all the other behaviours, except ***digging/burying*** and ***sniff bottle*** (identical score in both groups). The FIOE duration scores were lower for ***digging/burying***, ***propping***, ***displacement***, ***bar pressing*** and ***resting/sleeping***. Thus, for many of the non object-directed behaviours in the FIOE group, there were fewer bouts but of longer duration during the ***first 30 minutes*** of ***extinction***.

During the ***middle 30 minutes*** of ***extinction***, the FIOE frequency scores were lower for all but ***sniff bottle*** and ***bar-related behaviour***. The frequency of ***bar pressing*** was similar in both groups. The FIOE duration scores were lower for some of the other behaviours, except ***drinking***, ***sniff bottle***, ***propping***, ***bar-related behaviour*** and ***resting/sleeping***. The duration of ***bar pressing*** was similar in both groups. The duration of ***resting/sleeping*** was particularly high for the FIOE group.

For the other behaviours during the ***last 30 minutes*** of ***extinction***, the FIOE frequency scores were lower for all other behaviours except ***sniff bottle***. The FIOE duration scores were lower for ***digging/burying***, ***drinking***, ***chew/bite bottle***, ***sniff and touch bottle***, ***propping***, and ***resting/sleeping***. Duration scores of ***resting/sleeping*** were very high for both groups, but noticeably higher for the FIOS group.

9.4.4.3 HYPOTHESIS EIGHTEEN: WITHIN-SESSION CHANGES IN BEHAVIOUR DURING FI60-s SCHEDULES (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Hypothesis 18 predicted that late session decreases in ***bar pressing*** would occur during ***fixed-interval*** sessions, as a result of satiation or habituation to the reinforcer (McSweeney & Roll, 1998). There was ***partial support for this***. A habituation or satiation effect was only experienced if objects were absent during the 3.5-hour long ***fixed-interval*** sessions. For the FIOE group, there was indeed a late session decrease in frequency and duration of ***bar pressing***, as well as a decrease in the number of ***reinforcers*** obtained.

When objects were present during ***fixed-interval*** sessions (FIOS group), there were no late session decreases in frequency of ***bar pressing*** (the duration scores did decrease). Furthermore, the number of ***reinforcers*** obtained did not decrease (there was a minimal increase during the ***middle & last 30 minutes***). Thus rats did not appear to satiate or habituate to the reinforcer over the 3.5-hour session if objects were there to be explored.

Hypothesis 18 also predicted that there would be late session decreases in the ***object-directed behaviours***, as a result of habituation towards the objects. ***There was some support for this***. Certainly, there was a noticeable decrease in ***sniff object*** and ***sniff and touch object*** over the 3.5 hour long ***fixed-interval*** session. However, whilst the frequency of ***chew/bite object*** also showed a late session decrease, the duration of this behaviour in fact increased. The topography of the response towards the stimulus appeared to come into play. The time spent engaged in ***aggressive behaviour directed at the objects*** (***chew/bite object***), increased over the session, whereas ***exploratory sniffing and touching*** responses decreased.

Finally, Hypothesis 18 predicted that different behaviours might peak at different times throughout the ***fixed-interval*** session. There was ***partial support for this***. The frequency and duration measures for most of the behavioural categories peaked during the ***first 30 minutes***. However, there were a number of measures that peaked later in the session for both groups.

If objects were present during the ***fixed-interval*** sessions (FIOS group), the frequency score for most of the behaviours peaked during the ***first 30 minutes***. The exceptions were frequency and duration of ***propping***, ***resting/sleeping*** and ***displacement,*** frequency of ***bar pressing***, and duration of ***chew/bite object***. As already mentioned, habituation towards the objects (***sniffing & touching***) occurred early in the session, but ***aggression towards the objects*** increased over the session. ***Drinking*** and all the ***bottle-directed behaviours*** also peaked early in the session. Thus habituation towards the objects and bottle appeared to occur quickly. As a result, more time and effort was directed towards the ***peripheral areas of the box*** (***escape-directed propping***), ***displacement***, ***resting/sleeping*** (***inactivity***) and ***bar pressing***.

In the absence of objects (FIOE group), the frequency of all behaviours and most of the duration scores also peaked during the ***first 30 minutes***. The exceptions were frequency and duration of ***resting/sleeping*** and duration of ***chew/bite bottle***, ***sniff and touch bottle***, and ***displacement***.

Thus irrespective of presence or absence of objects during ***fixed-interval*** sessions, frequency and duration of ***resting/sleeping*** increased after the ***first 30 minutes***. This may have occurred as a result of fatigue. Duration of ***displacement*** also increased after the ***first 30 minutes*** in both groups. This suggests that the aversive features of the situation increased as the 3.5-hour session progressed.

9.4.4.4 HYPOTHESIS NINETEEN: WITHIN-SESSION CHANGES IN BEHAVIOUR DURING EXTINCTION (WHEN A WATER SOURCE IS CONCURRENTLY AVAILABLE)

Hypothesis 19 predicted that late session decreases in ***bar pressing*** would occur as this response extinguished. ***Hypothesis 19 was supported***. There was indeed a late session decrease in frequency and duration of ***bar pressing*** for both groups, as the ***bar pressing*** response extinguished over the 3.5-hour long session.

Hypothesis 19 also predicted that late session decreases in ***object-directed exploration*** would occur, as a result of habituation towards the objects. ***Hypothesis 19 was supported***, with respect to most of the measures of ***object-directed behaviours***. Rats in the FIOS group (first encountered objects during ***fixed-interval*** sessions) did indeed habituate to the objects during extinction. However, for the group that first encountered objects during ***extinction*** (FIOE group), the duration of ***sniff and touch object*** in fact increased quite noticeably. Thus, the time spent engaged in ***sniffing and touching the objects*** by the FIOE rats did not show a habituation effect. For this group, novelty of objects or arousal was greatest. The FIOS group had already encountered objects during ***fixed-interval*** sessions, and discovered that they did not provide an alternative source of food. They were less aroused when a second group of objects was encountered during ***extinction***. The FIOE group, on the other hand, encountered objects when the food source was depleted and objects were most novel (arousal was greatest). As the ***bar pressing*** response extinguished, they were able to direct more time and effort to this alternative source of stimulation or possible food source.

There was also ***partial support for Hypothesis 19***, with respect to the prediction that different behaviours might peak at different times throughout the session. The frequency and duration measures for most of the behavioural categories peaked during the ***first 30 minutes*** in both groups. That is, the rats appeared to be most active during the earliest part of session, when ***bar pressing*** activity was at its peak (as a result of spontaneous recovery in the last two sessions).

For the FIOS group, the frequency and duration of ***resting/sleeping*** and duration of ***propping***, ***displacement***, ***sniff and touch bottle***, and ***bar-related behaviour*** peaked in the latter parts of session. Thus as the ***bar pressing*** response extinguished and the rats habituated towards the objects (within each session), more time and effort was directed towards the outer perimeters of the box (***propping***) in an attempt to escape or explore outside the box. More time was also spent around the food trough area (***bar-related behaviour***), which may reflect foraging activity around the only known food source. These rats also spent more time in ***displacement activities***, indicating that the depleted food source, lack of alternative sources of food and inability to leave the box led to increased conflict. The FIOS rats spent more time ***sniffing and touching the bottle***, spending more time exploring the water source as the session wore on, and also became less active (more ***resting/sleeping***).

For the FIOE group, the frequency and duration of ***bar-related behaviour*** and ***resting/sleeping***, and the duration of ***sniff and touch object*** and ***displacement*** peaked later in the session. Thus, if objects were first encountered during ***extinction***, these rats also spent more time foraging around the only known food source, ***resting/sleeping*** and engaged in ***displacement activities***. Unlike the FIOS rats, these rats did not direct more time towards exploring the outer perimeters of the box. The ***sniffing and touching exploratory behaviour*** was directed towards the objects rather than the water source in this group as the session wore on.

Thus irrespective of presence or absence of objects during ***extinction*** sessions, frequency and duration of ***resting/sleeping*** increased after the ***first 30 minutes***. This may have occurred as a result of fatigue or in an attempt to conserve energy when there was no food immediately available (but would be at the end of the session, when the rat was returned to the home cage). Duration of ***displacement*** also increased after the ***first 30 minutes*** in both groups. Interestingly, these patterns and comments applied to both the ***fixed-interval*** and ***extinction*** sessions. Thus the aversive properties of both the ***fixed-interval*** schedule (with its predictable periods of non-reinforcement) and ***extinction*** (depletion of food source) increased as the 3.5-hour session progressed.

9.4.5 PERCENTAGE OF HALF-HOUR SESSION SEGMENT TIME SPENT ENGAGED IN EACH BEHAVIOURAL CATEGORY, OVER SESSIONS, AND BETWEEN GROUPS

(a) The schedule sessions

Not scored category

Both groups spent more than a third of total session time (<56%) engaged in behaviours that were ***not scored*** (except during the ***first 30 minutes*** of session 1 in the FIOS group). Although this study scored a wide range of behaviours, it was unable to cover every possible category. Much of this not scored category was ***general ambulatory behaviour***. Without objects to explore, the FIOE group spent less time engaged in ***not scored*** behaviours as each session lengthened (within-session decrease). There was a large within-session increase in session 1, but little change within-sessions for the later sessions for the FIOS group. If this category represented ***general ambulatory behaviour*** (mainly), then the presence of objects ensured that rats remained active throughout the session. In order to continue ***exploring*** and ***monitoring the objects***, the rats still moved actively around the apparatus. Once the apparatus itself had been investigated thoroughly, the FIOE rats probably spent less time moving away from the food source.

Behaviour directed at the bar and food-trough area

Both groups spent less than 20% of total session time (>7%) engaged in ***behaviour directed at the bar and food-trough area*** (except during one part of session). If objects were absent, rats spent more time engaged in ***behaviour directed at the bar and food-trough area*** (except during the ***first 30 minutes*** of session 1). Within-session decreases in these behaviours occurred in the FIOS group. Perhaps as a result of satiation, the rats spent more time exploring the objects. Clearly the presence of objects resulted in less behaviours centred at the food source. For both groups there was a decrease in ***behaviour directed at the bar and food-trough area*** over sessions, as the ***fixed-interval*** performance became more efficient.

Behaviour directed at the stimulus objects

During ***fixed-interval*** sessions, the FIOS group spent less than 20% (but >6.5%) of total session time engaged in ***object-directed behaviours***. More time was directed towards the objects over sessions, suggesting that habituation did not take place. That is, the objects retained novelty for 10.5 hours of contact. In fact, during the third ***fixed-interval*** session, these rats still engaged in ***object-directed exploration*** for more than 15% of total session time. The objects, and behaviours directed towards them, may have helped the rats more accurately time the interval between reinforcements. There was no clear within-session pattern.

Behaviour directed at the peripheral areas of the box

Both groups devoted less than 8% of total session time (>1.5%) to ***propping***. There were no clear within-session or between-session patterns. Thus although rats did direct ***behaviours towards the peripheral areas of the box***, in an attempt to escape or explore outside the apparatus, in many cases very little session time was actually spent ***propping***. Therefore, the regular availability of food at the only known food source limited the amount of time spent exploring the outer perimeters of the apparatus (or attempting to escape).

Behaviour directed at the water bottle

If objects were present (FIOS group) during ***fixed-interval*** sessions, rats spent noticeably more time (>10%) engaged in ***bottle-directed behaviours*** (***chew/bite bottle***, ***sniff bottle*** & ***sniff & touch bottle***) during the ***first 30 minutes*** of each session. The presence of objects, when they were most novel or arousing (start of each session), appeared to increase ***exploratory behaviour*** directed at other sources as well (the bottle). For this group of rats, there was a clear within-session decrease in percentage of total session time engaged in ***bottle-directed behaviours***. A decrease over sessions also tended to occur. Thus, the longer they were exposed to the stimulus objects, the less they explored the bottle (a habituation effect). If objects were absent, rats tended to direct more activity towards the bottle (within and between sessions) over time. That is, the opposite effect was seen. With no other objects to explore, the rats directed more behaviour towards the only object in the apparatus (the bottle). The FIOE rats spent almost 20% of total session time in ***bottle-directed behaviours*** during the ***middle 30 minutes*** of session 3.

Both groups spent less than 10% (>1.9%) of total ***fixed-interval*** session time ***drinking*** (except the FIOS group during the ***first 30 minutes*** of session 3). The percentages tended to show a within-session decrease, but a between-session increase. Possibly as a result of satiation to the reinforcer (& therefore less ***thirst***), the rats spent less time ***drinking*** towards the end of each 3.5-hour session. However, over sessions, ***drinking*** had not yet reached a ceiling effect and continued to increase slightly.

Aggressive behaviours

The FIOS group spent up to 21% of the ***first 30 minutes*** of ***fixed-interval*** time engaged in ***aggressive behaviours*** (***chew/bite object*** & ***chew/bite bottle***). The rats tended to devote less time to these behaviours as the session drew to a close (within-session decrease), but tended to spend more time in ***aggression*** over sessions (between session increase). That is, the more time that they spent with the bottle and objects overall, the more ***aggressive*** they became. In the absence of conspecifics (who represent competition for food), the bottle and objects may provide convenient targets (Holme, 1990; Lucas, Timberlake & Gawley, 1988), during aversive periods negatively correlated with reinforcement. These levels of ***aggression*** appear to be quite ***excessive*** most of the time. Less than 10% of total session time was spent ***chewing/biting the bottle*** in the FIOE group. In the absence of objects, this group displayed low levels of ***aggression***, except during the ***middle 30 minutes*** of session 3 (almost 10%). Thus, the more targets there are, the more ***aggression*** rats direct towards inanimate objects during ***fixed-interval*** sessions. The amount of time spent ***chewing/biting the bottle*** tended to show a within-session and between-session increase.

Other behavioural categories

Both groups spent more than 10% of total (part of session) time engaged in ***displacement*** in a number of cases (between 5% & 15%). If objects were present during ***fixed-interval*** sessions (FIOS group), less time was spent in ***displacement*** during the ***first 30 minutes***. Thus the presence of objects (when they were most novel) reduced the apparent conflict or aversiveness of the ***fixed-interval*** schedule (with its predictable periods of non-reinforcement). When food was not available, the FIOS rats were able to leave the food source and explore the objects (potential sources of food or stimulation). Both groups tended to spend more time in ***displacement*** as the session wore on (within-session increase), and they tended to spend more time in this activity over sessions. Thus the ***fixed-interval*** schedule, with its extinction-like periods of non-reinforcement (Flory, 1969), appears to become more aversive over time. During the latter parts of session in the FIOS group and in all parts of session (except one) in the FIOE group, the amount of time (>10%) devoted to ***displacement*** appears to be ***excessive***. It had probably not yet reached its peak or ceiling (particularly in the FIOE group), since the levels tended to increase over sessions. ***Displacement*** may have become an ***adjunctive behaviour*** and resemble the ***over-grooming*** observed in some zoo (or other captive) animals (Shepherdson, 1989).

Very little total session time was spent ***digging/burying*** by both groups (<3%). It tended to decrease within each session. Perhaps as a result of satiation to the reinforcer, the rats spent less time foraging through sawdust or attempting to escape the box via ***digging***. Without objects to explore, the FIOE group tended to spend slightly more time ***digging/burying***.

If objects were present, rats spent relatively little time (<7%) engaged in ***resting/sleeping*** (with the exception of the ***last 30 minutes*** of session 1). Without objects to explore, the FIOE rats tended to spend more than 10% of total session time during the latter parts of session (& even >20% in one part of session) engaged in this behaviour. Thus, the lack of objects or potential alternative sources of food (or stimulation) for the rats to investigate resulted in greater levels of ***inactivity*** (once satiated or fatigued). The levels could be considered ***excessive*** in this group, although not necessarily maladaptive, since energy was being conserved.

(b) The extinction sessions

Not scored category

In most cases, both groups spent less than a third of total session time (>7%) engaged in behaviours that were ***not scored***. The amount of time spent in this category was much lower during ***extinction*** (than ***fixed-interval*** sessions), when the rats spent more time ***resting/sleeping***, and less time moving around the apparatus. There was a marked within-session decrease and also a slight decrease over sessions for both groups. Thus as ***bar pressing*** extinguished, less time was spent in ***not scored*** behaviours, or ***general ambulatory activities***.

Behaviour directed at the bar and food-trough area

Once the food source was depleted, both groups spent less total session time (between 2% & 15%) engaged in ***behaviour directed at the bar and food-trough area*** (with two exceptions during the ***last 30 minutes***). Once food was no longer available, the rats spent more time exploring other areas of the apparatus (searching for alternative food sources or stimulation). There tended to be a noticeable within-session increase in time spent centred at the only known food source. That is, once the objects and other areas had been investigated and food was not discovered, the hungry rats returned to the only known food source. The time spent engaged in ***behaviour directed at the bar and food-trough area*** decreased over sessions as the ***bar pressing*** response extinguished (except during the ***last 30 minutes*** for the FIOE group). Since between 3.49% and 14.59% of the ***last 30 minutes*** of the third ***extinction*** session was still spent in ***activities centred at the bar and food trough area***, clearly more sessions were required to completely extinguish ***bar pressing***. However, hungry rats may continue to check a depleted food source, no matter how much time has passed, if it is the only known food source. In the wild, food sources may be seasonal or sporadic, so returning to these areas periodically would be adaptive.

Behaviour directed at the stimulus objects

During ***extinction***, both groups spent less than a third (but >8%) of total session time engaged in ***object-directed behaviours***. For the FIOE group, this figure never fell below 15%. Although a within-session decrease was observed for both groups (except session 5 for the FIOE group), habituation did not appear to take effect over the three sessions. Again, the objects retained novelty for 10.5 hours of contact. During the third ***extinction*** session, these rats still engaged in ***object-directed exploration*** for more than 10% of total session time (>20% in two parts of session). ***Extinction*** certainly seemed to elicit more ***exploratory behaviour*** initially (see Forster, 1995). That is, even for the FIOS group that had already encountered objects prior to ***extinction***, the levels of ***object-directed exploration*** were higher during the first ***extinction*** session and ***first 30 minutes*** of every ***extinction*** session. For the FIOE group, which had no prior contact with stimulus objects, the levels of ***object-directed exploration*** in the first ***extinction*** session were noticeably higher than for the FIOS group's encounter with either set of objects.

Behaviour directed at the peripheral areas of the box

Both groups spent less than 10% of total session time (>2.5%) engaged in ***propping***. The FIOS group spent more time engaged in this ***escape-directed behaviour*** in all parts of session. Thus previous experience with objects that did not provide an alternative source of food appeared to lead to increases in ***behaviour directed at the outer perimeters of the box***. Although not an ***excessive*** amount, there was a clear increase over sessions for both groups. The depletion of the food source (& extinction of ***bar pressing***) coupled with the fact that the objects did not provide an alternative source, led to rats that attempted to explore outside the box. In the wild, hungry rats would clearly need to leave a depleted food source and search for food elsewhere (in or beyond their home range).

Behaviour directed at the water bottle

As much as 23% of total session time was spent in ***bottle-directed behaviours*** (***chew/bite bottle, sniff bottle & sniff & touch bottle***) during the ***first 30 minutes*** of ***extinction*** sessions (>7% in both groups). Thus the earliest parts of ***extinction*** (food source depletion) tended to increase all ***exploratory activity directed towards the bottle***, especially in the FIOE group. For the FIOE group there was a clear within-session decrease, similar to the one observed in the FIOS group during ***fixed-interval*** sessions (habituation effect). Once again, the earliest exposure to stimulus objects resulted in high levels of ***bottle-directed exploration***. However, over ***extinction*** sessions, once the food source was depleted (& ***bar pressing*** became extinguished), the time spent in ***bottle-directed exploration*** tended to increase. The FIOS group patterns were less clear cut.

Percentage of total session time spent ***drinking*** dropped to very low levels (between 0% & 2.51%) during ***extinction*** in both groups. Clearly, ***drinking*** was linked to ***bar pressing*** activity and ***reinforcement***. Once the food source was depleted and ***bar pressing*** extinguished, very little

drinking took place. Thirst alone may have resulted in the ***drinking*** observed in this study. There was a within-session decrease in time spent ***drinking*** during ***extinction***. As the rats became less active over the 3.5-hour session, they also ***drank*** less.

Aggressive behaviours

Very high levels of total time spent engaged in ***aggressive behaviour*** tended to occur during the ***first 30 minutes*** of ***extinction*** sessions for both groups (between 19% & 25% in most cases). Thus the depletion of the food source resulted in far more ***aggression***, especially in the FIOS group (with two exceptions). The levels of aggression are quite low (<3%) during the latter parts of session for the FIOE group. For the FIOS group, objects had been present during both ***fixed-interval*** and ***extinction*** sessions. ***Aggression*** tended to decrease quite markedly within each ***extinction*** session, and decreased over sessions in some cases. Thus the earliest encounters with the depleted food source and objects that were at their highest level of novelty, resulted in higher levels of ***aggressive behaviour***. Whilst this activity may be related to minimising the competition from conspecifics for resources during ***fixed-interval*** sessions, it is unlikely that the rats would so actively protect a depleted food source. Thus, it may be related to frustration or have become an extinction-induced ***adjunctive behaviour*** (& was possibly already an ***adjunctive behaviour*** during ***fixed-interval*** sessions in the FIOS group).

Other behavioural categories

For the FIOS group, once the food source was depleted, the amount of time spent in ***displacement*** increased markedly during the ***first*** and ***middle 30 minutes*** of all three sessions. For four of the six parts of session, more than 20% of total session time was devoted to these activities. The situation had become more aversive. The food source was depleted, but previous experience with objects had shown that these objects did not present alternative sources of food. Furthermore, it was not possible to search for other food sources outside the box. There was a within-session decrease in ***displacement*** for this group. The percentage of total session time spent in ***displacement*** tended to be lower (<20%) for the FIOE group, although almost 30% of the ***first*** and ***last 30 minutes*** of session 5 were devoted to these activities. ***Extinction*** provided this group of rats with its first encounter with objects (maximum impact of novelty). It may not yet have reached its peak or ceiling, since the levels tended to increase over sessions (mainly in the earlier parts of session). The time spent in ***displacement*** tended to be excessive in all parts of session during ***extinction*** (aberrant or ***adjunctive behaviour*** like ***over-grooming***).

Despite the depletion of the food source, both groups of rats spent low amounts of total session time (<3%) engaged in ***digging/burying***. Levels were marginally higher during the ***first 30***

minutes of each session (when object novelty was highest). Irrespective of whether this behaviour represented a form of ***foraging*** or ***escape-directed behaviour***, total lack of reinforcement did not result in higher levels of this activity.

Both groups spent very little time ***resting/sleeping*** (<5%) during the ***first 30 minutes*** of ***extinction*** sessions (although the levels tended to be slightly higher than during ***fixed-interval*** sessions). These percentages increased dramatically in the ***middle*** and ***last 30 minutes*** of each session. The level of ***inactivity*** tended to peak during the ***middle 30 minutes*** in the FIOE group (>30%) and during the ***last 30 minutes*** in the FIOS group (up to 46%). Since the food source was depleted, the session was quite long (3.5 hours), escape from the box was not possible, and the objects did not provide an alternative source of food, the rats appeared to conserve energy by ***resting/sleeping***. Thus although apparently ***excessive***, such ***inactivity*** could not be considered maladaptive.

9.4.6 PATTERNS OF CHANGE IN EACH BEHAVIOURAL MEASURE OVER SESSIONS, AND BETWEEN GROUPS

Visual inspection of Figures 9.14(I) – 9.18:III (inclusive) showed a number of different patterns over the ***fixed-interval*** and ***extinction*** sessions. Since there are two groups of rats, with three parts of session presented on each graph, the patterns would require a lengthy discussion. The reader is urged to inspect these graphs if interested. The Figures were merely presented as an adjunct to statistical analysis.

9.4.7 CHANGES IN BEHAVIOURS OVER SESSIONS, BETWEEN PART OF SESSION AND BETWEEN OBJECT CONDITIONS

Visual inspection of the Figures mentioned in the previous section identified general patterns or trends, whereas this section discusses the statistically significant differences that were found.

9.4.7.1 SCHEDULE SESSIONS

(a) Changes over schedule sessions

Over the three ***fixed-interval*** sessions, measures of five behavioural categories showed statistically significant differences (between session effect). The frequency of ***bar pressing*** tended to increase over ***fixed-interval*** session, whereas the duration of ***bar-related behaviour*** declined over the same sessions, for both groups. This suggests that the rats' operant performance may have been improving over sessions. More ***bar presses*** were made, and less time was spent foraging in and around the food trough.

The frequency and duration of ***sniff object*** decreased sharply over sessions for the ***first 30 minutes***, whereas these measures tended to increase for the other parts of session. The sharp decline in ***exploratory behaviour*** in the form of ***sniffing*** reflects a habituation effect. There were more bouts and more time was spent ***sniffing objects*** during the ***first 30 minutes*** of each session. Repeated exposure to the objects showed a habituation effect within sessions and between sessions, for the early part of the session. However, later in each session, rats still directed ***exploratory behaviour towards the objects***. Thus the objects were still able to elicit orienting and ***sniffing*** responses. In fact, later in the sessions, there was an increase in this behaviour over sessions.

The duration of ***drinking*** increased noticeably over the three ***fixed-interval*** sessions for both groups. This suggests that ***drinking*** had not reached a ceiling effect yet, and may have continued to increase if more sessions had been run. It is probably unlikely that the rats would have become ***polydipsic***, as there was no indication of ***excessive drinking*** during any sessions, in any rat.

Over the three ***fixed-interval*** sessions, the frequency of ***digging/burying*** tended to decrease in both groups. This behaviour may be related to foraging or an attempt to escape or explore beyond the box. As the operant performance became more stable over time, the rats spent less time engaged in this particular form of foraging or escape.

(b) Differences between parts of session

The differences between the ***first***, ***middle*** and ***last 30 minutes*** (parts of session) were statistically significant for measures of seven behavioural categories (within-session effect).

Both measures of ***sniff object*** were higher during the ***first 30 minutes*** of the first two sessions. In addition, the scores showed a marked decrease over sessions for the ***first 30 minutes*** (slight increase over sessions for the latter parts of session). The frequency of ***sniff and touch object*** also reflected this trend. Scores were higher in every session, and tended to decrease over sessions for the ***first 30 minutes*** alone. Thus ***exploration of the objects*** showed a habituation effect within each session. However, a habituation effect over sessions was only observed during the ***first 30 minutes*** (but since this is when most exploratory behaviour took place, it may reflect a general habituation trend over sessions).

The frequency of ***sniff bottle*** showed noticeable within-session decreases for the FIOS group. These rats ***sniffed the bottle*** more often in the earlier parts of each session. The scores also tended to be higher during the ***first 30 minutes*** for the FIOE group, and then the ***last 30 minutes***. Thus, the presence of objects appeared to result in an orderly within-session decrease (habituation effect) in ***sniffing directed towards the bottle***.

The frequency and duration of ***drinking*** scores tended to be higher during the ***first 30 minutes*** of each session for both groups. A within-session decrease in both measures was evident for the FIOE group. If objects were absent, rats tended to engage in more bouts of ***drinking*** and spent more time devoted to this behaviour in the earlier parts of each session. This may reflect a satiation effect.

Less time was spent engaged in ***displacement*** activities in the ***first 30 minutes*** of each session in both groups. In the FIOS group, the duration of ***displacement*** tended to be highest during the ***middle 30 minutes*** of each session. The aversive nature of the situation (predictable periods of non-reinforcement) appeared to increase as the session progressed.

In the FIOE group, most bouts of ***digging/burying*** took place during the ***first 30 minutes*** of each session. The frequency of this behaviour tended to decrease within each session. Thus, if objects were absent, the number of bouts of ***digging/burying*** tended to decrease as the session wore on. Such an orderly pattern was not evident in the FIOS group. Without objects to explore, rats directed more effort towards foraging in the sawdust or attempting to escape or explore beyond the box, the longer they spent in the apparatus.

The frequency and duration scores of ***resting/sleeping*** were very low during the ***first 30 minutes*** in each group. That is, little time was spent engaged in this activity early in each session. Rats were more likely to ***rest*** or ***sleep*** during the latter stages of each 3.5-hour session. This may be as a result of fatigue or satiation. That is, they conserved energy once they were satiated or fatigued.

(c) Differences between object conditions

No measures of behaviour showed statistically different differences between the object conditions (although statistically significant ***object by part of session*** & ***object by session*** interactions were found). Whether objects were first present during ***fixed-interval*** or ***extinction*** sessions had no effect upon the frequency and duration of the various behavioural categories.

(d) Interaction effects

Object by part of session interaction effect

An ***object by part of session*** interaction was found for the frequency of ***propping***, indicating that both the object condition (present or absent), and the part of session (***first***, ***middle*** or ***last 30 minutes***) affected this behavioural measure. When objects were absent (FIOE group), frequency of ***propping*** was noticeably higher in most sessions during the ***first 30 minutes***. That is, these rats attempted to escape or explore beyond the box in the early part of each session. A decrease in this measure over sessions was also marked for the latter parts of session. Over time, these rats spent less time and effort trying to explore outside the box. When objects were present, the frequency of ***propping*** showed less noticeable differences between the parts of session.

Object by session interaction effect

The frequency of ***displacement*** yielded a statistically significant ***object by session*** interaction. Both the object condition (present or absent) and session had an effect upon this measure. When objects were absent (FIOE group), the frequency of ***displacement*** was higher in all three sessions, and showed a slight decrease over sessions. The decrease over sessions was more pronounced for the latter parts of session. For the FIOS group, which had objects present, this measure peaked in the second session (but decreased overall for the three sessions) for all three parts of session. Thus the presence of objects appeared to reduce the aversive nature of the ***fixed-interval*** schedule, since the amount of conflict-related ***displacement*** was less. The objects provided an alternative source of stimulation or potential food source.

9.4.7.2 EXTINCTION SESSIONS

(a) Changes over extinction sessions

Over the three ***extinction*** sessions (between session effect), only three measures showed statistically significant differences (although a number of behaviours yielded statistically significant ***object by session*** & ***part of session by session*** interactions). The frequency of ***bar-related behaviour*** decreased over ***extinction*** for both groups, and all parts of session, as the instrumental response was extinguished. That is, once the food source was depleted, less bouts of behaviour were centred at the food trough area.

The frequency and duration of ***propping*** increased noticeably over sessions for both groups, and all parts of session. Thus, as the ***bar pressing*** response was extinguished, the rats directed more ***behaviour towards the peripheral areas of the box***. ***Propping*** may be a form of ***escape-directed***

exploration, and since food was no longer available, the rats were attempting to explore (or search for alternate sources of food) beyond the confines of the box.

(b) Differences between parts of session

The differences between the parts of session (***first***, ***middle*** & ***last 30 minutes***) were statistically significant for measures of seven behavioural categories (within-session effect).

The duration of ***chew/bite object*** tended to decrease over ***extinction***. The scores showed a dramatic decline in the second session during the ***first 30 minutes***, in both groups. Thus, ***extinction*** did not appear to lead to increases in this behaviour, which might be considered to be an ***aggressive behaviour***.

The frequency of ***sniff and touch bottle*** was highest during the ***first 30 minutes*** of each session. Thus there was a slight within-session decrease as a result of habituation to the bottle itself. The frequency of ***chew/bite bottle*** was also highest during the ***first 30 minutes*** of every session in FIOE group, and scores tended to be lowest in the ***last 30 minutes***. For this group, the bottle was ***chewed*** most when the stimulus objects were most arousing or novel. For the FIOS group, ***chew/bite bottle*** scores were highest during the ***first 30 minutes*** of the first ***extinction*** session and then highest in the ***last 30 minutes*** for the later ***extinction*** sessions, showing the opposite effect.

The frequency and duration of ***drinking*** scores were highest in most cases during the ***first 30 minutes*** of each session. In fact, very few bouts of ***drinking***, of short duration, took place during the latter parts of session. Thus there was a slight within-session decrease during ***extinction*** sessions. In the absence of food, ***drinking*** was less likely to occur, although it tended to reappear at the start of each ***extinction*** session, when it was most likely that "spontaneous recovery" of the ***bar pressing*** response would occur. Since drinking was not ***excessive***, and may have only occurred as a result of thirst during ***fixed-interval*** sessions, the lack of food and lower energy expenditure in the form of ***bar pressing*** during ***extinction*** may account for this finding.

The frequency of ***displacement*** was highest during the ***first 30 minutes*** of each session. For the FIOS group there was a steady within-session decrease in each ***extinction*** session. Thus the depletion of the food source resulted in more conflict-related behaviours. That is, rats could either remain near the only known food source or explore other areas (objects or peripheral areas) or even attempt to escape. The scores tended to peak in the second ***extinction*** session for all parts of session.

The frequency and duration of ***digging/burying*** was highest in the ***first 30 minutes*** of each session, and tended to be lowest in the ***last 30 minutes***. A within-session decrease in the measures of this behaviour was apparent. That is, rats spent more time and effort trying to forage in the sawdust or trying to escape the box during the earliest part of every session, when the food source was depleted.

The frequency and duration scores of ***resting/sleeping*** were extremely low during the ***first 30 minutes*** of each ***extinction*** session. The frequency scores were highest during the ***last 30 minutes***, whereas duration scores were at times highest during the ***middle 30 minutes***. Thus ***resting/sleeping*** was a feature of the latter parts of session during ***extinction***. Once the food source was depleted, the objects explored and no escape was possible from the box, the rats conserved their energy by ***resting/sleeping*** more towards the end of the session.

(c) Differences between object conditions

The differences between the object conditions were not statistically significant for any measure of behaviour (although statistically significant ***object by part of session*** & ***object by session*** interactions were found). Whether objects were first present during ***fixed-interval*** or ***extinction*** sessions had no effect upon the frequency and duration of the scored behaviours.

(d) Interaction effects

Object by part of session interaction effect

An ***object by part of session*** interaction was found for the frequency of ***chew/bite object*** and the frequency of ***bar pressing***. The number of ***bar presses*** and bouts of ***chew/bite object*** were highest during the ***first 30 minutes*** of ***extinction*** sessions, indicating a within-session decrease or effect of part of session. Frequency of ***chew/bite object*** was lowest during the ***last 30 minutes*** of each session. The frequency of ***bar pressing*** was much higher during the ***first 30 minutes*** of the first ***extinction*** session and frequency of ***chew/bite object*** was higher in all ***extinction*** sessions for the FIOS group, indicating an effect of object. That is, if objects were first encountered during ***extinction***, rats engaged in less ***bar pressing*** and bouts of ***chew/bite object*** during ***extinction***. That is, ***bar pressing*** appeared to extinguish more rapidly if objects were most novel (first encounter with any), and less ***aggressive behaviour*** was directed towards those objects.

Object by session interaction effect

The frequency of ***drinking*** yielded a statistically significant ***object by session*** interaction. The scores tended to decrease slightly over ***extinction*** for the FIOE group, whereas they tended to increase or remain unchanged for the FIOS group. That is, if objects were most novel (first encountered during ***extinction***), fewer bouts of ***drinking*** took place over sessions. However, it should be noted that the frequency scores were so low during ***extinction***, that statistical analysis may not be appropriate.

Part of session by session **interaction effect**

A statistically significant ***part of session by session*** interaction was found for measures of five behavioural categories, including the frequency measures of the three ***object-directed behaviours***. The frequency and duration of ***bar pressing*** tended to be highest during the ***first 30 minutes*** of each ***extinction*** session (effect of part of session) and these scores decreased over sessions (effect of session). Thus, during ***extinction***, ***bar pressing*** measures demonstrated both within-session and between-session decreases as the response was extinguished.

The frequency of ***sniff object***, ***sniff and touch object*** and ***chew/bite object*** was highest during the ***first 30 minutes*** of each ***extinction*** session (effect of part of session). The frequency of ***sniff object*** and ***chew/bite object*** tended to decrease over ***extinction***. The frequency of ***sniff and touch object*** also decreased over sessions in the FIOE group. However, in the FIOS group, the scores increased during the latter parts of session. Thus for both groups there was a within-session decrease (habituation effect), but after the initial decrease early in the session, the group that had encountered objects during ***fixed-interval*** sessions, ***sniffed and touched objects*** more often over ***extinction*** during the latter parts of session. The frequency of ***sniff bottle*** decreased over sessions and was highest during the ***first 30 minutes*** of each ***extinction*** session, showing a within-session and between-session decrease (habituation effect).

9.4.7.3 ALL SIX SESSIONS

(a) Changes over all six sessions

Six behavioural categories showed statistically significant differences over the six sessions (between session effect). In addition, ***object by session***, ***part of session by session*** and ***object by part of session by session*** interactions, were found for a number of behavioural measures (to be discussed subsequently).

The frequency and duration of ***bar pressing*** tended to increase over ***fixed-interval*** sessions, whereas both measures of ***bar-related behaviour*** decreased over these sessions. Since the ***fixed-interval*** schedule was fairly predictable and more time was spent ***bar pressing***, the rats spent less time foraging around the food-trough area (and only did so to retrieve pellets). Both ***bar pressing*** measures and the frequency of ***bar-related behaviour*** then plummeted dramatically in the first ***extinction*** session, when the response was no longer reinforced. By contrast, the duration of ***bar-related behaviour*** increased in the first ***extinction*** session in most cases. The sudden absence of reinforcement resulted in rats spending more time in and around the food-trough area, which was the previous source of food. There was a large overall decrease in both of the ***bar pressing*** measures, and the ***bar-related behaviour*** measures also showed an overall decline across the six sessions in most cases.

The duration of ***propping*** showed an overall increase across the six sessions. The increases across ***extinction*** sessions were pronounced in both groups, although the scores tended to decrease in the first ***extinction*** session. Objects were present in both groups for the first time, in that session. More time was spent ***propping***, which may have been ***escape-directed exploration***, when the objects had been in longer. Thus during ***extinction***, when food was no longer available at the previous source, and the objects had not provided an alternative source of food, the rats spent more time ***propping*** in an attempt to leave the confines of the box.

There was an overall decrease in the frequency of ***sniff bottle*** across the six sessions, with a noticeable decrease in the first ***extinction*** session in most cases. If objects were absent during ***fixed-interval*** sessions (FIOE group), the frequency of ***sniff bottle*** tended to increase over sessions, whereas it decreased for the FIOS group. Thus the longer objects were present, the less the rats ***sniffed the bottle***. The frequency and duration of ***drinking*** tended to increase over ***fixed-interval*** sessions, and then dropped dramatically in the first ***extinction*** session. There was an overall decrease across the six sessions. More bouts of ***drinking*** occurred, and more time was spent engaged in this behaviour when food was available during ***fixed-interval*** sessions. Very little ***drinking*** took place during ***extinction*** sessions. This behaviour was ***schedule-induced*** (although not ***excessive*** like most ***schedule-induced behaviours***) rather than ***extinction-induced***.

The frequency of ***displacement*** showed an overall decrease across the six sessions, whereas the duration measure tended to increase. The number of bouts of ***displacement*** decreased in the first ***extinction*** session, but the duration of bouts increased in a number of cases. The highest overall duration scores were obtained during ***extinction*** sessions. Thus, over time the rats tended to engage in fewer bouts of ***displacement***, but actually spent more time engaged in these activities (in many cases).

(b) Differences between parts of session

A statistically significant main effect of part of session (***first*, *middle*** or ***last 30 minutes***) was found for measures of seven behavioural categories, excluding ***bar pressing***, ***propping***, ***chew/bite bottle*** and the three ***object-directed behaviours*** (within-session effect).

For the FIOS group (objects present) there was a clear within-session decrease in the frequency of ***bar-related behaviour*** during ***fixed-interval*** sessions, and the scores tended to be higher during the earlier parts of session during ***extinction***. These rats tended to forage around the food trough more (bouts) during the early parts of session, whether food was available or not. For the FIOE group the frequency scores were similar for the ***middle*** and ***last 30 minutes*** of each sessions during the ***fixed-interval*** sessions, and a noticeable drop occurred during the second session. The frequency scores tended to be higher during the ***last 30 minutes*** during ***extinction*** for this group. Unlike the FIOS rats, this group of rats directed more bouts of activity towards the food trough area in the latter parts of session, whether food was available or not.

An orderly within-session decrease in the frequency of ***sniff bottle*** was apparent for the FIOS group during ***fixed-interval*** sessions, and the scores remained noticeably higher for the ***first 30 minutes*** of each ***extinction*** session. For the FIOE group, the frequency scores were higher during the ***first 30 minutes*** in most sessions. The frequency of ***sniff and touch bottle*** was also highest during the ***first 30 minutes*** in all but one session for both groups. Thus, the decreasing number of bouts of ***exploratory behaviour directed towards the bottle*** (in the form of ***sniffing & touching***) suggests that the rats habituated to the bottle within each session. The frequency and duration of ***drinking*** also tended to be highest during the ***first 30 minutes*** of most sessions, and lowest for the ***last 30 minutes***, for both groups. Thus, rats tended to ***drink*** most during the earlier parts of each session (less during ***extinction***).

The frequency of ***displacement*** was highest during the ***first 30 minutes*** of every session for the FIOE group. For the FIOS group, which had objects present during every session, the frequency of ***displacement*** tended to be low during the ***first 30 minutes*** of ***fixed-interval*** sessions, but then highest during the ***first 30 minutes*** of ***extinction*** sessions. For this group, there was a within-session increase in this behaviour during ***fixed-interval*** sessions, but a within-session decrease during ***extinction***.

There was a within-session decrease in the duration of ***digging/burying*** in all sessions for the FIOE group, and in all but the first two sessions for the FIOS group. Thus when objects were first encountered during ***fixed-interval*** sessions, the duration of this ***foraging*** or ***escape-directed***

behaviour was low.

There were very few bouts of ***resting/sleeping*** during the ***first 30 minutes*** of any session. The frequency of this behaviour tended to be higher during the ***last 30 minutes*** of sessions. Thus, as the 3.5-hour session wore on, rats were more likely to engage in bouts of ***resting/sleeping***, as a result of fatigue or satiation.

(c) Differences between object conditions

No measures of behaviour showed statistically significant differences between the object conditions (objects first present during ***fixed-interval*** or ***extinction*** sessions). However, statistically significant ***object by part of session*** interactions, ***object by session*** interactions, and ***object by part of session by session*** interactions were found for some behavioural measures.

(d) Interaction effects

Although the independent variables were found to have a main effect on a number of behavioural measures, there were a large number of statistically significant interaction effects.

Object by part of session interaction effect

A statistically significant ***object by part of session*** interaction was found for two frequency measures. Whenever objects were present, the frequency of ***chew/bite object*** tended to be highest during the ***first 30 minutes*** of each session. The scores were also notably lower for the FIOE group during ***extinction***, which is when they first encountered objects. Thus, rats tended to ***chew and bite*** the objects during the early part of each session, which is also when they tended to ***drink*** most. The objects would have been most novel and arousing during the early part of each session, but if this behaviour was ***aggressive*** and most ***drinking*** also occurred at this time, it could have been a mild form of ***adjunctive behaviour***. The scores were, however, much lower for the rats that first encountered objects during ***extinction***. The frequency of ***digging/burying*** tended to be highest during the ***first 30 minutes*** of each session (an effect of part of session). It also tended to be lower in the FIOS group, which had objects present in every session (an effect of object).

Object by session interaction effect

Five measures of behaviour yielded statistically significant ***object by session*** interactions. The duration of ***sniff and touch object*** tended to decrease over ***fixed-interval*** sessions (except during the ***last 30 minutes***) in the FIOS group, increase substantially in the first ***extinction*** session (except during the ***last 30 minutes***), and then increased over ***extinction***. Thus, when objects were present during ***fixed-interval*** and ***extinction*** sessions (FIOS group), a habituation effect was only observed over ***fixed-interval*** sessions during the earlier parts of session. During the ***last 30 minutes*** of each session, rats spent more time ***sniffing and touching objects*** over sessions. In addition, rats in the FIOS group spent more time engaged in this behaviour over ***extinction*** sessions. The duration of ***sniff and touch object*** scores were substantially higher in many instances for the FIOE group during ***extinction***, when objects were first encountered.

A statistically significant ***object by session*** interaction was found for both measures of ***sniff and touch bottle***. During ***fixed-interval*** sessions, the frequency and duration scores tended to be higher for the FIOE group (an effect of object). That is, when objects were absent, rats engaged in more bouts and spent much more time ***sniffing and touching*** the bottle. For the FIOE group, both measures tended to increase over ***fixed-interval*** sessions, plummet in the first ***extinction*** session, and then tended to decrease over ***extinction*** (an effect of session). Whereas both measures decreased over the six sessions for the FIOE group, they tended to increase for the FIOS group. Thus, if objects were present in every session, more time was spent ***sniffing and touching the bottle*** over time.

Both measures of ***digging/burying*** yielded statistically significant ***object by session*** interactions. If objects were present only during ***extinction*** (FIOE group), both measures tended to decrease over the six sessions (whereas they tended to increase for the FIOS group). That is, the presence of objects in every session appeared to result in more ***digging/burying*** over the six sessions.

***Part of session by session* interaction effect**

Statistically significant ***part of session by session*** interactions were found for the frequency and duration of ***chew/bite object*** and the duration of ***resting/sleeping***. During ***extinction***, most of the time spent ***chewing and biting objects*** took place during the ***first 30 minutes*** of each session, in both groups. The lowest scores tended to be obtained during the ***last 30 minutes*** of session. Thus, there was a within-session decrease for ***chew/bite object***. There was also a decrease over ***extinction*** sessions (in most cases) for both groups. For the FIOS group, the frequency and duration of ***chew/bite object*** increased over ***fixed-interval*** sessions, for all parts of session. Thus, the longer the objects were present during ***fixed-interval*** session running, the more likely rats were to ***chew and bite*** the stimulus objects.

The frequency and duration of ***resting/sleeping*** tended to increase over the six sessions, most noticeably during ***extinction***. Thus, as the ***bar pressing*** response was extinguished, the rats spent more time ***resting or sleeping***. Very little time was spent ***resting/sleeping*** during the ***first 30

minutes of every session. There was a marked within-session increase in this behaviour. During ***fixed-interval*** sessions this may have reflected a satiation or habituation to the reinforcer effect. During ***extinction***, once the stimulus objects and perimeters of the box had been thoroughly investigated and no more food was available at the known source, the rats were more likely to lie down and ***rest*** or even ***sleep***.

***Object by part of session by session* interaction effect**

A statistically significant ***object by part of session by session*** interaction was found for frequency and duration of ***sniff object*** and the frequency of ***sniff and touch object***. These ***object-directed behaviours*** were affected by all three grouping variables over the six sessions. The FIOE rats spent more time engaged in ***sniff object*** in every ***extinction*** session, which was their first encounter with objects. This group also directed very high amounts of ***sniffing and touching towards the objects*** during the first ***extinction*** session. Habituation towards the objects then took place over sessions.

9.4.7.4 TOTAL NUMBER OF LICKS AND BAR PRESSES FOR EACH SESSION, AND OTHER NOTABLE BEHAVIOURS

For both groups, more than 1000 ***bar presses*** (in one case >5000) were made during each ***fixed-interval*** session, whereas few ***bar presses*** occurred during ***CRF*** and ***extinction*** sessions (by comparison). With the exception of rats that did not always trigger the lick counter (or disconnected/damaged it), a peak in the total number of ***licks*** (between 500 & 6000 in most cases) was also observed in the ***fixed-interval*** sessions in a number of cases for both groups. That is, the highest total number of ***bar presses*** and ***licks*** appeared to occur during ***fixed-interval*** sessions. This is hard surprising, with respect to the ***bar pressing*** measures. During ***CRF*** sessions, rats became satiated more quickly as every ***bar press*** resulted in a food pellet. During ***extinction***, the ***bar pressing*** response was extinguished. Clearly, number of ***licks*** was correlated with number of ***bar presses***. That is, more ***licks*** occurred when more ***bar presses*** were made, perhaps as a result of thirst (since the rats were not ***polydipsic***).

A number of rats literally chewed the bottle housing to pieces. That is, they were very ***aggressive*** and were not merely directing ***exploratory behaviour towards the bottle***. Two rats in each group ***attacked*** the bottle in all experimental sessions (except Rat 2 in session 1 & 2). If a loose bottle was present on the floor of the experimental box, most rats were also ***aggressive towards the loose bottle***. Rat 1 was so ***aggressive towards the bottles*** that this activity resulted in him ripping out a nail (front paw). The ***stimulus objects***, which had moving parts or plastic parts, were also ***attacked***. That is, the objects that could be readily chewed or destroyed were (fan part of the

windmill object & springs on the ***scrap metal*** object). Some rats also chewed up and destroyed the wire that connected the bottle to the lick counter. Holme (1990) concluded that the rats ***attacked*** whatever was closest, and the bottles provided a convenient target. The rats in this study appeared to ***attack*** whatever was most easily chewed or destroyed. However, the closest targets were the easily destroyed objects and bottles (& lick-counter wire). The ***aggression*** observed in this study was directed at multiple targets. Section 9.5.6 discusses the possible reasons for such high levels of ***aggressive behaviour***.

All rats engaged in bouts of ***coprophagia*** (typically between 1 & 10 bouts) during some (or all) experimental sessions. At least one rat (Rat 9) developed some unusual behavioural patterns linked to his bouts of ***coprophagia***. That is, the fecal pellets were sometimes carried to the water source and consumed there. Sometimes fecal pellets were immediately consumed, whereas on other occasions they were first buried (& dug up & consumed later). Whilst the levels of ***coprophagia*** could not be considered ***excessive***, this behaviour could be considered aberrant. ***Coprophagia*** has been observed in many species under captive conditions. For these food-deprived rats it may have provided an alternative source of nutrients, or it may have represented the beginnings of an ***adjunctive behaviour***. At the low levels observed, it was probably not maladaptive.

In a number of cases quite large mounds of sawdust were created as a result of ***burying behaviour*** (or ***sawdust pushing***). Most of these mounds developed near the bottle or back wall areas. Thus although this study has tended to suggest that this behaviour may have been related to ***foraging*** or ***escape-directed behaviour***, it could at times have been related to the ***defensive burying*** observed in rats under aversive conditions in other laboratory situations.

An ***escape-directed exploratory behaviour*** was observed in some rats, during some of the sessions. By ***propping*** against the wall and stretching their heads up, these rats were able to ***push at the lid with their snouts***. One rat even managed to escape from the box. This behaviour (& possible reasons for its occurrence) is discussed in some detail in section 9.5.3.

Thus, a variety of behaviours took place during this study. It was not possible to include them all during event recording (& many occurred infrequently), but most of the notable ones have been discussed. Clearly a number of individual differences existed, with respect to the diversity and frequency of behaviours (whether “normal” or “aberrant”).

9.4.7.5 BEHAVIOURAL CATEGORIES ENGAGED IN FOR MORE THAN 10% OF TOTAL SESSION TIME

A particular behaviour may be ***excessive*** if it occurs for more than 10% of total (session) time. A number of behavioural categories were engaged in for less than 10% of session time, but there were others that took up more than 30% of total session time.

Less than 10% of total ***fixed-interval*** or ***extinction*** session time (all parts of session) was spent engaged in ***drinking***, ***digging/burying*** or ***propping*** by either group. Thus, none of these categories of behaviour can be considered to be ***excessive***.

Importantly, it is not possible to define the ***drinking*** observed in this study as ***polydipsia***. There are several possible reasons for the lack of ***excessive drinking*** (as observed by Falk, 1971). Certainly, Falk (1971) also ran his rats on a 3.5-hour long FI60-s schedule of intermittent food reinforcement. However, he did not provide an "open-field" style Skinner box, stimulus objects (for one group at least), a soft substrate or bottle located within the box itself (rather than just the spout). Thus, the opportunity to engage in a variety of behaviours in Experiment 3 clearly prevented the development of ***polydipsia***. The absence of objects during ***fixed-interval*** sessions in the FIOE group did not result in ***excessive*** amounts of ***drinking***. Thus, the other features of the exploration box rather than stimulus objects *per se* prevented ***polydipsia*** from occurring.

Propping may have been an ***escape-directed behaviour*** or attempt to explore beyond the confines of the box. This behaviour was not ***excessive*** in either group during either ***fixed-interval*** or ***extinction*** sessions. By contrast, both groups in Experiment 1 engaged in ***excessive*** (>10%) amounts of ***propping*** during both ***fixed-interval*** and ***extinction*** sessions. Thus the presence of the water source reduced the amount of activity directed towards the ***peripheral areas of the box***. If a water source was not present, rats were perhaps attempting to explore outside the box for water (as well as food or stimulation). Both groups of rats in Experiment 1 and Experiment 3 spent less than 10% of their time ***digging/burying***. Clearly, neither the presence nor absence of water resulted in ***excessive*** amounts of this behaviour occurring.

The concurrent availability of a water source reduced the amount of time spent around the ***bar and food trough area*** in both ***fixed-interval*** and ***extinction*** sessions. Although both groups in Experiment 3 spent more than 10% of session time (all parts of session) engaged in ***behaviours directed at the bar and food-trough area*** during ***fixed-interval*** sessions, the rats in Experiment 1 spent more than 20% of their session time engaged in these activities. During ***extinction***, Experiment 3 rats spent less than 10% of session time (all parts of session) engaged in

behaviours directed at the bar and food-trough area (except for the FIOE group during the ***last 30 minutes***). The Experiment 1 rats, on the other hand, spent more than 10% of their time engaged in these behaviours. Therefore, the amount of time spent engaged in ***bar pressing*** and ***bar-related behaviour*** could not be considered ***excessive*** when a concurrent water source was available.

The FIOS group spent more than 10% of total ***fixed-interval*** session time (all parts of session) engaged in ***behaviours directed at the stimulus objects*** (objects were <u>absent</u> for the FIOE group). Overall, the levels were slightly higher than for the same group in Experiment 1. Thus, the presence of a water source resulted in slightly higher levels of ***exploratory behaviour directed towards the objects***. These behaviours are certainly adaptive, since the objects represent a source of stimulation or potential source of food. Thus it is reassuring, that at least 10% of total ***fixed-interval*** session time was spent engaged in such behaviours, even when a water source was available (& no ***polydipsia*** was evident). During ***extinction***, both groups spent more time overall engaged in these ***exploratory behaviours***. In fact, during the ***first 30 minutes***, more than 20% of total time was spent ***exploring the stimulus objects***. This is not surprising, since one would expect ***stimulus novelty*** to be greatest during the early part of each session. On average, both Experiment 3 groups of rats spent more time engaged in ***behaviours directed at the stimulus objects*** than their Experiment 1 counterparts during ***extinction***. Thus, ***extinction*** did result in higher levels of ***object exploration***, as Forster (1986; 1992; 1995) also found. Furthermore, the levels in this Experiment were higher than those reported in Experiment 1, apparently as a result of the longer session time and the availability of a concurrent water source.

The FIOS group spent more than 10% of the ***first 30 minutes*** of ***fixed-interval*** time engaged in ***bottle-directed behaviours*** (excluding ***drinking***), whilst the FIOE group engaged in these behaviours for more than 10% of the ***middle 30 minutes*** of ***fixed-interval*** session time. These behaviours represented ***exploratory behaviour directed at the water bottle***. That is, the rats were directing attention towards the bottle, which was also an object to be explored. The bottle provided a source of water and stimulation. If stimulus objects were also present (FIOS group), then bottle exploration peaked earlier in the session, when all objects were most novel. During ***extinction***, slightly higher levels were observed. The FIOS group spent more than 10% of time engaged in ***behaviours directed at the water bottle*** during the ***first*** and ***last 30 minutes*** of ***extinction***. More than 10% of the ***first 30 minutes*** of ***extinction*** time was spent engaged in these activities by the FIOE group. Again, ***bottle exploration*** peaked earlier in the session for both groups, when all objects were most novel. Since these behaviours were most likely a form of ***exploratory behaviour***, it is unlikely that the levels observed could be considered ***excessive***.

If objects were absent during ***fixed-interval*** sessions (FIOE group), then more than 10% of all parts of session were spent engaged in ***displacement***. The FIOS group spent less than 10% of the ***first 30 minutes*** of ***fixed-interval*** sessions in ***displacement*** activities. However, in the latter parts of session, more than 10% of total time was also spent engaged this ***conflict-related behaviour***. Thus, the absence of objects or the habituation towards the objects (lack of ***novelty***) resulted in higher levels of ***displacement***. Since these behaviours are considered to be ***conflict-related***, then these levels could be considered ***excessive***. Certainly, in a zoo situation, such levels of this behaviour could be akin to ***over-grooming***, and thus a cause for concern (Shepherdson, 1989). Overall, both groups spent more time engaged in this category of behaviour during ***extinction*** (even reaching a level of >20% in the ***middle 30 minutes*** for the FIOS group). The FIOS group levels varied quite substantially within-sessions, from greater than 20% (***middle 30 minutes***), to less than 10% (***last 30 minutes***). Thus, the lack of reinforcement tended to result in higher levels of ***displacement***, and level of habituation towards the stimulus objects may have had an effect. By contrast, neither group in Experiment 1 devoted more than 10% of ***fixed-interval*** or ***extinction*** session time to ***displacement***. This suggests that the length of the session (3.5-hours compared to 30 minutes) and the concurrent availability of water, rather than lack of reinforcement (predictable periods during ***fixed-interval*** sessions & complete absence during ***extinction***) or object novelty increased the levels of ***displacement activities*** seen.

The presence of objects during ***fixed-interval*** sessions clearly reduced the amount of time spent ***resting/sleeping***. If objects were present, less than 10% of any part of session was spent engaged in this behaviour. Without objects, more than 10% of the ***middle*** and ***last 30 minutes*** of these sessions were spent ***resting/sleeping***. For this latter group, ***inactivity*** could be considered ***excessive***. By the latter parts of session, the rats may be satiated, and since there are no opportunities to ***explore objects*** or leave the box, these rats spend more time ***resting/sleeping***. Importantly, if objects are available to explore, the rats are more active. During ***extinction***, the amount of time that rats spent ***resting/sleeping*** increased markedly for both groups for the ***middle*** and ***last 30 minutes***. Less than 10% of the ***first 30 minutes*** was spent ***inactive***. The objects would have been most novel during the early part of each session. For the latter parts of session, both groups spent more than 20% of session time engaged in ***resting/sleeping***, and in one part of session this jumped to more than 30% of session time. This is not surprising, since the operant response would be extinguishing over the session, the rats would be habituating to the objects, and fatigue might be setting in. This level of inactivity may be ***excessive***, but perhaps not maladaptive, since the rats are conserving energy. That is, the food source is depleted, and there are no further food sources available until the end of the session when the rats are returned to the home cage. Therefore too much vigorous activity would be a waste of energy.

Since only the FIOS group had objects present during ***fixed-interval*** sessions, the combined ***aggressive behaviour*** category is only relevant to this group during those sessions. The FIOS group spent more than 10% of ***fixed-interval*** session time ***chewing/biting the water bottle and objects*** during the ***first*** and ***last 30 minutes*** of ***fixed-interval*** sessions. Such levels of ***aggressive behaviour*** may be considered ***excessive***. Interestingly, they are most prevalent early and late in the session. Thus ***aggression*** is least likely to occur when the stimulus objects are at an "intermediate level of arousal" (Hebb, 1955). During ***extinction***, more than 20% of the ***first 30 minutes*** was spent engaged in these ***aggressive behaviours*** by the FIOS group (& >15% for the FIOE group), whilst the figure decreased to less than 10% of session time for the latter parts of session. Thus, when the stimulus objects are most arousing and the hungry rats first encounter the depleted food source, ***aggression*** is at its peak. The levels of ***aggression*** observed in the early part of session could certainly be considered ***excessive***. It is difficult to determine whether such ***aggression*** was really ***maladaptive***. It was not possible to see whether the rats consumed any of the debris from the destroyed bottle housings or objects. Certainly, if they did consume any of this plastic, such ***pica*** could be considered detrimental to their health.

9.4.7.6 TIME AND "EFFORT" SPENT OBTAINING REINFORCEMENTS

The mean frequency of ***bar presses*** per reinforcement was lowest for the two groups in Experiment 3 (compared to Experiment 1 counterparts). The presence of the water bottle resulted in more ***optimal foraging***. In the absence of a water source, Experiment 1 rats exerted at least twice (FIOS group) or three times (FIOE group) as much energy per reinforcement as the Experiment 3 counterparts. Of course, a rat that is run on a half-hour session may be able to exert more energy per reinforcement than a rat that is run on a session that is six times longer (since the latter presumably would need to conserve energy).

The effect of stimulus objects on ***optimal foraging*** differed depending upon the length of session. During short sessions (30 minutes in Experiment 1), the presence of stimulus objects resulted in far fewer ***bar presses*** per reinforcement and consequently more ***optimal foraging*** (less energy spent ***bar pressing*** per reinforcement). However, during longer sessions (3.5 hours in Experiment 3) slightly more energy was spent ***bar pressing*** per reinforcement when objects were present. Overall, the most ***optimal foraging*** condition during ***fixed-interval*** sessions was when a water bottle was concurrently available, and stimulus objects were absent.

9.5 CONCLUSIONS BASED ON THE FINDINGS OF EXPERIMENT 3

This section presents a summary of the general findings of this study. Following this, some practical implications of these findings are discussed, specifically with respect to other "real life" captive environments in which animals are provided with food on an intermittent schedule of food reinforcement (*e.g.*, zoo enclosures).

9.5.1 BEHAVIOUR DIRECTED AT THE BAR AND FOOD-TROUGH AREA

Whilst both groups in Experiment 3 spent more than 10% of session time (all parts of session) engaged in ***behaviours directed at the bar and food-trough area*** during ***fixed-interval*** sessions, they spent far less time than their Experiment 1 counterparts engaged in these activities. The presence of the water bottle increased the range of behaviours that were possible, which reduced the time and effort that was directed at the food source (whether depleted or not). When not involved in activities centered at the food source, rats could ***drink*** or direct a range of ***exploratory responses*** or ***aggression*** towards the bottle. Given that the rats had to ***bar press*** (in order to be reinforced) and had to retrieve the pellets from the food trough, it is unlikely that these levels of ***behaviours directed at the bar and food-trough area*** could be considered excessive or maladaptive.

During ***extinction***, Experiment 3 rats spent less than 10% of session time (all parts of session) engaged in ***behaviours directed at the bar and food-trough area*** (except for the FIOE group during the ***last 30 minutes***). Clearly the amount of time spent engaged in ***bar pressing*** and ***bar-related behaviour*** was not ***excessive*** when a concurrent water source was available. The Experiment 1 rats, with a more limited range of behavioural opportunities available, spent more than 10% of their time engaged in these behaviours.

Bouts of ***bar-related behaviours*** were more likely to occur outside the PRPs, although just over half of the duration took place during PRPs in the FIOE group in the latter parts of session. For both groups, only about a third of the frequency and duration of ***bar-related behaviour*** took place during the PRPs in the ***first 30 minutes*** of sessions for both groups. Thus rats were just as likely to forage around the food trough area outside the PRPs, in an attempt to check for food at the only known source.

In summary, ***behaviours directed at the bar and food-trough area,*** were not found to be ***excessive*** during ***fixed-interval*** or ***extinction*** sessions in either group. Less than 51% of the bouts of ***bar-related behaviour*** (frequency & duration) took place during the PRPs.

9.5.2 BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS

The FIOS group spent more than 10% of total ***fixed-interval*** session time (all parts of session) engaged in ***behaviours directed at the stimulus objects*** and the levels were slightly higher than for its Experiment 1 counterpart. The presence of a water source resulted in slightly higher levels of ***exploratory behaviour directed towards the objects***. The objects represent a source of stimulation or potential source of food, and such levels of ***exploratory behaviour*** are adaptive and should not be considered ***excessive***. Higher percentages of total frequency and duration of ***behaviours directed at the stimulus objects*** took place during the PRPs as the session progressed (*i.e.*, more of each of the measures occurred during the PRPs in the latter parts of session). This may reflect the increased stability or predictability of the PRP as the session progressed.

During ***extinction***, both groups spent more time overall engaged in these ***exploratory behaviours***. During the ***first 30 minutes***, more than 20% of total time was spent ***exploring the stimulus objects***. ***Stimulus novelty*** would be greatest during the early part of each session. ***Extinction*** resulted in higher levels of ***object exploration*** (Forster, 1986; 1992; 1995). The longer session time and the availability of a concurrent water source resulted in higher levels of ***object exploration*** during ***extinction*** (since the levels were lower in for the Experiment 1 counterparts). Again, such levels of ***exploratory behaviour*** are adaptive and should not be considered ***excessive***. Rats should direct their activities towards alternative sources of food and stimulation once the food source is depleted.

In summary, levels of ***behaviours directed at the stimulus objects*** were not found to be ***excessive*** during ***fixed-interval*** or ***extinction*** sessions. For the FIOS group, more than a third of ***object exploration*** (frequency & duration) took place during the PRPs in the ***first 30 minutes***. During the latter parts of session, most of these behaviours occurred during the PRPs (ranging from >70% to >90%).

9.5.3 BEHAVIOUR DIRECTED AT THE PERIPHERAL AREAS OF THE BOX

Propping may have been an ***escape-directed behaviour*** or attempt by the rats to explore beyond the confines of the box. This behaviour was not ***excessive*** in either group during either ***fixed-interval*** or ***extinction*** sessions, whereas both groups in Experiment 1 engaged in ***excessive*** (>10%) amounts of ***propping*** during both ***fixed-interval*** and ***extinction*** sessions. The presence of the water source reduced the amount of activity directed towards the ***peripheral areas of the box***. If a water source was not present, rats were perhaps attempting to explore outside the box for water (as well as food or stimulation).

Another form of ***escape-directed exploratory behaviour*** was observed in some rats. By ***propping*** against the wall and stretching their heads up, these rats engaged in ***push at the lid with snout***. This behaviour was only observed in the FIOE group during the ***fixed-interval*** sessions, in the absence of objects. Once objects were present during ***extinction***, this behaviour was no longer observed. In the FIOS group (Table 9.33), two rats engaged in ***push at lid with snout*** during session 3 (***fixed-interval*** session). For the FIOS group, ***push at lid with snout*** was only observed during the last ***fixed-interval*** sessions, after the objects had begun to "lose novelty", or once the food source was depleted (in one rat). Thus, this behaviour was least likely to occur when objects were first encountered (maximum novelty). With objects to explore within the box, they were less likely to attempt to explore beyond the box.

During ***extinction***, one rat (Rat 1) actually succeeded in escaping from the box (***first 30 minutes*** of session 5 & ***last 30 minutes*** of session 6). He persisted with using his ***nose to push the lid***, until a large enough gap existed for him to climb out through. He climbed around on top of the lid and returned to the box of his own accord each time. Although he never physically explored beyond the apparatus, he was able to monitor the surroundings outside the box visually.

Interestingly, "escape-oriented behaviour dominated" Holme's (1990, p.98) study, and far exceeded the levels of ***aggressive behaviour*** recorded. Her category of ***escape-oriented behaviour*** (p.68) included ***propping*** (labeled as exploratory behaviour ancillary to escape) and actual ***escape behaviour*** (pushing lid with forepaws &/or nose, and partial or complete physical escape from the apparatus). One of her rats also escaped from the box. He was considered ***polydipsic*** and engaged in up to three times as many ***bar presses*** as the other rats. As in the current study, this rat also returned to the apparatus. Holme (1990) suggests that the rat returned to a "seemingly aversive situation" as a result of "hunger and/or its limited life history" (p.102). She concluded that the rats were attempting to leave the aversive situation, which was negatively correlated with food, in order to search for food or even return to the nest (or a less open &

brightly-lit area). Lucas, Timberlake and Gawley (1988) postulate that rats may have evolved an "out-of-nest time" that minimises risk of predation (& foraging costs) and maximises reproductive gains (p.27). Their rats spent more time within the available nest area as the inter-food intervals increased.

The current study found that ***aggressive behaviour*** was more common than ***escape-directed behaviour***, especially ***pushing at lid*** and actual ***escape***. That is, these ***excessive behaviours*** were reversed in the Holme (1990) study. The apparatus size was the same, but no objects were provided (other than bottles attached to walls) and the inter-food interval was longer (FI120-s instead of FI60-s schedule). Certainly in this apparatus, without any areas to hide in or find cover, the rats would theoretically be exposing themselves to a greater risk of predation for fewer food pellets on the FI120-s schedule. That is, the cost-benefit analysis is different for the two schedules. Thus attempts to escape from the Holme's (1990) apparatus were higher. On the FI60-s schedule, theoretically, the food source was richer (pellets more often), and thus risk of loss of food to conspecifics (rather than predators) may have been greater and resulted in higher levels of ***aggressive behaviour***.

Clearly individual differences exist in whether rats are actually capable of escape from the apparatus. One rat in the current study and one rat in Holme's (1990) study successfully climbed out of the box. These rats demonstrated superior climbing abilities (since they had to be at full stretch to reach the lid, move it and then drag themselves out of the box with their front paws), and appeared to be more motivated to explore beyond the box (to find shelter or food). Once out of the box, they were able to observe the whole experimental room, and then return to the only known food source. One might argue that these two rats represented members of the species that would be more likely to survive and reproduce under natural conditions. That is, they were excellent climbers and successfully extended their search for food and shelter (although no food or shelter was actually found). However, such behaviour may have carried higher costs under natural conditions (no shelter or food obtained & possible increased risk from predators).

In summary, levels of ***propping*** (& ***push lid with snout***) were not ***excessive*** during ***fixed-interval*** or ***extinction*** sessions in either group. More than half of this behaviour (frequency & duration) took place during the PRPs in the latter parts of session.

9.5.4 BEHAVIOUR DIRECTED AT THE WATER BOTTLE

The low levels of ***drinking*** observed in this study mean that this behaviour could not be regarded as ***polydipsia***. Falk (1977) maintains that ***schedule-induced behaviours*** may be affected (reduced) if increased behavioural opportunities exist (*e.g.*, apparatus size is increased). The current study provided a larger apparatus and the opportunity to engage in a variety of behaviours, which may have prevented the development of ***polydipsia***. Features of the exploration box (size & soft substrate) rather than stimulus objects appeared to prevent ***polydipsia*** from occurring.

No rat in this study ***drank excessively***. By contrast, Holme (1990) found that nine out of her twelve rats displayed ***polydipsia*** whilst run on a FI120 schedule of intermittent food reinforcement. The size of the apparatus, soft substrate, position of the bar and food-trough and type of bottle used were similar (even identical) to the ones used in the current study. However, her sessions were three hours long, no novel stimulus objects were provided, and there were six water bottles present (only one served as a water source), and discrimination stimuli (cards) behind the spout of each bottle. Thus larger apparatus and soft substrate are not enough to prevent ***polydipsia*** from occurring on a FI120-s schedule, but they may contribute to the lack of ***excessive drinking*** on a FI60-s schedule. It should be pointed out, that Holme (1990) used level of water intake (in ml) to measure ***drinking***. Experiment 3, on the other hand, used actual frequency and duration of ***drinking*** (scored from videotapes) and then calculated the percentage of total session time spent ***drinking*** to measure whether this behaviour was ***excessive*** or not.

Holme (1990) calculated the percentage of total frequency of ***drinking*** that took place immediately after reinforcement for four of the rats in her study. Of these, only two had the water bottle positioned close to the feeder (similar to the location of the bottle in the current study). Holme's (1990) figures refer to ***drinking*** that occurs immediately after pellet consumption, rather than at some time during the PRP (when other behaviours may occur prior to ***drinking***). The two figures varied substantially, from 78.57% to 31.82%. Gilbert (1974) demonstrated the "ubiquity of schedule-induced polydipsia, *i.e.*, the phenomenon's capability of appearing anywhere in the interval" (Gilbert, 1974, p.280). He also found that the peak ***drinking*** period varied between individual rats. In the current study more than 70% of ***drinking*** in both groups took place during the PRP. However, it may not always have been the first behaviour engaged in immediately after pellet delivery and consumption (as many of the other behaviours also took place during the PRPs).

The rat that drank less immediately after reinforcement actually drank twice as much during the session in Holme's (1990) study. That is, the peak level of water intake also varied noticeably between individuals (21.5ml for Rat 2 & 42.5ml for Rat 3). Thus ***polydipsic*** rats that drink immediately after pellet consumption are not necessarily more ***polydipsic***. ***Drinking***, whether excessive or not, does not always take place immediately after pellet delivery or during the PRPs. It can take place at any time during periods of non-operant responding, just as Gilbert (1974) suggests.

The FIOS group spent more than 10% of the ***first 30 minutes*** of ***fixed-interval*** time engaged in ***bottle-directed behaviours*** (excluding ***drinking***), whilst the FIOE group engaged in these behaviours for more than 10% of the ***middle 30 minutes*** of ***fixed-interval*** session time. Such ***bottle exploration*** peaked earlier in the session for both groups (only relevant for the FIOS group during ***fixed-interval*** sessions), when all objects were most novel or arousing. Since these behaviours were most likely a form of ***exploratory behaviour***, it is unlikely that the levels observed could be considered ***excessive***.

In summary, ***drinking*** was not found to be ***excessive*** during ***fixed-interval*** or ***extinction*** sessions in either group. That is, ***polydipsia*** did not develop. Most instances of this activity (frequency & duration) took place during the PRPs (>70%). Levels of ***bottle-directed behaviours*** were also not considered to be ***excessive***. More than half of the ***bottle-directed behaviours*** (frequency & duration) took place during the PRPs (>80% in a number of cases).

9.5.5 OTHER BEHAVIOURAL CATEGORIES

Both groups of rats in Experiment 1 and Experiment 3 spent less than 10% of their time ***digging/burying***. This behaviour may be ***escape-directed*** or it may be related to ***foraging***. Neither the presence nor absence of water resulted in ***excessive*** amounts of this behaviour occurring.

If objects were absent during ***fixed-interval*** sessions (FIOE group), then more than 10% of all parts of session were spent engaged in ***displacement***. The FIOS group also spent more than 10% of the latter parts of session engaged in this ***conflict-related behaviour***. Overall, both groups spent more time engaged in this category of behaviour during ***extinction*** (>20% in the ***middle 30 minutes*** for the FIOS group). Excessive levels of ***displacement*** were not observed in the Experiment 1 counterparts (***fixed-interval*** or ***extinction*** sessions). Therefore, increased session length and the concurrent availability of water, rather than lack of reinforcement or decreased object novelty resulted in the excessive levels of ***displacement activities*** seen. These activities may not be considered ***maladaptive***, unless they develop into ***over-grooming*** (a behavioural disorder observed in some zoo animals), since such activities typically delay the rat's next response (which may save its life).

Without objects, more than 10% of the ***middle*** and ***last 30 minutes*** of these sessions were spent ***resting/sleeping***. This level of ***inactivity*** could be ***excessive***. These rats may have been satiated at that point and they were unable to ***explore objects*** or leave the box. During ***extinction***, the amount of time spent engaged in ***resting/sleeping*** increased markedly for both groups for the ***middle*** and ***last 30 minutes*** (<10% for the ***first 30 minutes***). For these latter parts of session, both groups spent more than 20% of session time engaged in ***resting/sleeping*** (>30% for one part of session). At this point, the operant response was extinguishing, the rats were habituating to the objects, and fatigue could have been setting in. Although ***excessive***, this level of ***inactivity*** was perhaps not maladaptive, since the rats were conserving energy.

In summary, levels of ***digging/burying*** were not ***excessive***, whereas ***displacement activities*** were ***excessive*** during both ***fixed-interval*** and ***extinction*** sessions. ***Resting/sleeping*** was at times ***excessive*** in the FIOE group during ***fixed-interval*** sessions and ***excessive*** for both groups during ***extinction***. More than 50% of the frequency and duration of ***digging/burying*** and ***displacement*** (>80% in a number of cases) took place during the PRPs for all parts of session. Almost all ***resting/sleeping*** took place during the PRPs for the latter parts of session.

9.5.6 AGGRESSIVE BEHAVIOUR DIRECTED AT THE STIMULUS OBJECTS AND WATER BOTTLE

Holme (1990) defined ***aggressive behaviour*** as "vigorous biting and/or pawing of anything within the apparatus" (p.68). The current study used a combined category, comprised of ***chew/bite object*** and ***chew/bite bottle*** (see section 6.2.3.3 & 9.2.3.3 for the complete definitions). The definitions are very similar, except that there were never any stimulus objects present in Holme's (1990) study, and there was only one bottle present in the current study. Holme (1990) found very few instances of ***aggressive behaviour*** during either baseline (***massed reinforcement*** or ***extinction***) or the last week of ***fixed-interval*** sessions (mean frequencies all <3 per session). Any ***aggressive behaviour*** that was recorded was directed at any of the six water bottles, not just at the single source of water. The rat, which ***attacked*** its water source the most, was not ***polydipsic*** (Rat 5). Holme (1990) concluded that the rats ***attacked*** whatever was nearby (not necessarily the water source), with the bottles providing a convenient target. That is, they were not directing ***aggression*** towards the water source, but rather towards the target that the closest water bottle(s) provided.

Unpublished studies by Clode et al (1987) and Lee et al (1989) observed ***aggressive behaviour directed at a water bottle*** located in a standard sized Skinner box on a FI120-s schedule. A rat in the former study managed to dislodge the bottle from the wall, and two of the three ***polydipsic*** rats that became ***aggressive*** in the latter study bit through the bottle. It should be noted, that these studies, along with Holme's (1990) study and the current study, differ from most published studies (*e.g.*, Falk, 1971; Gilbert, 1974), because the actual water bottle itself is present in the experimental chamber, instead of just the waterspout.

The current study found numerous instances of ***aggression*** in both groups of rats during both ***fixed-interval*** (only the FIOS group had objects present) and ***extinction*** sessions (see Table 9.13). In fact, this behaviour was very prevalent during the ***first 30 minutes*** of every session in the FIOS group. In four of the six sessions, more than 19% of total session time was spent engaged in these activities. During ***extinction***, the time spent in ***aggressive behaviours*** tended to be higher in the group that had first encountered objects during ***fixed-interval*** sessions.

The important difference between the rats in this study, and those in the studies just cited, is that the rats in the current study were not ***polydipsic*** (although they all ***drank*** throughout the session) and they were run on a FI60-s schedule rather than a FI120-s schedule. On the latter schedule, increased size of the experimental apparatus and/or more targets (bottles) to attack appears to reduce the frequency of ***aggression*** but not ***polydipsia***. This pattern appears to be reversed for the FI60-s schedule. That is, the current study found that the larger apparatus and numerous targets (objects & bottle) increased the frequency of ***aggression*** but not ***polydipsia***. As mentioned previously, on the FI60-s schedule (theoretically), the food source was richer (pellets more often), and thus risk of loss of food to conspecifics (rather than predators) may have been greater and resulted in higher levels of ***aggressive behaviour***. In the current study, the inter-food interval may not have been long enough to develop ***polydipsia*** under open-field conditions (with objects present).

Holme (1990) reports that most of the ***aggressive behaviours*** "occurred towards the end of the run", which she attributes to the "accumulating aversiveness of the situation" (p.96). In the current study, higher percentages of total frequency and duration of ***aggressive behaviours*** took place during the PRPs as the session progressed in the FIOS group (*i.e.*, more of each of the measures occurred during the PRPs in the latter parts of session). This may reflect the increased stability or predictability of the PRP as the session progressed. It may also indicate that the aversive properties of the stimuli present during PRPs (negative predictors of food) increased as the session progressed (Dinsmoor, Lee & Brown, 1986). For the FIOS group, the actual amount (frequency & duration) of ***aggressive behaviour*** decreased as the session progressed. That is, more ***aggressive behaviours*** took place during the ***first 30 minutes*** (within-session decrease). However, more ***aggressive behaviours*** took place over sessions (between-session increase). This suggests that the aversiveness of stimuli present (or situation) may have decreased within each session but increased over repeated sessions.

During ***extinction***, the frequency and duration of ***aggressive behaviours*** showed a marked within-session decrease. That is, the levels were much higher during the ***first 30 minutes*** of sessions. Overall, there was no decrease over sessions in the percentage of total session spent engaged in these behaviours during the ***first 30 minutes***, and little change for the latter parts of session. Holme (1990), Clode et al (1987) and Lee et al (1989) did not run their rats on extinction following ***fixed-interval*** sessions, so no comparison is possible.

In summary, ***excessive*** amounts of ***aggressive behaviour directed at the objects*** and ***water bottle*** were observed in the FIOS group during ***fixed-interval*** sessions (no objects present in the other group) and in both groups during ***extinction***. Furthermore, most instances of this activity (frequency & duration) took place during the PRPs (ranging from >60% to >90%). Thus the aversive properties of stimuli present during the PRPs (negative predictors of food) appear to result in higher levels of ***aggressive behaviour*** than other periods of non-operant responding (Dinsmoor, Lee & Brown, 1986).

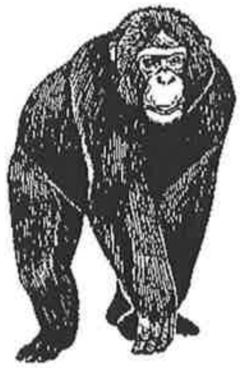
9.5.7 PRACTICAL IMPLICATIONS OF THESE FINDINGS

The findings of this study, coupled with the findings of Holme's (1990) study, indicate that it is difficult to predict which behaviours will occur excessively in an open-field situation on a ***fixed-interval*** schedule, with a concurrently available water source. The shorter interval (FI60-s) resulted in high levels of ***aggressive behaviour***, but acceptable levels of ***drinking*** and ***escape-directed behaviour***. The longer interval (FI120-s) appeared to evoke ***polydipsia*** and extremely high levels of ***escape-directed behaviour***, but minimal ***aggression***. Since Holme (1990) did not provide her rats with stimulus objects, it is not possible to determine whether the presence of objects to explore would have mediated some of the observed effects.

Zoo enclosures provide an excellent opportunity to investigate "open-field" behaviour, with a concurrently available source of water. Animals in zoos are often on a fixed-time schedule of food reinforcement. That is, they tend to be fed at predictable times on predictable days. Even if keepers attempt to vary the feeding times, food still appears at a particular time of day. That is, only some flexibility is possible. The presentation of novel stimulus objects (or other behavioural enrichment techniques) and the opportunity to engage in exploratory behaviour may eliminate or minimise the development of aberrant behaviours. However, based on the findings of this study, it would be difficult to accurately predict the effect of stimulus objects or schedules of reinforcement in the zoo environment, with its long inter-food intervals.

CHAPTER 10

FACILITATION OF EXPLORATORY BEHAVIOUR AND REDUCTION OF ABERRANT BEHAVIOURS IN CAPTIVE CHIMPANZEES (*Pan troglodytes*) AND CARACALS (*Felis caracal*): PRELIMINARY STUDIES AT ADELAIDE ZOO



10.1 INTRODUCTION TO PRELIMINARY STUDY 4: CHIMPANZEES

In 1991 and 1992, this author visited each of the major zoos in Australia (Adelaide, Melbourne, Taronga & Perth) that maintained a group of chimpanzees. In addition, the chimpanzees housed at the Rockhampton Botanical Gardens/Zoo and a young female (Holly) in a private facility were also visited. Differences in the type and size of enclosures, as well as the social structure of the various groups were observed (but will not be discussed in detail here). At the time, the following numbers of chimpanzees were held:

- 6 at Adelaide Zoo (2.4)- in an outdoor enclosure with a water moat
- 5 at Melbourne Zoo (2.3)- in an outdoor enclosure with a dry moat
- 24 at Taronga Zoo (7.17) + 5 that were about to be transferred overseas (3.2)- in an outdoor enclosure with a water moat
- 2 at Perth- in an outdoor, off-exhibit enclosure (1.1)
- 2 at Rockhampton Botanical Gardens/Zoo (2.0)- in an outdoor cage
- 1 at a private home in Wallacia, New South Wales (0.1)
- A further three (2.1) were held at locations that could not be visited.

Different methods of food presentation and environmental enrichment techniques were employed at each zoo. Artificial termite mounds were present at Adelaide, Perth and Taronga Zoo, and were used frequently by all the chimpanzees. Browse material (in the form of branches) was provided at Adelaide, Taronga and Melbourne Zoo, but there were size restrictions for such browse material at Melbourne Zoo, since the chimpanzees were known to throw branches at zoo visitors. Food was buried in a sandpit at Melbourne Zoo to encourage foraging. In the spacious night quarters (indoors) at Taronga Zoo, the chimpanzees were provided with shredded paper, tyres, plastic modular toys, phone books, poster rolls, plastic closed bins with holes and peanuts inside, tubs of water with floating Macadamia nuts, sacks and boxes with food hidden inside, and so on. Honey, jam and malt extract, were smeared at the top of climbing structures at Melbourne and Taronga Zoo to encourage use of these structures.

Only the chimpanzees at Adelaide and Taronga Zoo were breeding successfully. The inter-birth interval was as low as two or three years at Taronga. Many of the females there gave birth to their first progeny at nine-years of age, and some had their second infant by 11-years of age (Sacha). The pair of chimpanzees at Perth Zoo was housed in an off-exhibit enclosure.

Interesting similarities and differences in a number of behaviours were observed between groups. For example, ***wading in the water moat*** and extensive use of the termite mound was found at both Adelaide and Taronga Zoo. Similarly, ***fecal art*** using the ***mouth only*** (not finger painting) was found at both Adelaide and Melbourne Zoo. Interestingly, ***coprophagia*** appeared to be at its peak in the late afternoon (3.30 – 4.00 p.m.) at all zoos across the country. Not surprisingly, ***play*** and ***general activity*** was greatest in the two groups containing infants and juveniles (Adelaide had three chimpanzees under the age of 10-years, & Taronga had 17 in this age group).

10.2 METHOD FOR PRELIMINARY STUDY 4

10.2.1 SUBJECTS

The group of six chimpanzees (2.4.0) housed at Adelaide Zoo served as subjects (Figure 10.1). This group was comprised of an adult male (***Peter***), an infant male (***Tyce***), two adult females (***Susie*** & ***Fanny***) and two juvenile females (***Penny*** & ***Sandy***). The four youngest chimpanzees were all captive born, whilst the three adults were either wild born (***Susie***) or of "unknown birth type" (*Adelaide Zoological Garden Taxon Report*, 13th Dec. 1990). The chimpanzees ranged in age from 2-years to 38-years, at the start of the study (June 1991). Both Peter and Susie have since died.

According to the zoo records, ***Peter***'s (ID=550001`F') origin of birth is unknown, having arrived at Adelaide zoo on the 18th of March 1955, at approximately two-years of age. Donated by Taronga Zoo, his date of birth is given as 18th March 1953. At the start of the study, he was 38-years of age (Figure 10.1). He is the sire of the juveniles and infants in this group (***Penny***, ***Sandy*** & ***Tyce***).

Susie was born somewhere in Africa on approximately the 19th of April 1954 (ID=760009`O', referred to as ***Susie Cameo*** in the zoo records). She arrived at Adelaide Zoo on the 13th of April 1976, at the age of 22-years, having been donated by Perth Zoo. At the start of the study, ***Susie*** was 37-years of age (Figure 10.1). She has only given birth to one infant (9th February 1980) who lived for one day. ***Susie*** was almost 26 years old when her first and only offspring was born.

The third adult of the group was ***Fanny*** (ID=780030`Q'), whose origin of birth is unknown. She was born on the 16th of September 1965, and arrived in Adelaide on the 31st of July 1978, at the age of 13-years (just under), having been donated by Munich Zoo. At the start of the study ***Fanny*** was 25-years of age (Figure 10.1). She is the dam of ***Sandy*** and ***Tyce***, her only two surviving offspring. At the age of 15-years, ***Fanny*** gave birth to ***Jenny***, who lived for five years (until 10th October 1986). ***Fanny*** was 19-years old when she gave birth to ***Sandy*** and 24- years old when her son ***Tyce*** was born. (***Fanny*** has been renamed ***Fimi***).

Penny (ID=830056`U') was born at Adelaide Zoo on the 24th of March 1983. Her dam was ***Marlene***, who was 25-years old when she gave birth to ***Penny***. ***Marlene*** died when ***Penny*** was only 16-months old. According to keeping staff there at the time, ***Susie*** "adopted" ***Penny***, taking the role of adoptive mother. At the start of the study ***Penny*** was 8-years of age (Figure 10.1). Her unusual gait was immediately noticeable, since she usually walked on her wrists, rather than her knuckles. This mode of locomotion resulted in large and distinctive calluses on the back of her wrists. (***Penny*** has been renamed ***Panga***).

The youngest female, ***Sandy*** (ID=850063`V'), was born at Adelaide Zoo on the 10th of April 1985. Her sister ***Jenny*** was still alive at this point, being approximately four and a half years old. ***Sandy*** was 6-years of age at the start of the study (Figure 10.1). Her brother ***Tyce*** (ID=890148, referred to in the zoo records as ***Tryce***), was born on the 25th of June 1989, when ***Sandy*** was 4-years old. He was exactly 2-years old at the start of the study. (***Sandy*** has been renamed ***Sanda***, & ***Tyce*** has been renamed ***Totsie***).

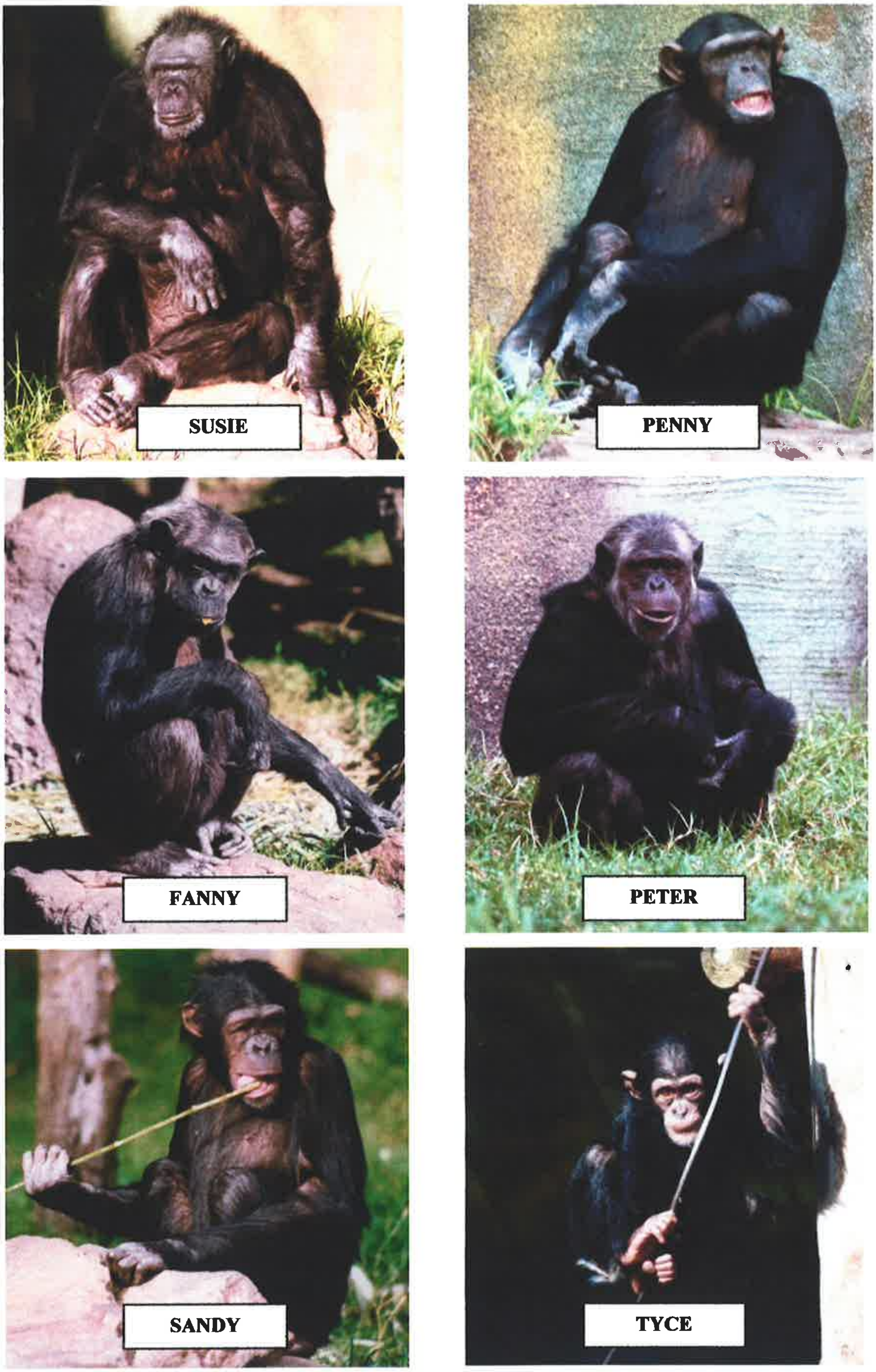


Figure 10.1. The six members of the chimpanzee group at Adelaide Zoo (in late 1991)

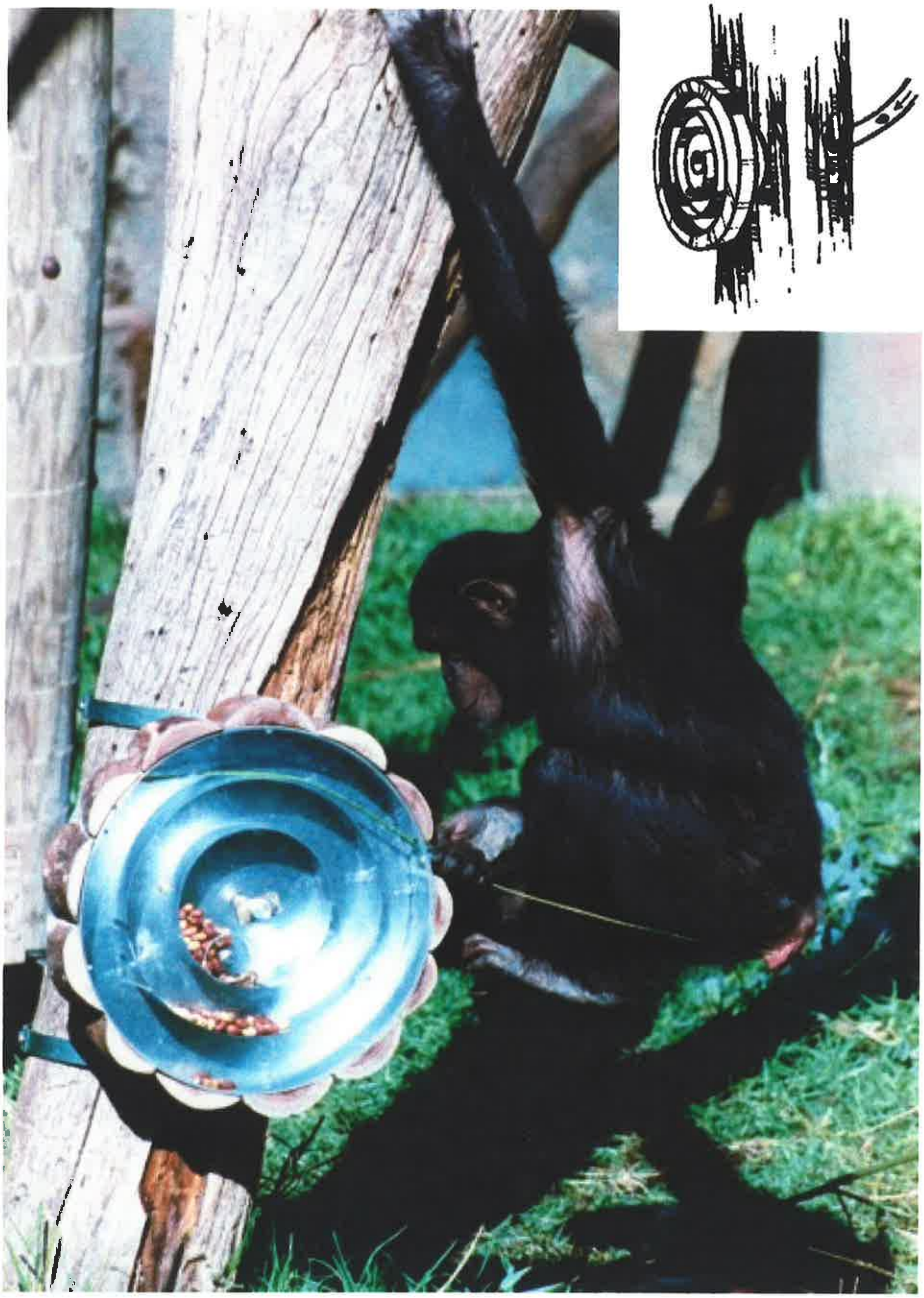


Figure 10.3. Sandy inserting a stick into the "peanut-wheel maze" (insert- diagram of the "nut maze" used at Copenhagen Zoo, taken from Figure 15, Lunding Andersen, 1987, p.48)

Figure 10. 2. Chimpanzees using the hollow "tree trunk" feeding device in the Copenhagen Zoo "Ape Jungle" (Photo 13 from Lunding Andersen, 1987, p.47)

10.2.2 APPARATUS

10.2.2.1 EXPERIMENTAL APPARATUS

Two groups of three removable objects were introduced into the enclosure during the "novel stimuli" phases of the experiment. These were securely bolted onto the climbing poles and anchored with wire cables where necessary to prevent heavy objects from becoming dangerous by swinging around, or being used by the chimpanzees as possible swinging "weapons". The safety of the chimpanzees was the prime concern during the construction, introduction and use of the apparatus. The objects were designed for easy installation and removal (without damaging the existing enclosure & facilities). The materials used were as strong and weather-resistant as possible. The food-related objects were designed to be easily loaded with food and cleaned. Timber and mid-green paint were used wherever possible, to give the objects as naturalistic an appearance as possible. Steve Tupper and Geoff Matthews constructed the objects in the Psychology Department workshop at the University of Adelaide. Adam Litchfield bored out the large log drum at Keith Litchfield Motor Engineers. Some of the objects were based upon objects in use at Copenhagen Zoo (Figure 10.2). The drawings from Copenhagen Zoo are also provided in the following pages. Members of staff at Adelaide Zoo were consulted throughout all phases of object construction and introduction. The stimulus objects were as follows:

FOOD-RELATED OBJECTS

- **"peanut wheel-maze"**: this object (based on the "nut maze" at Copenhagen Zoo) consisted of two main parts, namely, the fixing bracket and the wheel itself.

The fixing bracket was made of two adjustable (in diameter) metal hoops, which could be tightly bolted closed. These hoops were constructed from mild steel (25mm x 3mm), and rolled into a circle (310mm diameter), to suit the climbing pole to which they were clamped. The two hoops were welded top and bottom to a piece of square tube (30mm wide & 420 mm in length). A 16mm diameter x 100mm shaft was welded in the center of the tube, on the opposite face to the hoops (Figure 10.3).

The wheel consisted of three main components. The first component was the main frame. Flat mild steel (25mm x 3mm thick) was used to make two rings (410mm diameter). The rings were welded one above the other using four spacers (leaving a 30mm gap). A cross brace was welded to the back, with a bearing fixed in the centre. Thirteen small log segments were fixed to the outside of the frame. These created a more naturalistic look, as well as providing the chimpanzees with a "multiple handle" for ease of turning. A gap of 40mm was left for the nuts to fall out of. This size was judged to be small enough to prevent a chimpanzee from inserting his/her whole hand, but large enough to avoid getting a finger stuck.

The second component of the wheel was the internal maze structure (inside the main frame), which consisted of three circles on a 0.7 mm galvanised sheet backing (65mm in height). The two inner circles each had a gap of 10mm, at 90^0 to each other. The outer circle gap was 40mm, in line with the gap in the main frame, and at 180^0 to the gap in the middle circle. A spacer was required in the centre cavity of the maze, in order to secure the filler cap.

The final component was the clear acrylic front cover (10mm thick & 410mm in diameter). This was secured inside the main frame and held the nut maze assembly in place. A block of brass was fixed in the centre of the cover, to act as a bearing for the main shaft on the fixing bracket, thus supporting the wheel. A two-inch diameter hole with individual lid was cut within the front cover (sitting flush within it), so that the peanuts could be easily loaded into the centre of the maze. Once the wheel was positioned on the shaft, it was held in place with a domed end cap, which was screwed and pinned in place. Figure 10.3 shows the completed object, set up inside the zoo enclosure.

- **"foraging box"** : this object (combining features of Copenhagen Zoo's "shaking table" & "tilting table") consisted of four sides made of prepared pine timber (35mm thick & 195mm high). The sides of the square measured 570mm (outside dimension). A 10mm thick plywood floor and 10mm thick acrylic lid slid into grooves in the top and bottom of the box. A false galvanised sheet (0.7mm thick) bottom formed a 50mm high "hump" in the floor. This hump prevented the food from simply falling or rolling out of the hole. A 75mm diameter hole, with a 50mm deep tube (flush with the base) was created in the center of the "hump". This tube allowed the food inside the box to drop out of the base.

  Steel cable (4mm thick) was used to suspend the box from a horizontal climbing beam in the enclosure. At a height of 450mm above the box, a pulley system allowed the box to be suspended by a two cable cross assembly, which was anchored at the four top corners of the box. This pulley system allowed the chimpanzees to "wobble" the box. Greater movement increased the likelihood of food rolling over the "hump" and out of the box. Restraining cables were attached to the base of the box, to prevent excessive swinging, which may have endangered the chimpanzees. Figure 10.4 shows the completed object, set up inside the zoo enclosure.

- **"seed-shaker"**: A small River Red Gum (*Eucalyptus camaldulensis*) log formed the basis of this object (approximately 160mm in diameter & 250mm in length), which was similar in design to the "sunflower castor" used at Copenhagen Zoo. The centre of the log was bored out to a diameter of 110mm. A thin metal cylinder with a baffle system (15mm below the top) and a floor with a gap of 20mm were tightly fixed into the bore of the log. A flat piece of timber was bolted to the top of the log as a lid. Two metal straps were fixed to the outside of the log (top & bottom) to prevent the log from splitting open. At 50mm below the top of the log, a shaft (12mm diameter, 780mm long) was positioned through the centre of the log and cylinder. Metal collars on each side of the log held it in place on the shaft, whilst it was suspended in the fork of a climbing tree in the enclosure. Holes were drilled into the branches that created the fork in the tree, so that the shaft could be bolted into place. The log could be rotated through 360° by the chimpanzees, which would allow the seeds to fall out of the gap. Figure 10.5 shows the completed object, set up inside the zoo enclosure.

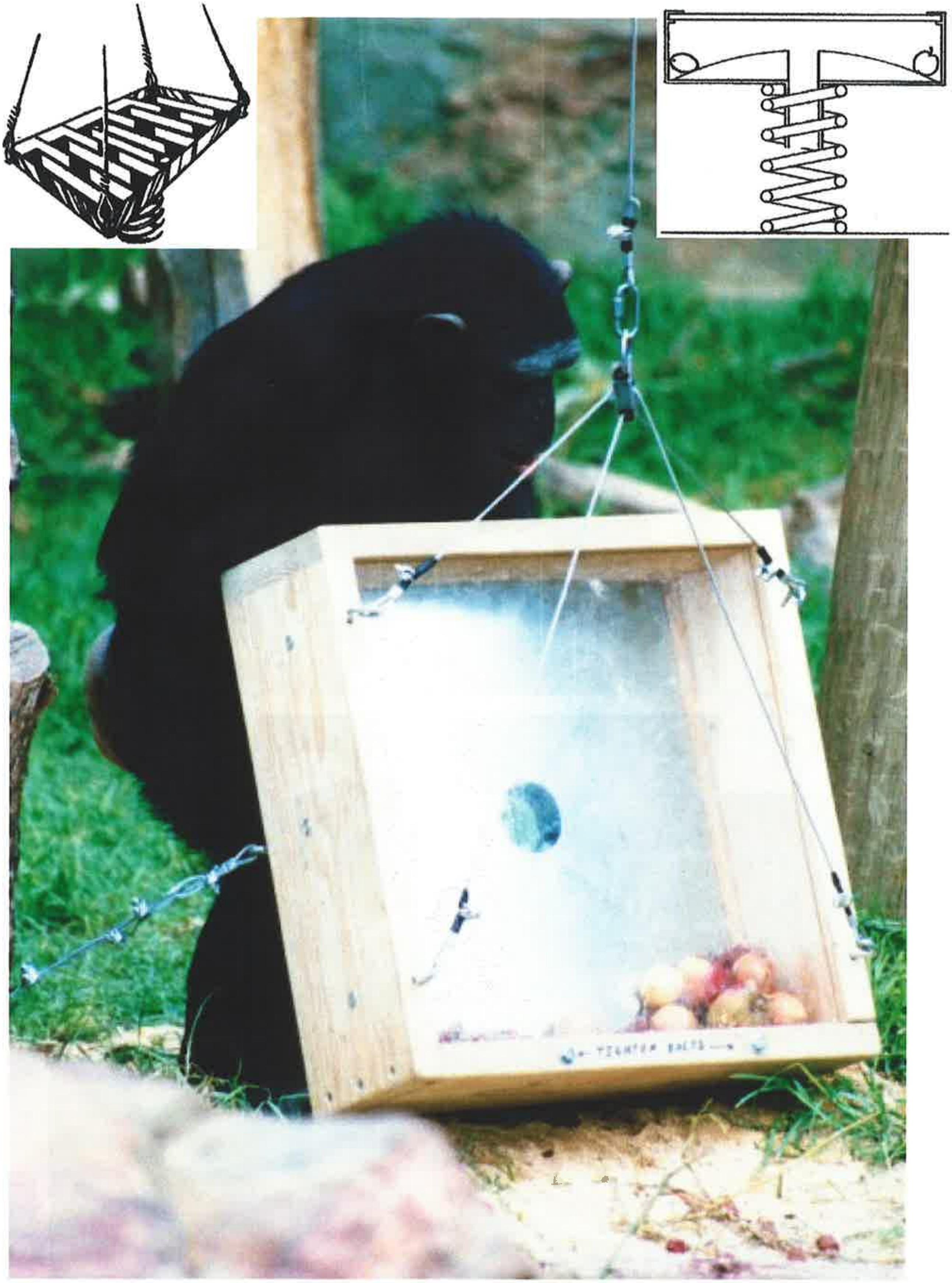


Figure 10.4. Penny tilting the "foraging box" and inspecting the fruit inside (insert left- "shaking table" & right- "tilting table" at Copenhagen Zoo, taken from Figures 15 & 17, Lunding Andersen, 1987, pp.48 & 49)

NON-FOOD-RELATED OBJECTS

- **"rotating seat"** : this object was created by re-modelling an office swivel chair. The cushioned seat and back were removed, and replaced with a timber disc (470mm diameter & 20mm thick). The four legs of the seat were welded to an angle iron frame, with open hoops fixed to the ends of this frame. In the zoo enclosure, these hoops were opened around the climbing posts, and then bolted tightly closed. The flat timber seat was 540mm above the ground. The steel was painted a mid-green colour (Figure 10.6).

- **"barrel-swing"**: this object was constructed from half a wooden 45-gallon wine barrel (420mm deep, open diameter of 730mm & floor diameter of 580mm). The staves were approximately 20mm thick. Three metal hoops were fixed around the barrel, to hold it together. Four fixing rings were welded to these hoops, and 6mm steel cables were attached through the rings, allowing the barrel to be suspended from an horizontal climbing pole in the zoo enclosure. Restraining cables were also attached to the base of the barrel, and fastened to nearby climbing posts, in order to limit the swing of the barrel. Figure 10.7 shows the completed object, set up inside the zoo enclosure.

- **"log drum"**: was an object (based on Copenhagen Zoo's "Ape drum") made from a large pine log (370mm diameter & 660mm in length). The center was bored out to a diameter of 250mm. In order to reproduce a synthesised drum beat, a large speaker and electronic circuitry were secured into the cavity. A 0.5mm thick metal cover was fixed to each end of the log. If the chimpanzees tapped or thumped the flexible metal ends of the drum, a button switch situated just behind the cover was activated, which in turn elicited a single drumbeat. The drum was suspended at a height of 600mm from the ground, by ropes attached to two eyelets on the log, and then to a horizontal climbing pole. Figure 10.8 shows the completed object, set up inside the zoo enclosure.

10.2.2.2 OBSERVATIONAL EQUIPMENT

Interesting behavioural patterns were recorded onto VHS videotapes, using a Panasonic NV-M7A video camera, with time and date onscreen display. The video camera was mounted on a tripod when the chimpanzees were at rest (or moving around very little), or hand-held if the chimpanzees were very active (to prevent them from being obscured by the climbing structures in the enclosure). The camera was in view of the chimpanzees at all times, being situated at the front of the enclosure, in the public viewing area.

Figure 10. 6. Tyce playing on the "rotating seat" by climbing up and spinning on his back

Figure 10.7. Sandy sitting in the "barrel-swing" (main picture), and Sandy climbing in and out of it with Tyce clinging dorsally (inserts).

Figure 10.8. Sandy, Fanny and Tyce using or playing on the "log drum" (insert- "Ape drum" at Copenhagen Zoo, taken from Figure 15, Lunding Andersen, 1987, p.48)

10.2.3 PROCEDURE

The study was divided into five phases, including three baseline phases and two phases involving the introduction of novel objects. Observations were made over eight weeks, with six observation sessions of one hour's duration taking place every day (*i.e.*, 6 hours per day, for 56 consecutive days). General observations were conducted over a period of three weeks (first baseline), in order for the chimpanzees to become accustomed to the observer. At the start of Week 4, the food-related objects were introduced into the enclosure (remaining in the enclosure at all times), and general observations were again conducted at the same times.

At the end of the fourth week (*i.e.*, after 7 days), the food-related objects were removed and the chimpanzees were again observed for a period of one week (second baseline). At the beginning of Week 6, the non-food-related objects were introduced into the enclosure. These objects remained there for a week, and general observations were made. At the end of this week, the objects were again removed, and the chimpanzees were observed for a period of two weeks (third baseline).

Table 10.1
The experimental design of preliminary Study 4.

Week	Dates	Phase of Study	Object Condition
1 - 3	Mon. 24th June 1991 to Sun. 14th July 1991	General observations (Baseline 1)	No Objects
4	Mon. 15th July 1991 to Sun. 21st July 1991	Presentation of Novel Stimuli	Food-related Objects
5	Mon. 22nd July 1991 to Sun. 28th July 1991	General observations (Baseline 2)	No Objects
6	Mon. 29th July 1991 to Sun. 4th August 1991	Presentation of Novel Stimuli	Non-food-related Objects
7 - 8	Mon. 5th August 1991 to Sun. 18th August 1991	General observations (Baseline 3)	No Objects

No changes were made to the usual zoo routine. Adelaide Zoo is open every day of the year, from 9.30 a.m. to 5.00 p.m. (extended hours during summer). The chimpanzees were given access to their "night quarters", but could remain in the outdoor enclosure at all times, except when they were locked away in the "night quarters", while the enclosure was being cleaned (once daily, typically at approximately 10.00 a.m.). The chimpanzees were fed three times per day, with keepers scattering the morning feed around the enclosure, once it had been cleaned (chimpanzees were still locked away in the "night quarters"). The feeds comprised a variety of fresh fruit and vegetables, and a measured portion of "primate cake" (containing extra protein, vitamins & minerals), which was passed to each chimpanzee through the bars of the gate at the back of the enclosure. The chimpanzees were also given a cup of "herbal tea" every morning, thus establishing a routine that would allow medication to be given if the need arose. There was a strict "hands-off" policy, with no physical interaction between the chimpanzees and their keepers.

Table 10.2
Observation times, feeding times and feeding location for preliminary Study 4.

Observation Times	**Feeding times (between)**	**Feeding Location**	**Zoo Visitors present?**
8.00 a.m. – 9.00 a.m.			No
	9.00 a.m. – 10.00 a.m.	Scattered & hidden throughout the enclosure	Yes – after 9.30 a.m.
10.00a.m. – 11.00a.m.			Yes
12.00 p.m. – 1.00 p.m.			Yes
	1.00 p.m. – 1.30 p.m.	Food passed through the bars of the back gate	Yes
1.30 p.m. – 2.30 p.m.			Yes
3.00 p.m. – 4.00 p.m.			Yes
	4.00 p.m. – 4.30 p.m.	Food in the night quarters & at the back gate	Yes
4.30 p.m. – 5.30 p.m.			No – after 5.00 p.m.

When the food-objects were in the enclosure, the keepers filled the "foraging box" with the food items that were usually hidden around the enclosure during the morning feed (*i.e.*, fruit & vegetables). The keepers also filled the "peanut-wheel-maze" with nuts, and the "seed-shaker" with sunflower seeds at the same time (after the enclosure was cleaned & the chimpanzees were still locked away). The nuts and seeds were additional food items (*i.e.*, not typically provided on a regular basis).

10.3 PRELIMINARY FINDINGS AND DISCUSSION FOR STUDY 4

10.3.1 GENERAL BEHAVIOURAL OBSERVATIONS (BASELINES)

Although this section focuses on a description of aberrant behaviours, this should not imply that the chimpanzees did not engage in a wide variety of "normal" or interesting behaviours. There were notably few instances of ***aggression*** throughout the eight-week study. All members of the group fashioned tools from the bamboo sticks or browse provided (Figure 10.12), which were then used to extract honey from the artificial termite mound. All members of the group utilized the climbing poles and structures in the enclosure, demonstrating their remarkable climbing and balancing abilities (Figure 10.11). Browse was used in a number of ways- as food, as nesting material, as ladders (Figure 10.11) and even to interact with birds (Figure 10.10) or stimulus objects (Figure 10.19). The chimpanzees groomed, played, foraged and rested together. ***Penny*** succeeded in destroying a number of objects in the enclosure during the study, ranging from pulling out tree stumps, to collapsing a large wooden platform by jumping on it and pulling at it (Figure 10.21).

10.3.1.1 UNUSUAL BEHAVIOURS

WADING IN THE MOAT

On a number of occasions, ***Penny*** and ***Sandy*** waded in the water moat, walking bipedally along the top step (Figure 10.9). As the steps were slippery, members of the zoo staff were concerned about the risks of drowning. After completion of the study, the water moat as a barrier was replaced with a high wall and window, thereby eliminating any risk of drowning.

10.3.1.2 ABERRANT BEHAVIOURS

STEREOTYPIC PACING

Stereotypic pacing was observed in ***Peter*** on numerous occasions during the afternoon, immediately prior to the afternoon feed, suggesting that it was a food-anticipatory stereotypy.

Typically the ***pacing*** occurred at a walk, and took place at the back of the enclosure, parallel to the back gate, where food was presented. At times, he appeared to pace out an exact number of steps before turning around, and sometimes slapped his foot with his hand as he turned around. ***Stereotyped pacing***, which may include pivoting and turning movements, is one of the ***aberrant movements*** sometimes observed in captive chimpanzees (Jane Goodall Institute, 1990).

MASTURBATION

Susie engaged in a behaviour that may have been ***masturbation***. Captive female chimpanzees sometimes rub their sexual swellings with a hand or an object (Jane Goodall Institute, 1990). However, ***Susie*** rubbed her rear end against the walls for extended periods of time (>30-minutes), not only when she was "swollen" (in estrous), and this masturbation appeared to be a food-anticipatory behaviour. Typically, she rubbed her swelling against the walls when she was standing or lying forwards, resting on her arms. If the behaviour took place immediately prior to the afternoon feed, it tended to take place in the area adjacent to the back gate, where the food was to be presented. At other times, it took place against the back wall (balcony).

FOOD BEGGING

Occasional bouts of ***food begging*** (from the zoo public) were observed in ***Susie*** and ***Fanny*** (Figure 10.14). Thus, there were individual differences in some of the aberrant behaviours observed (***pacing***, ***masturbation*** & ***food begging***). It should be noted, that not all researchers might consider ***food begging*** as an aberrant behaviour. Three other aberrant behaviours were observed in all members of the group, which will now be discussed.

COPROPHAGIA

Five main ***aberrant oral behaviours*** have been observed in captive chimpanzees (Jane Goodall Institute, 1990), namely: ***coprophagy*** (eat or orally manipulate feces), ***self bite*** (grip & apply pressure to parts of the body with the teeth), ***self orality*** (prolonged sucking of fingers or toes), ***re-ingesting vomit*** (vomit into hand & then eat the vomit) and ***urine drinking*** (urinate into hand or container & then swallow it). A few brief bouts of ***urine drinking*** were observed in ***Susie*** and ***Penny***, but ***self bite***, ***self orality*** and ***re-ingesting vomit*** were not observed in any member of the group. ***Coprophagia***, on the other hand was observed on numerous occasions (Figure 10.13), with bouts that lasted for more than 10-minutes in some instances (***Sandy*** & ***Susie***). It appeared to occur most frequently in the morning and late afternoon, prior to the first and last feeds of the day, suggesting that this behaviour may also have been a food-anticipatory behaviour.

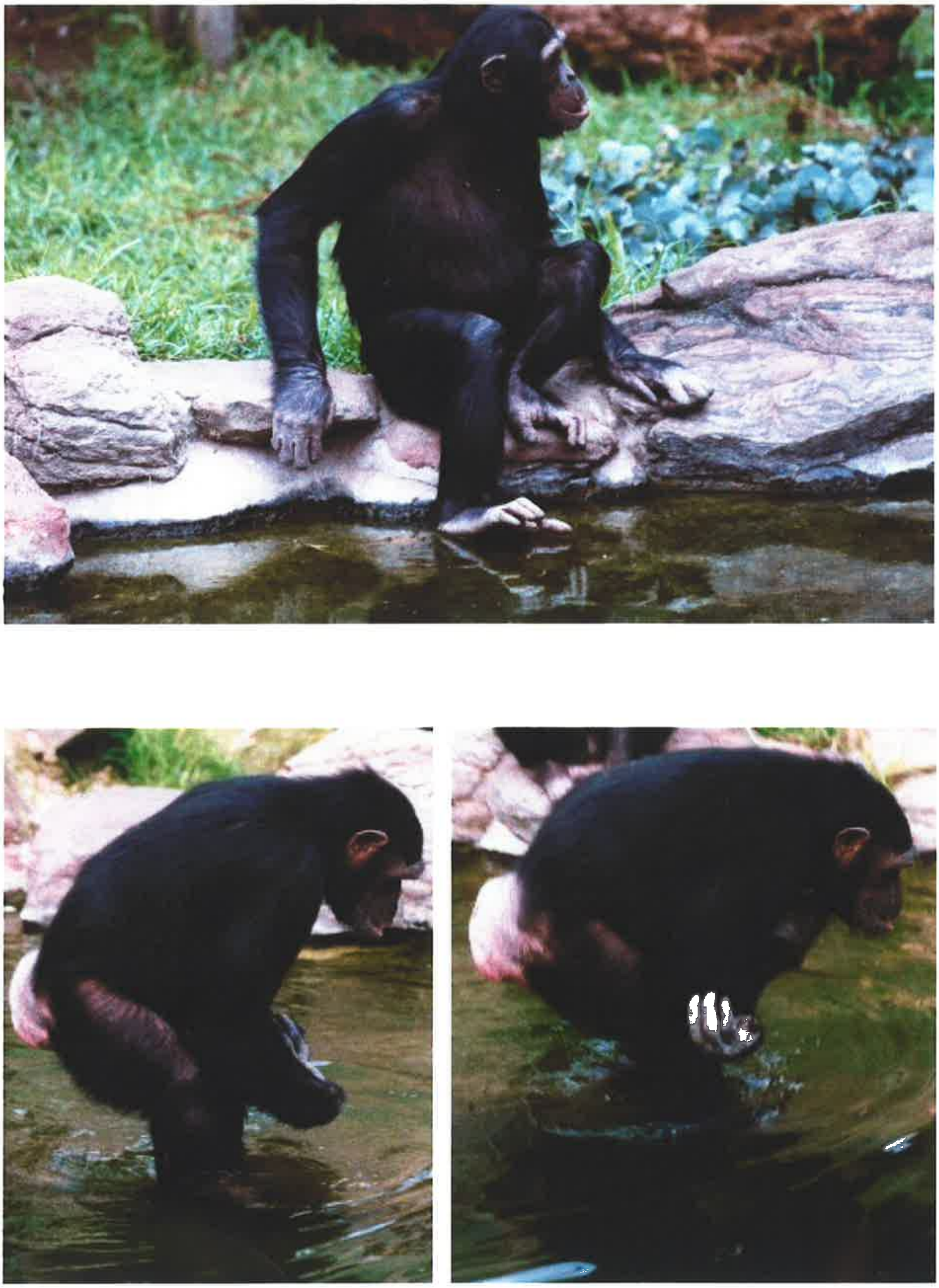


Figure 10.9. Both Sandy (top) and Penny (bottom) were observed wading in the shallow end of the water moat on several occasions

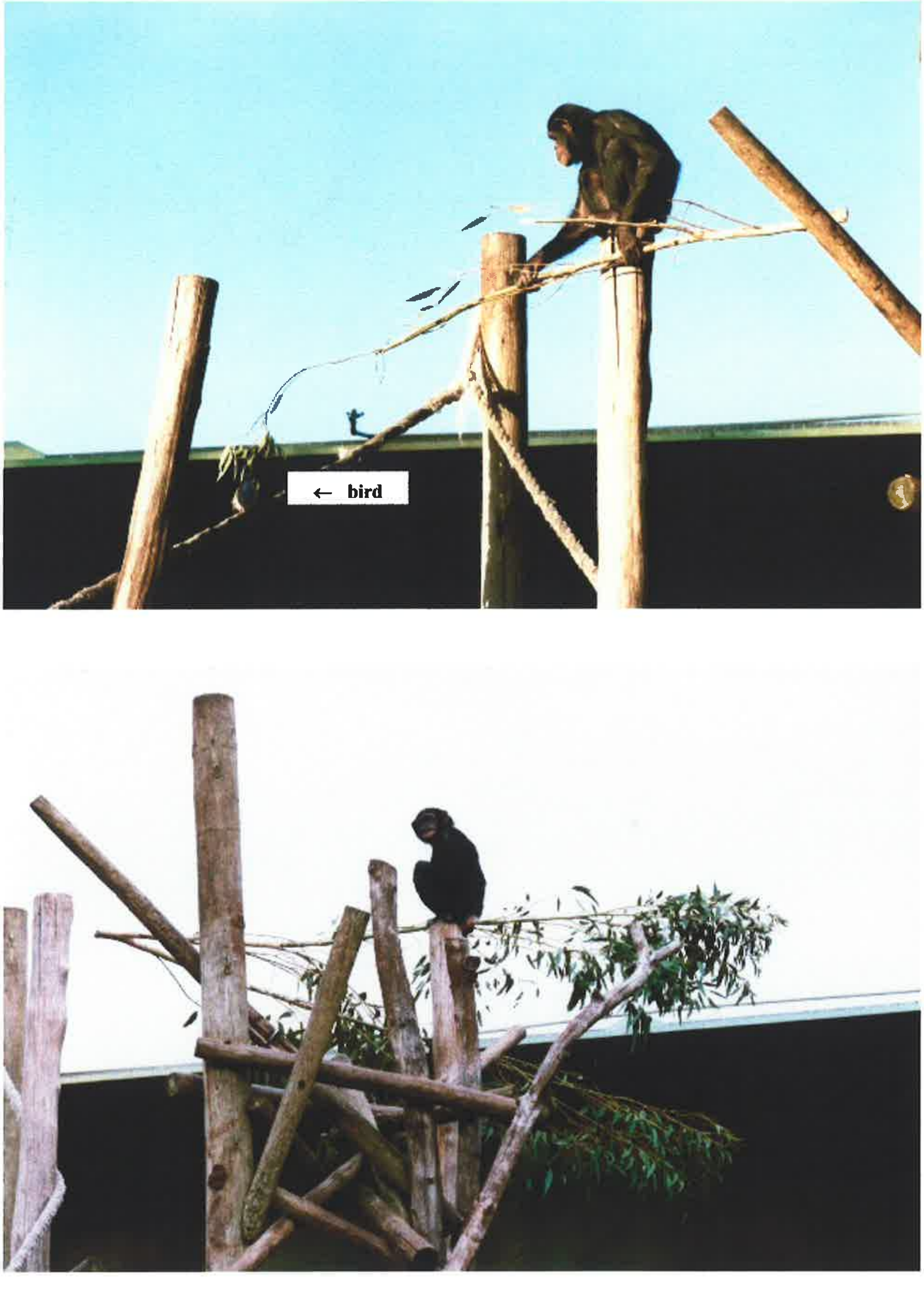
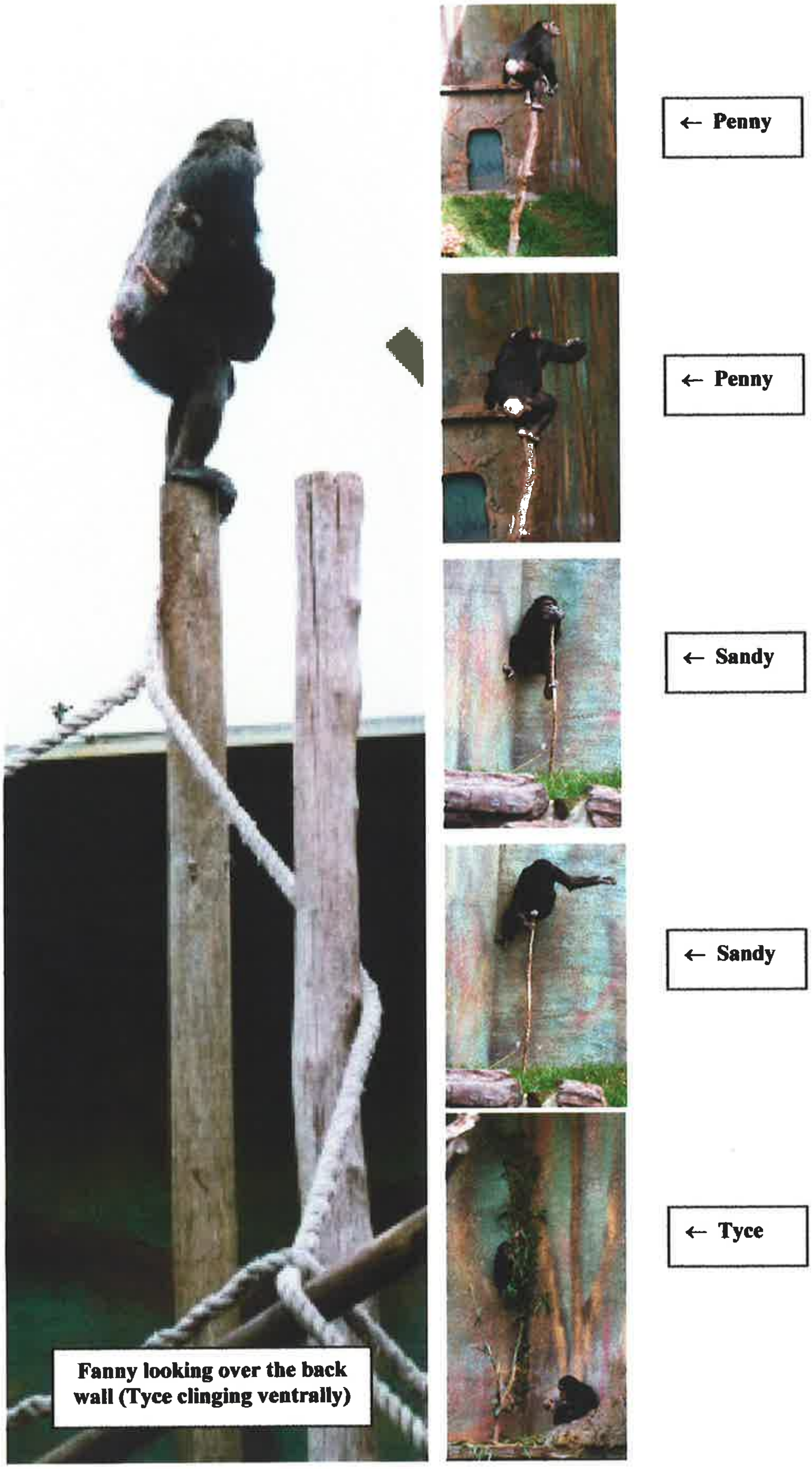


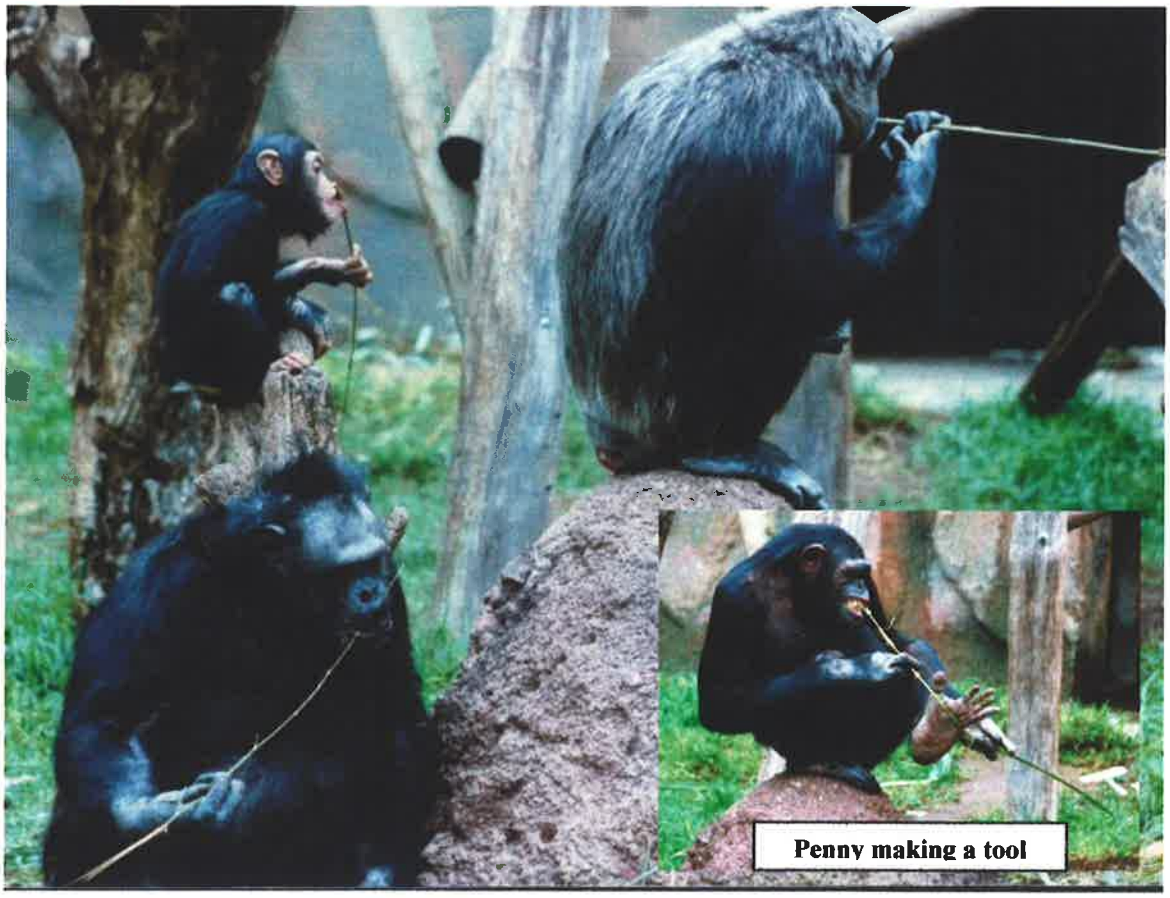
Figure 10.10. Sandy, in particular, used the larger branches of browse in interesting ways, such as to interact with birds (top) or to carry to the top platforms (or elsewhere) and make nests or manipulate them in other ways (*e.g.*, breaking, dragging, using as poles or ladders)



Fanny looking over the back wall (Tyce clinging ventrally)

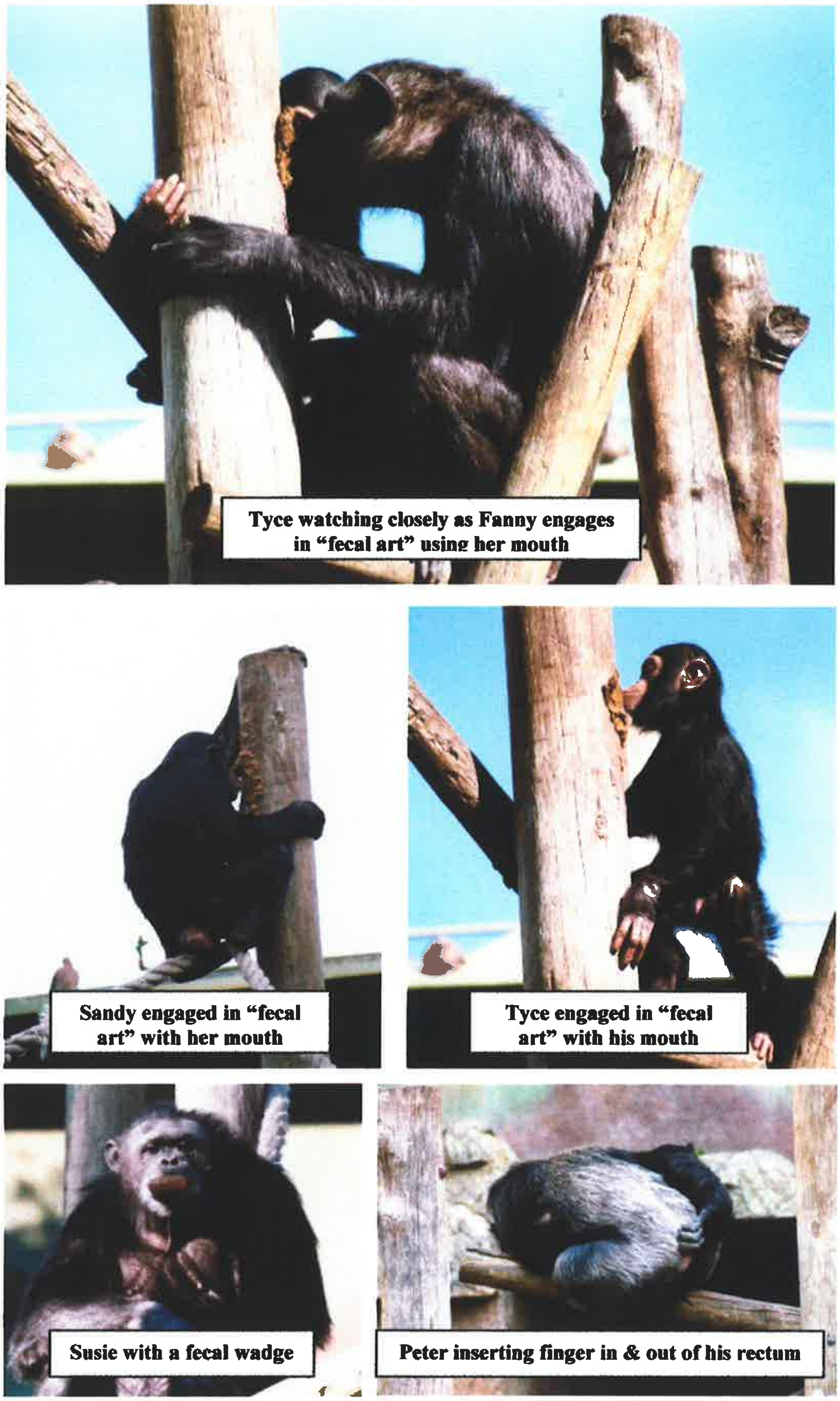
Figure 10.11. Onlookers are often astounded by the climbing abilities of the chimpanzees at Adelaide Zoo, yet "wild" chimpanzees feed and move through trees that are often 20-40 metres in height (personal observation)

Sandy making a tool by stripping leaves off a bamboo stick



Penny making a tool

Figure 10.12. All members of the group used the artificial termite mound, and fashioned their own tools from the bamboo sticks or browse provided



Tyce watching closely as Fanny engages in "fecal art" using her mouth

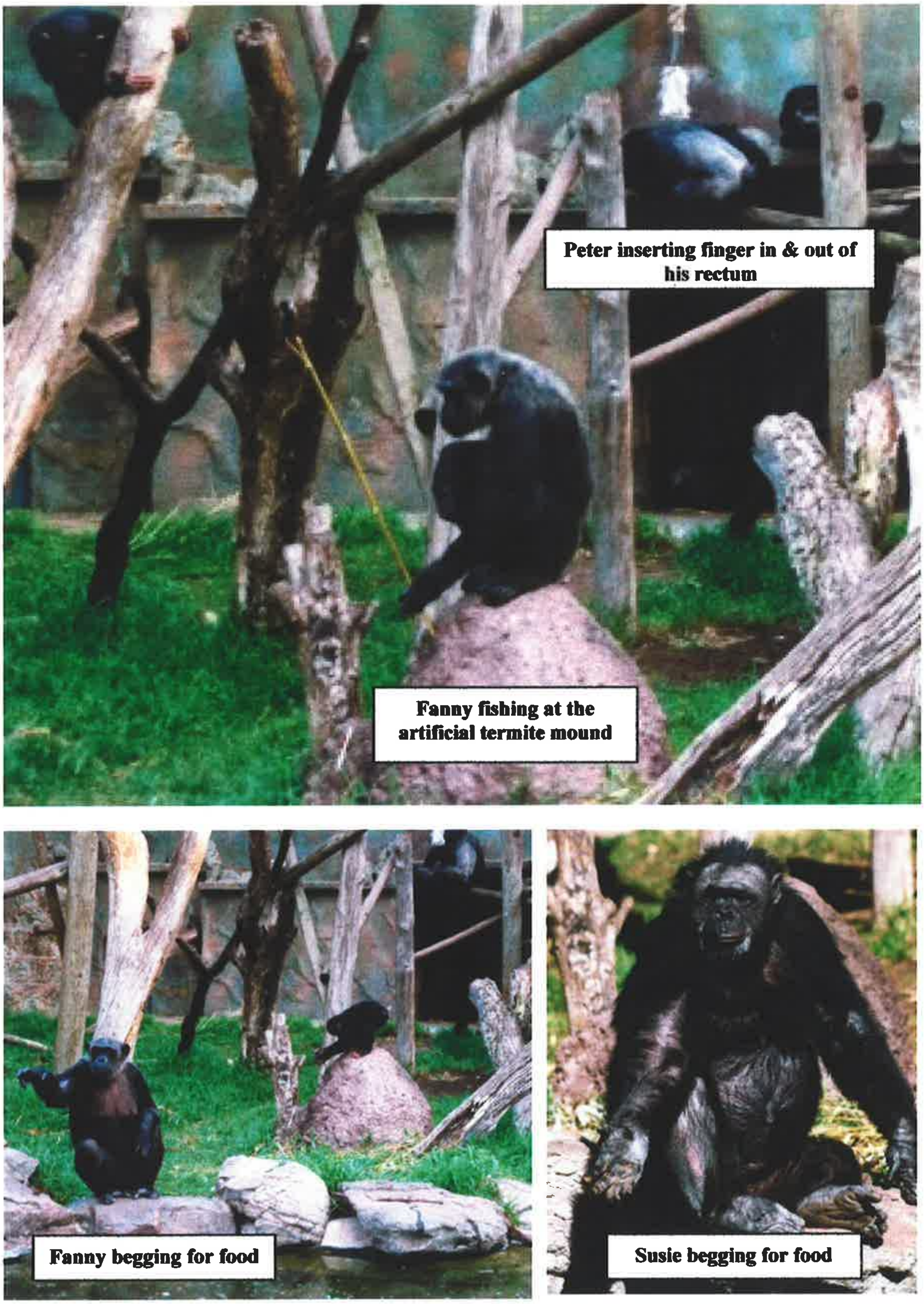
Sandy engaged in "fecal art" with her mouth

Tyce engaged in "fecal art" with his mouth

Susie with a fecal wadge

Peter inserting finger in & out of his rectum

Figure 10.13. Fanny, Penny, Sandy and Tyce were observed engaging in "fecal art" (using the mouth rather than the typical finger painting) on a number of occasions. All group members were observed to engage in ***coprophagia***, & also to insert fingers in-&-out of their own rectums- but this behaviour was most often observed in Peter (usually in the late afternoon just prior to the last feed of the day)



Peter inserting finger in & out of his rectum

Fanny fishing at the artificial termite mound

Fanny begging for food

Susie begging for food

Figure 10.14. Food begging was observed on a few occasions (bottom). Apart from fecal art and ***coprophagia***, the most aberrant behaviour observed was the insertion of fingers in-&-out of the rectum, which usually took place immediately prior to the late afternoon feed (top)

FECAL ART

Captive chimpanzees sometimes engage in ***fecal art***, which involves the smearing of feces onto the walls or floors of enclosures with the fingers (Jane Goodall Institute, 1990). Interestingly, all members of the group at Adelaide Zoo were only observed to use their mouths for painting feces onto the walls at the back of the enclosure (balcony), and onto the posts of the climbing structures (Figure 10.13). That is, they engaged in ***fecal mouth art*** (not ***finger painting***). Thus, cultural variations in this behaviour may exist. ***Fanny***, ***Penny***, ***Sandy*** and ***Tyce*** engaged in this behaviour most frequently.

INSERTION OF FINGERS INTO THE RECTUM

This behaviour might be considered the most aberrant of all. It is not included in the widely used ethogram for captive chimpanzees (Jane Goodall Institute, 1990). Whilst in a standing or lying position, the chimpanzee repeatedly inserted his/her index or middle finger into the rectum (Figure 10.13). This behaviour only took place in the afternoon, immediately prior to the last feed of the day, and appeared to be a food-anticipatory behaviour. It was observed in all members of the group, but most often and most noticeably (for longer bouts) in ***Peter*** and ***Fanny***.

10.3.2 BEHAVIOURS WHEN FOOD-RELATED OBJECTS WERE PRESENT

This section presents a descriptive analysis of some of the behaviours directed at the food-related novel stimulus objects, and changes in other behaviours observed prior to the presentation of objects.

10.3.2.1 OBJECT-DIRECTED BEHAVIOURS

All members of the group successfully obtained food from the three objects. The adult females mastered the response requirements of each object at the first attempt. Throughout the week, the area around the ***peanut wheel-maze*** and ***foraging box*** was a focus for activity (Figure 10.16). These two objects were constantly manipulated until they were empty of food, and then they were clambered on and up during bouts of play.

The speed with which the adult chimpanzees approached the novel objects was somewhat startling (***neophilia***). Within seven seconds of emerging from the locked dens, the three adults (with ***Tyce*** clinging to his mother) were inspecting and manipulating the ***peanut wheel-maze*** and ***foraging box***. By contrast, ***Penny*** and ***Sandy*** clearly avoided the objects for the first few minutes (***neophobia***), initially watching the adults from as far away as possible, and up high (presumably giving the best vantage point). Of particular interest are the initial approaches made by ***Sandy***, who was the last to approach and touch the objects. The following general observations were made after ***Sandy*** entered the enclosure at 11.05 a.m.:

- 11.10 a.m. (5-mins after entry)- ***Sandy*** was comforted (appeasement & grooming) by both ***Peter*** and her mother, and she and ***Penny*** approached the objects, but remained out of reach above them.
- 11.14 a.m. (9-mins after entry)- ***Sandy*** approached the ***peanut wheel-maze***, standing directly behind ***Fanny***, who was turning it. After four seconds, ***Sandy*** climbed away.
- 11.15 a.m. (10-mins after entry) ***Sandy*** approached and touched the ***wheel-maze***.
- 11.16 a.m. (11-mins after entry) ***Sandy*** sat and tipped the ***seed-shaker***.
- 11.19 a.m. (14-mins after entry) ***Sandy*** touched the ***foraging box*** and then immediately climbed above the ***wheel-maze*** and touched it.
- 11.23 a.m. (18-mins after entry) ***Sandy*** tipped and inspected the ***seed-shaker*** and ate the seeds which had fallen onto the log below.
- 11.24 a.m. (19-mins after entry) ***Sandy*** watched ***Fanny*** turn the ***wheel-maze*** and eat the nuts, from over her shoulder.

Thus, within the first 20 minutes, even ***Sandy***, who was the most hesitant to approach and touch the objects, had visually inspected and successfully obtained food from at least one object.

PEANUT WHEEL-MAZE

Susie monopolized this object, and showed a wide range of topographical variations of responses. Unlike the other members of the group, she did not always adopt a standing or sitting position, when turning the wheel with her hands. Sometimes she lay on her back, turned the wheel with her feet, and collected the nuts with her hands (Figure 10.15). At other times she lay on her side and turned the wheel with one hand (Figure 10.16). Since ***Susie*** was the most overweight member of the group, and she obtained most of the nuts, her access to peanuts would have been restricted if this object had been present for more than a week. Options might have included occasional use of the object (*e.g.*, only fill it up once a week), or use of other small food items that might have been less fattening (*e.g.*, other nuts or seeds).

Peter and ***Sandy*** were both observed to use sticks on this object. ***Peter*** hit the clear front cover of the maze on a number of occasions (Figure 10.15), in an apparently frustrated attempt to obtain the nuts inside. Unlike the adult females, he did not successfully turn the wheel on the first attempt. ***Sandy*** inserted bamboo sticks (used as tools to obtain honey from the artificial termite mound) into the hole from which the nuts fell out (Figure 10.3). That is, she appeared to be using a tool in order to obtain the nuts.

Peter hitting the maze with a bamboo stick

Tyce standing to inspect the maze

Susie lying on her back & turning the wheel-maze with her feet

Penny standing & turning the maze

Susie collecting the nuts

Figure 10.15. The wheel-maze was used in a number of ways, with chimpanzees adopting a standing, sitting or even lying down position (only Susie), and turning the wheel clockwise and counter-clockwise

Penny stands & turns the wheel-maze while Sandy with Tyce clinging dorsally watch on

Susie lying down & turning the maze, & Sandy vigorously tilting the foraging box

The area around the wheel-maze & foraging-box becomes a center of activity for the group- Susie & Penny at the maze, & Tyce & Sandy play on & around the foraging box

Tyce watching as Fanny & Sandy turn the wheel-maze

Figure 10.16. Throughout the week, the area around the "peanut-wheel maze" and "foraging box" was a focus for activity

Sandy tickling Fanny (open play-face) & Penny watching Susie turn the maze

Peter playing "chase" with Tyce (clambering up the cable) & Susie turning the maze

Figure 10.17. The "foraging box", in particular, was often incorporated into bouts of play

Figure 10.18. Most of the chimpanzees vigorously tilted the "foraging box" in order to obtain the fruit (top- Penny), but Fanny (bottom) was able to insert her long thin hands into the hole and pull the fruit out

Figure 10.19. The "foraging box" was firmly anchored with cables and strong enough to withstand the chimpanzees hitting it with large branches (Sandy- middle pictures) and sitting or jumping on the box itself (Sandy- top, & Tyce- bottom)

Figure 10.20. The "seed-shaker" was mainly used by the three youngest members of the group, especially Sandy, who supplemented her late afternoon feeds with the seeds

FORAGING BOX

All members of the group used this object successfully. Sometimes the box was shaken, whilst at other times it was vigorously tilted (Figure 10.18). ***Sandy*** sat on, jumped on or hit the foraging box with sticks (10.19). ***Fanny*** was able to insert her long thin hands into the hole at the bottom, and pull the food items out (Figure 10.18). At some stage, all the chimpanzees had to lean under the box to pick up the fruit from the ground. Otherwise, the chimpanzees did not appear to adhere to a single topography of response.

SEED-SHAKER

All members of the group used this object at some stage. However, the youngest members of the group used it the most (Figure 10.20). ***Sandy***, in particular supplemented her late afternoon feeds with the seeds. Although the keepers attempted to distribute this last feed of the day evenly, throughout the eight-week study, ***Sandy*** often had her food taken from her by other members of the group (mainly adults). Thus, this object served as an important source of food for this individual, who otherwise received no food for a period of up to 20-hours.

10.3.2.2 OTHER BEHAVIOURS

Aberrant behaviours declined dramatically upon presentation of the food-related objects. Almost no ***coprophagia*** or ***fecal art*** took place, with only a few instances recorded towards the end of the week. Although it was completely absent during the first three days, it gradually began to reappear as the chimpanzees habituated to the novel objects. ***Foraging***, ***play*** and ***exploration*** were observed more frequently during this week, in all members of the group.

10.3.3 BEHAVIOURS WHEN NON-FOOD-RELATED OBJECTS WERE PRESENT

As with the previous section, this section presents a descriptive analysis of behaviours directed at the novel stimulus objects, and changes in other behaviours observed prior to the presentation of objects. The three non-food-related objects were designed purely for play and manipulation. Although the adults investigated the objects, and occasionally sat on the ***rotating seat*** as they ate, or incorporated them into bouts of play (*i.e.*, climbing over or up them), they were largely ignored. The younger chimpanzees, however, played with the objects throughout the week.

10.3.3.1 OBJECT-DIRECTED BEHAVIOURS

ROTATING SEAT

Tyce, in particular, was the most playful around this object. He was often observed to climb onto the seat, lie on his back displaying a "play face" while it rotated, and then leap off (Figure 10.6). During bouts of play (*e.g.*, chase), he and the other younger chimpanzees (***Sandy*** & ***Penny***) clambered onto the object, or chased each other around it.

BARREL-SWING

The three youngest members of the group primarily used the ***barrel-swing*** as a climbing structure. Sometimes they sat in it (Figure 10.7), but most often they rapidly climbed in and out of it, incorporating it into bouts of play.

LOG DRUM

The ***log drum*** was used in a number of ways. Towards the end of the first day, ***Fanny*** successfully tore the cover from one end of the drum, watched closely by ***Tyce*** and ***Sandy*** (Figure 10.8). After hitting the end of the drum, and hearing the synthesized drum noise, she appeared to tear and pick at the end with her fingers, in order to discover the source of the sound. When it became apparent that she would succeed in pulling off the cover, the keepers called in and locked up the chimpanzees, in order to remove the drum so that it could be repaired (since the internal parts may have posed a risk of choking). A stronger metal cover was attached, and the drum remained in tact for the rest of the week. All members of the group hit the drum at some stage, but ***Sandy***, ***Tyce*** and ***Penny*** again incorporated this object into bouts of play-chasing each other up and over it.

10.3.3.2 OTHER BEHAVIOURS

Fewer bouts of ***coprophagia*** and ***fecal art*** appeared to take place during this week. However, ***Peter*** and ***Fanny*** were observed to engage in ***insertion of fingers into the rectum*** prior to the last feed of the day. The three youngest members of the group appeared to benefit greatly from the presence of these objects, with many lengthy bouts of ***play*** observed in or around the objects.

10.3.4 SOCIABILITY OF GROUP MEMBERS

Figures 10.23a and 10.23b provide a visual summary of the percentage of total sample points, that each member of the group spent alone, or with each of the other members of the group, prior to the commencement of the study (Week 1 Baseline) and after completion of the study (Week 8 Baseline). This allows a comparison of associations between group members to be made, and may indicate whether the study itself may have affected the time spent alone or time spent with each other individual.

It must be noted, that the percentages do not reflect actual durations (*i.e.*, ***instantaneous sampling*** was used), but are based on a large number of total sample points (*i.e*, 840 for Week 1 & 832 for Week 8). For each one-hour observation session (6 per day), 40-minutes worth of "association" data were collected (*i.e.*, 2 x 20-mins), divided into 2-minute sample intervals (20 per session). A chimpanzee was considered to be alone, if s/he was more than two meters away from another chimpanzee. The names of any individuals located within 2-meters were recorded for every sample interval. The two-meter criterion was somewhat arbitrary, and it must be noted that a chimpanzee may have appeared to be alone, but actually engaged in an interpersonal interaction. As Goodall (1986) points out, any such analysis may not take into account: "the many subtle glances, soft grunts, inconspicuous avoidances, and so on that characterize chimpanzee communication" (p.192). In addition, the association patterns presented here do not indicate whether the interactions were friendly or aggressive. Nevertheless, general patterns of association and time spent alone can be determined.

10.3.4.1 TIME SPENT ALONE

Prior to the presentation of novel stimulus objects (Week 1 Baseline), ***Fanny*** (mother) and ***Tyce*** (infant) spent the least amount of time alone (≤ 30%). This is not surprising, since ***Tyce*** was not weaned, and they were in each other's company for more than 40% of the total sample points. The other members of the group spent between 40% and 50% of total sample points alone. After exposure to novel stimulus objects (Week 8 Baseline), the time spent alone decreased for four of the chimpanzees. Whilst ***Tyce*** and ***Fanny*** still spent more than 40% (≤ 50%) of total sample points in each other's company (a slight increase), they both spent less time alone (≤ 22%). For ***Fanny***, a 10% decrease in time spent alone was recorded. ***Penny*** and ***Susie*** also spent noticeably less time alone, after exposure to objects. For ***Penny***, there was an 8% decrease, with about a third of her time spent alone during Week 8. The decrease in time spent alone was greatest for ***Susie***. Prior to presentation of objects, she spent half of the total sample points alone, which decreased by 12% in Week 8. For ***Sandy*** and ***Peter***, there was no change at all in time spent alone, and the values for both differed by only 1% (≤ 45%). That is, exposure to objects had no effect upon the time spent alone for these two individuals.

10.3.4.2 TIME SPENT WITH OTHER INDIVIDUALS

During Week 1, ***Fanny*** spent more than a third of her time with ***Tyce*** (already mentioned) and ***Peter***, and more than 20% (≤ 27%) of total sample points with the others. She spent slightly more time with her daughter, ***Sandy***, than with ***Penny*** and ***Susie***. After exposure to objects (Week 8), ***Fanny*** spent slightly less time with ***Peter*** and ***Sandy*** (33% & 25%, respectively), but noticeably more time with ***Penny*** and ***Susie*** (> a third). She still spent the most time with her infant, ***Tyce***, but now spent the least total sample points with her oldest offspring, ***Sandy***.

For ***Tyce***, exposure to objects resulted in little change in time spent with other members of the group, although he spent slightly more time with his mother. This suggests that the changes in routine, and exposure to unfamiliar stimuli may have been somewhat unsettling. During both weeks, a large percentage of sample points were spent with his older sister (≥ 38%). This is not unexpected, since in natural environments, the next oldest sibling typically takes on an ***allo-parenting*** role. That is, the elder sibling cares for or takes control of the infant (Jane Goodall Institute, 1990). Indeed, ***Sandy*** was often observed to hold, groom or carry ***Tyce*** around on her back (Figure 10.16). ***Fanny*** only carried him ventrally (Figure 10.11), but ***Sandy*** was too small to do this. ***Tyce*** spent less than a third of total sample points with other members of the group, and the least amount of time with ***Susie*** (> 20%).

Sandy spent the most time with her younger brother, ***Tyce*** (35%), and about a quarter of her time with her mother, ***Fanny*** (Weeks 1 & 8). She was clearly engaged in ***allo-parenting***. She spent the least amount of time with ***Susie*** and ***Peter*** (< 20%). After exposure to objects, she spent slightly less time with the adults in the group, but exactly the same amount of time with the other younger members of the group.

Susie spent the most time with ***Penny*** during Week 1 and Week 8 (> 30%), but the amount increased by 10% after exposure to objects. Prior to introduction of objects, she spent about a quarter of her time with ***Peter*** and ***Fanny***, the other adults in the group. After exposure to objects, she spent noticeably more time with ***Fanny*** (11% increase), but not with ***Fanny***'s infant, ***Tyce***. That is, the increase in time spent together by ***Susie*** and ***Fanny***, took place when ***Tyce*** was away from his mother. ***Susie*** spent the least amount of time with ***Sandy*** (< 20%).

Exposure to novel objects had little effect on the time that ***Penny*** spent with ***Peter***, ***Sandy*** and ***Tyce*** (20% - 26% of her time was spent with each of these individuals). However, during Week 8 ***Penny*** spent noticeably more time with ***Fanny*** (7% increase) and ***Susie*** (10% increase), the two adult females. The increase in time spent with ***Fanny*** took place when ***Tyce*** was away from his

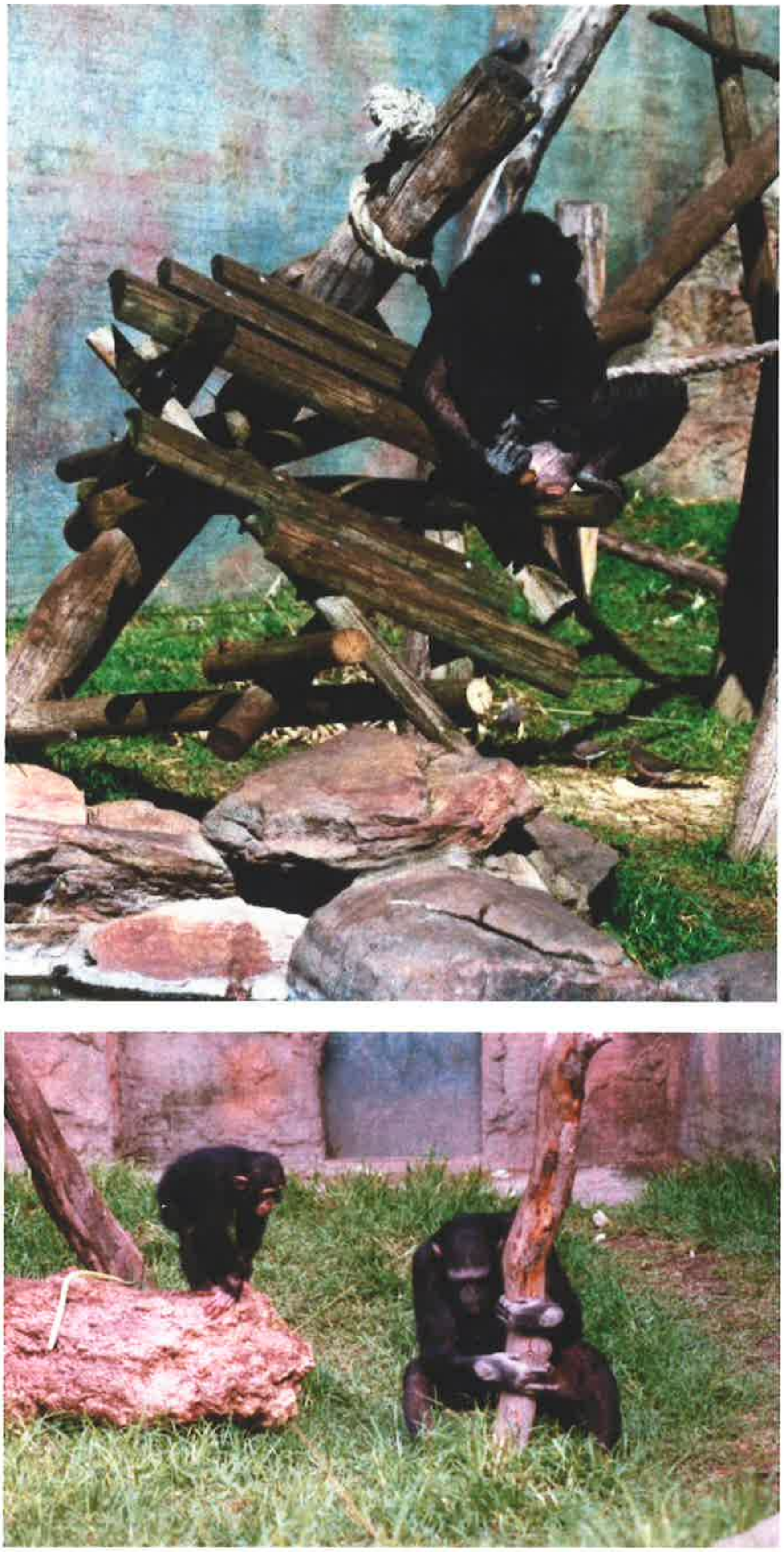


Figure 10.21. Penny destroyed a number of items in the enclosure during the study. She succeeded in collapsing the front platform by jumping on it and pulling at it (top), and she loosened and then pulled out a tree stump (bottom)

Figure 10.22. Chimpanzees should be provided with tall observation areas- platforms, trees or poles (top- adult chimpanzee, Peter, looking over the wall at Adelaide Zoo at adult orangutan, Punjac) and artificial termite mounds (an array of topographical responses can be observed at Taronga Zoo)

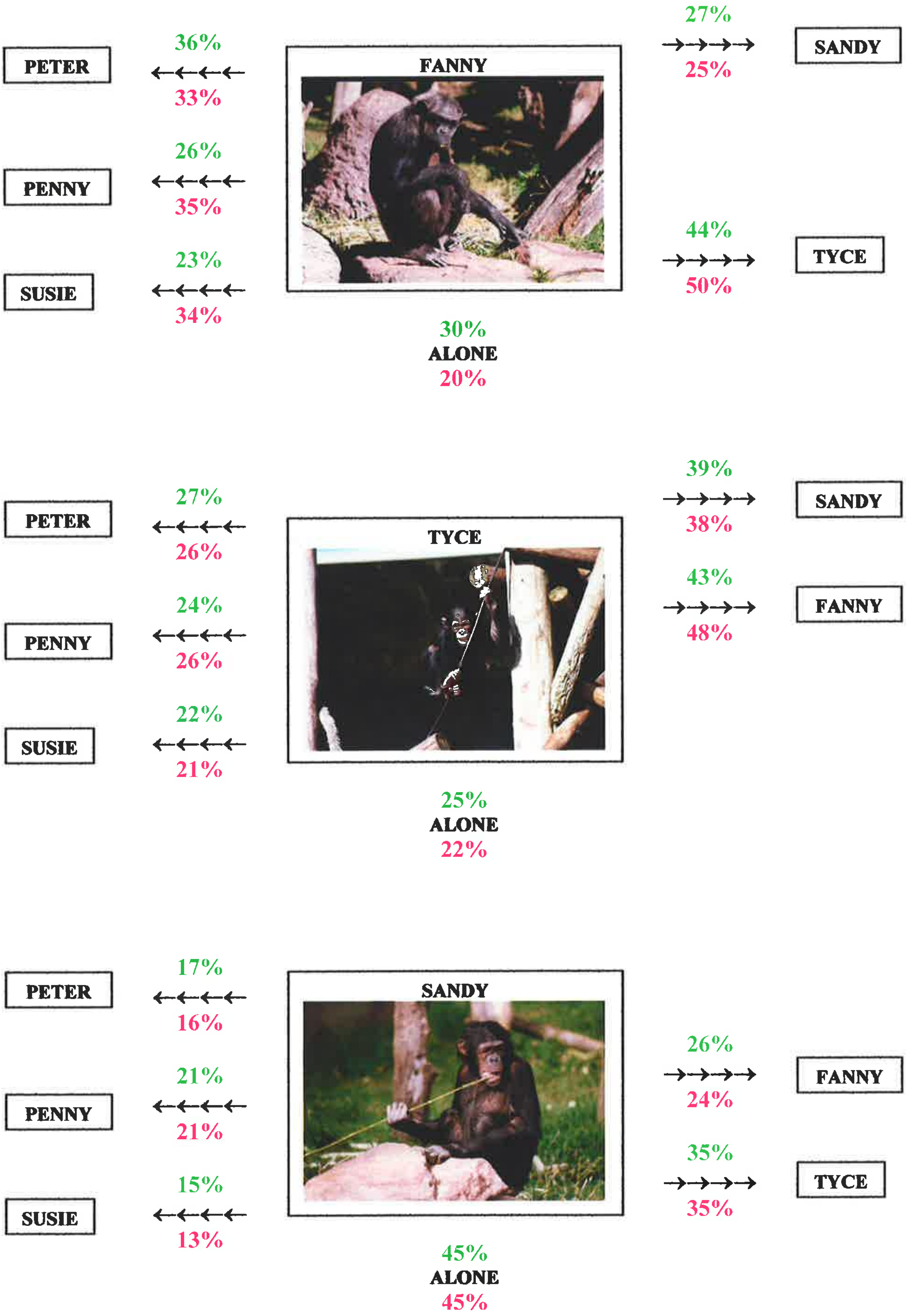


Figure 10.23a. The percentage of total sample points spent alone or with each individual during Week 1 baseline (green, above arrows) and Week 8 baseline (pink, below arrows).

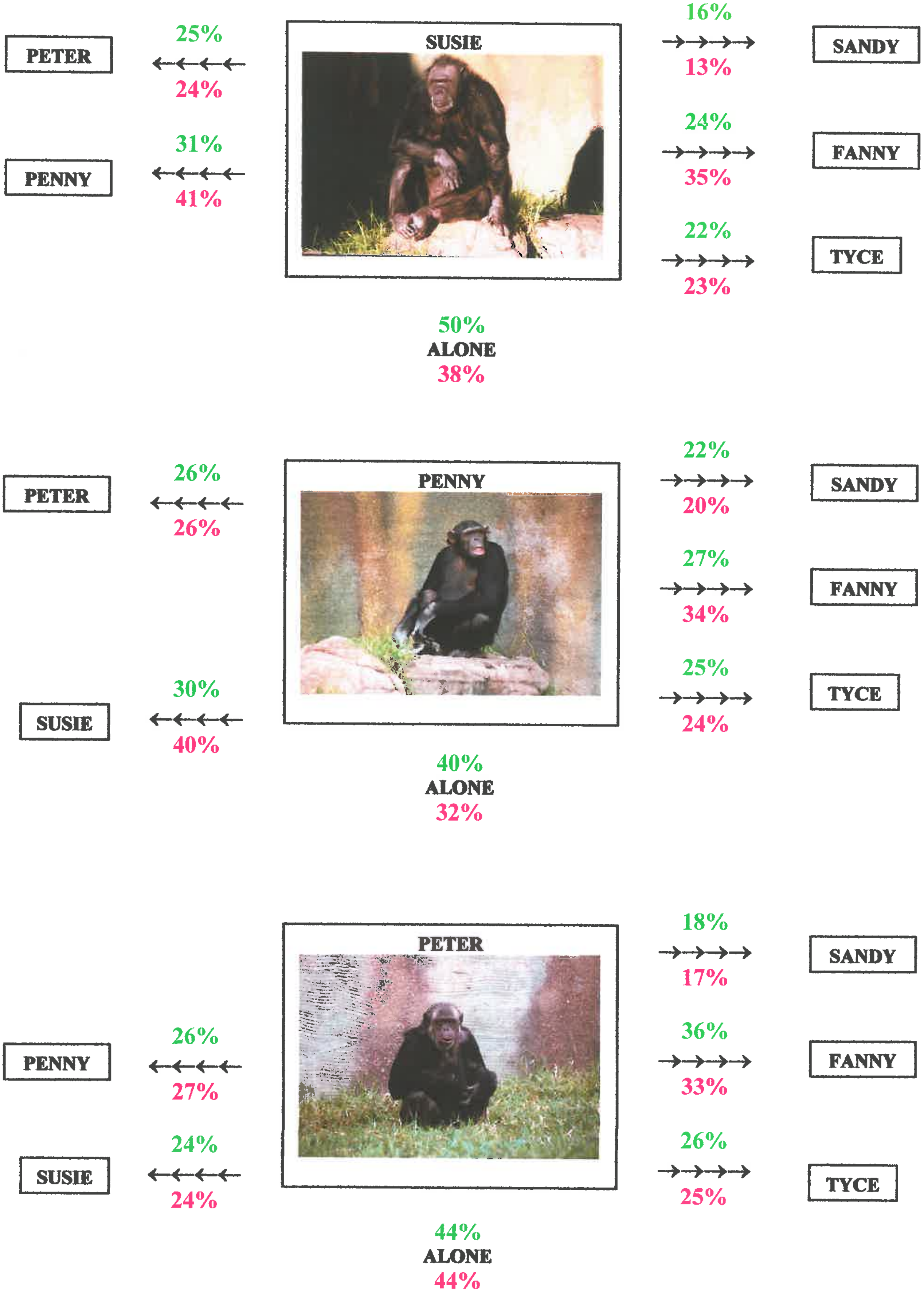


Figure 10.23b. The percentage of total sample points spent alone or with each individual during Week 1 baseline (green, above arrows) and Week 8 baseline (pink, below arrows).

mother, since time spent with the infant had decreased marginally. ***Penny*** spent the least amount of time with ***Sandy*** (< 22%).

There was little change in the time ***Peter*** spent with each individual, after exposure to novel objects. During both weeks he spent about a quarter of the total time with ***Penny***, ***Tyce*** and ***Susie***. He spent the least time with ***Sandy*** (< 20%), and the most time with ***Fanny*** (> 30%).

10.3.5 SUMMARY AND CONCLUSIONS

It is somewhat difficult to interpret the "sociability" information. For most of the members of the group, exposure to objects resulted in less time spent alone, and little change or increased amounts of time spent with others in the group. On the one hand, less time spent alone may suggest that exposure to objects resulted in increased "sociability". However, the change to routine, and exposure to different stimuli, may have resulted in individuals seeking "comfort" from each other- ***Tyce*** spent more time with his mother, ***Penny*** spent more time with her adoptive mother and ***Fanny***, and ***Susie*** spent more time with the only other adult female.

Other extraneous variables (*e.g.*, estrous cycles, seasonality, developmental factors) may have affected the "sociability" results. For example, as Penny got older, she would be expected to spend more time with adult females. Relationships among free-ranging chimpanzees change constantly, but there are noticeable sex differences, with adult males interacting with far more individuals, particularly other adult males (Goodall, 1986).

Thus, based on the "sociability" results alone, it is not possible to determine whether presentation of novel stimulus objects had a beneficial or deleterious effect. It is, however, possible to conclude that the presentation of objects appeared to have little effect on time spent alone or proportion of time spent with each individual, for ***Peter*** (only adult male) and ***Sandy*** (youngest weaned member of the group). This, in conjunction with the findings that presentation of novel objects reduced aberrant behaviours, whilst simultaneously increasing foraging, play and exploration, suggests that these objects indeed had a beneficial effect upon the members of this chimpanzee group.

Finally, extensive use was made of the tall poles and platforms providing areas from which the chimpanzees could observe their surroundings, and even look into adjacent enclosures (Figure 10.22). All members of the group also used the artificial termite mound extensively (Figures 10.12 & 10.22).

10.4 INTRODUCTION TO PRELIMINARY STUDY 5: CARACALS

As discussed at some length in Chapter 5, most of the enrichment techniques for small or medium-sized carnivores are designed to increase foraging activities. A number of studies have attempted to provide "artificial" hunting opportunities, in order to increase physical and mental stimulation (Lindburg, 1998). For example, African hunting dogs have "hunted" meat suspended from artificial metal zebras moving along a track (Gewalt, 1992), servals have been rewarded for leaping and hitting teflon rod "birdies" (Mellen et al, 1981) or pouncing on artificial rodents moving through a tube (Markowitz & LaForse, 1987), tigers have "hunted" plastic rabbits and squirrels along the ground (Markowitz & LaForse, 1987), and cheetahs have sprinted after non-edible ground lures (Lindburg, 1998). Although many of the "artificial" hunting techniques end with presentation or "capture" of a food reward, servals (& other cats) are known to stalk and jump at ropes or objects suspended above them (Mellen et al, 1981). This study examined responses to objects- both food-related and non-food-related. It also investigated changes in other behaviours as a result of presentation of novel stimuli.

10.5 METHOD FOR PRELIMINARY STUDY 5

10.5.1 SUBJECTS

A pair of adult caracals (*Felis caracal schmitzi*), housed together in an outdoor enclosure at Adelaide Zoo, served as subjects (Figure 10.30). Both caracals had been at Adelaide Zoo since 31st August 1990. The male was three-years of age at the start of this study, and the female was four-years old.

The male, ***Boozie*** (ID tag = CHIP 7F7F411077, transponder ID = 7F7F411077, Tel-Aviv ID = 890063), was born in the wild at Ein Gedi on 1st June 1989. He was captured at eight-weeks of age, taken to the "Petting Zoo" at Abu Cabir on 1st August 1989, and subsequently hand-reared. The Specimen Report (Adelaide Zoo) states that ***Boozie*** was traded from Abu Cabir to The Zoological Garden Society of Tel-Aviv on 1st August 1989 (this date corresponds to the date he arrived at Abu Cabir, making it unclear how long he actually spent at the Petting Zoo there). One year later, ***Boozie*** arrived at Adelaide Zoo as part of a direct exchange. He remained in quarantine from the 31st August 1990 until the 3rd October 1990 (ISIS/ARKS Specimen Report for Adelaide Zoo, 15th September 1992).

The female, ***Zili*** (tag ID = CHIP 241B8C, transponder ID = 7F7F410AOF, Tel-Aviv ID = 880060), was captive born at The Zoological Garden Society of Tel-Aviv on 12th August 1988. Her dam (Tel-Aviv ID = 830061) was also captive born, at Haifa Zoo of wild-caught parents (geographic origin unknown). ***Zili's*** sire (Tel-Aviv ID = 830060) was wild-born at Beer Sheeva and later kept at Haifa Zoo. Along with ***Boozie***, ***Zili*** arrived at Adelaide Zoo as part of the same direct exchange (31st August 1990). Her weight on 7th September 1990 was reported to be 8.0Kg. ***Zili*** was transferred to an enclosure off exhibit, when staff suspected she was pregnant on 2nd January 1991. Her mating with ***Boozie*** had indeed been successful, and on 27th February 1991 ***Zili*** gave birth to two kittens/cubs. Three days earlier, she had already been reported as spending all day in the "cubbing" box. One month later, ***Zili*** and the kittens/cubs were moved back into the outdoor exhibit (28th March 1991). Seven months after giving birth to these cubs, ***Zili*** was given an MPA contraception injection (24th October 1991), which was followed by another four months later (13th February 1992). ***Boozie*** was reintroduced to ***Zili*** on 22nd February 1992. Five months later (24th July 1992) ***Zili*** was anaesthetised and checked for pregnancy. She was not pregnant, but after this check-up was separated from ***Boozie*** and put on a diet. Her weight at this time was 12.9Kg.

Both ***Zili*** and ***Boozie*** were housed in the caracal outdoor exhibit at Adelaide Zoo throughout the study. However, as a result of an injury sustained by ***Boozie*** prior to the commencement of the study, he was removed from the enclosure on two separate occasions, during which time he was anaesthetised and his wound cleansed and dressed. The experiment was delayed for a number of weeks, to allow ***Boozie***'s puncture wound under his right front paw to heal. It became apparent, that it would take an indeterminate amount of time for ***Boozie***'s wound to heal, and the study could not be delayed indefinitely. The inclement weather resulted in wet and soggy bandages that further aggravated the wound. ***Boozie***'s front right leg remained bandaged for the first four weeks of the experiment, which hindered some activities during this period (*e.g.*, climbing trees or other parts of the enclosure).

Water was always freely available to the caracals. The feeding schedule remained unchanged for all phases of the experiment except the ten days involving the food objects (or alternative ways of presenting food). The usual feeding routine involved the keeper entering the caracal enclosure and presenting the animals with either horsemeat, half a chicken each, an adult rat each, or day old chicks, or occasionally a guinea pig or pigeon. The caracals either took the food from the keeper's hands or retrieved the food from wherever the keeper distributed it. It should be noted that Adelaide Zoo does not provide live prey. The caracals were fed once daily, in the afternoon (between 1p.m. & 4p.m.), except on Fridays, which was their "starve day".

10.5.2 APPARATUS

10.5.2.1 EXPERIMENTAL APPARATUS

FOOD-RELATED OBJECTS

- **"Flying fox":** This aerial apparatus consisted of a galvanised steel cable (2mm diameter), which was stretched 8-meters across the enclosure and fixed at a height of approximately 1.8 meters. A metal bracket was fitted to the inside of the wire mesh at one end of the cable. Connected to this was a small 12-volt D.C. motor, which was connected up to two (30mm diameter) rubber pinch rollers (with a small 2mm deep groove machined into them for the pull cord to run in). Also on the bracket were two brass guides, a 55mm diameter free running plastic pulley and an "eyebolt" guide. The 2mm steel cable was fixed 50mm above the pulley and pinch roller assembly. Opposite this main drive bracket (on the other fence), another free running 55mm diameter pulley was situated 50mm below the other end of the steel cable.

  The motor was run at 130 revolutions per minute. It drove a continuous loop of cord (2.5mm diameter) around the two pulleys. At the join of this loop, a piece of marine plywood (200mm x 100mm x 10mm thick) was attached. Two "eyebolts" (5mm diameter) were screwed to it. They extended up 55mm to allow the steel cable to run through the eyes, which supported, with considerable strength, the platform of marine plywood which could now be driven back and forth across the enclosure at a maximum speed of 8·6 Kilometers per hour.

  In the centre of the plywood, a piece of six-stranded electrical wire was securely attached. This hung down 500mm, and the meat was tied onto it. When it travelled to the fence line, it could be hooked out through the mesh and loaded up. The apparatus was activated from a switch on a 3-meter long control cable. When the caracals jumped and caught the meat, the motor was stopped. The steel cable supported the weight of the animals, so that the equipment wasn't dragged down too far. Figure 10.24 shows the ***flying fox*** in use.

Figure 10.24. Boozie leaping up at meat travelling above him on the “flying fox”

Figure 10.25a. Zili inspecting the "foraging box"

Figure 10.25b. Boozie inserting a paw into the "foraging box"

- **“Foraging box”:** The foraging box (235mm x 190mm x 165mm high) was constructed from 4·5mm thick gray Polyvinyl Chloride Plastic (P.V.C.), with a lockable hinged lid giving access to the inside. One of the end panels, which could be slid in and out when the lid was opened, was a piece of 6mm thick clear Perspex. A 110mm diameter hole was cut in the center of the front and back panels of the box. The complete box was then fastened to a piece of Plywood (900 x 300 x 18mm thick), which was pegged to the ground of the enclosure. During the study, the holes in the front and back panels were reduced in size to 65mm diameter, so that the caracals could not get their heads into the hole. Figures 10.25a and Figure 10.25b show the ***foraging box*** installed in the enclosure.

- **“Mouse tube”:** This piece of apparatus was a 7-meter long piece of flexible opaque tube (outside diameter of 60mm & inside diameter of 50mm). On the inside of one end, a 25mm diameter fee running pulley was fitted, so that when the tube was in the enclosure, the pulley was in a horizontal position. It was also on a sliding fitting, so that the cord’s tension could be adjusted. At the other end, a 12-volt D.C. motor (running at 40 revolutions per minute) was mounted in a waterproof box and bracket assembly. This in turn was coupled up to a 42mm diameter pulley. A continuous loop of cord (2mm diameter) was stretched inside the tube between the two pulleys. On one strand of the cord a black rubber toy mouse was fastened, so that when the motor was operated the mouse moved up and down along the inside of the tube. The motor was activated via a 3-meter long control wire and a 12-volt car battery was used as the power source. Figure 10.26a shows the toy mouse, which was visible through the clear ***mouse-tube***. The seven-meter long ***mouse-tube***, installed in the caracal enclosure, is shown in Figure 10.26b.

A feeder was attached to the eastern wall of the caracal enclosure. This stainless steel apparatus was 660mm in length (120mm deep), and consisted of 37 stainless steel plates (30mm deep with a 10mm lip), which were placed 25mm apart. These plates were riveted to a plastic fabric belt, which was driven by a 12-volt motor (8 R.P.M.). That is, small pieces of meat (reinforcements) were loaded onto the individual plates (one piece per plate), and could be delivered from the bottom of the feeder onto a large flat stone (Figure 10.44). The conveyor-belt style apparatus, was controlled by a manually operated the button, which also sounded a buzzer every time a reinforcement was delivered. The feeder was attached to a 1-inch mild steel tube, which was bolted to the sidewall mesh of the enclosure (Figure 10.44).

NON-FOOD-RELATED OBJECTS

- **"Bird":** A ***bird*** about the size of a pigeon (in flight) was carved from a piece of Radiata Pine with the 400mm wings being attached separately. The completed carving had a large number of feathers glued onto it and the eyes and beak were also marked. An "eyebolt" was fixed through the body of the ***bird*** which was then suspended form the roof of the enclosure by an adjustable length piece of cord/rope which allowed varying heights from the ground to be obtained. At the end of each operational session the ***bird*** was hoisted to the top of the roof and secured under a metal shelter in case of rain and this also helped to camouflage the ***bird*** until the next session. Figure 10.27a provides a close-up view of the ***bird***, and Figure 10.27b shows the placement of the ***bird*** in relation to the other non-food-related objects.

- **"Cane balls":** The diameter of each ball was 130mm and weighed 110grams. The three balls were purchased from Community Aid Abroad in Adelaide, and made from strands of 4mm wide cane, which were woven together in a criss-cross fashion. These balls were very robust, with no loose ends protruding, and were a natural light brown in colour. Pieces of catnip plant were threaded into the cane holes/mesh. Figure 10.28 shows ***Zili*** chewing one of the ***cane balls***.

- **"Hanging log":** A small log measuring 160mm in diameter and with a length of 250mm was suspended in the enclosure. A swivel bracket allowed the log to rotate when it was manipulated. A second log attached to the rope served as an anchor. Figure 10.28 shows this object installed in the enclosure.

10.5.2.2 OBSERVATIONAL EQUIPMENT

Notable behaviours were recorded onto VHS videotapes, using a Panasonic M7 video camera (model NV-M7A), which also provided an onscreen record of the date and time of recording. The video camera was mounted on a tripod when the caracals were at rest (or moving around very little), whereas the camera was hand-held if the cats were moving around a lot (enabling them to remain in sight, instead of continually becoming obscured behind the trees or other features). The camera was in view of the caracals at all times, being situated at the front of the enclosure, in the public viewing area. It should be noted, that the caracals were not always in view to zoo visitors, but the area set aside for the observer, consisted of a narrow strip, that encompassed three of the four enclosure fences, allowing the animals to remain in view for most of the time.

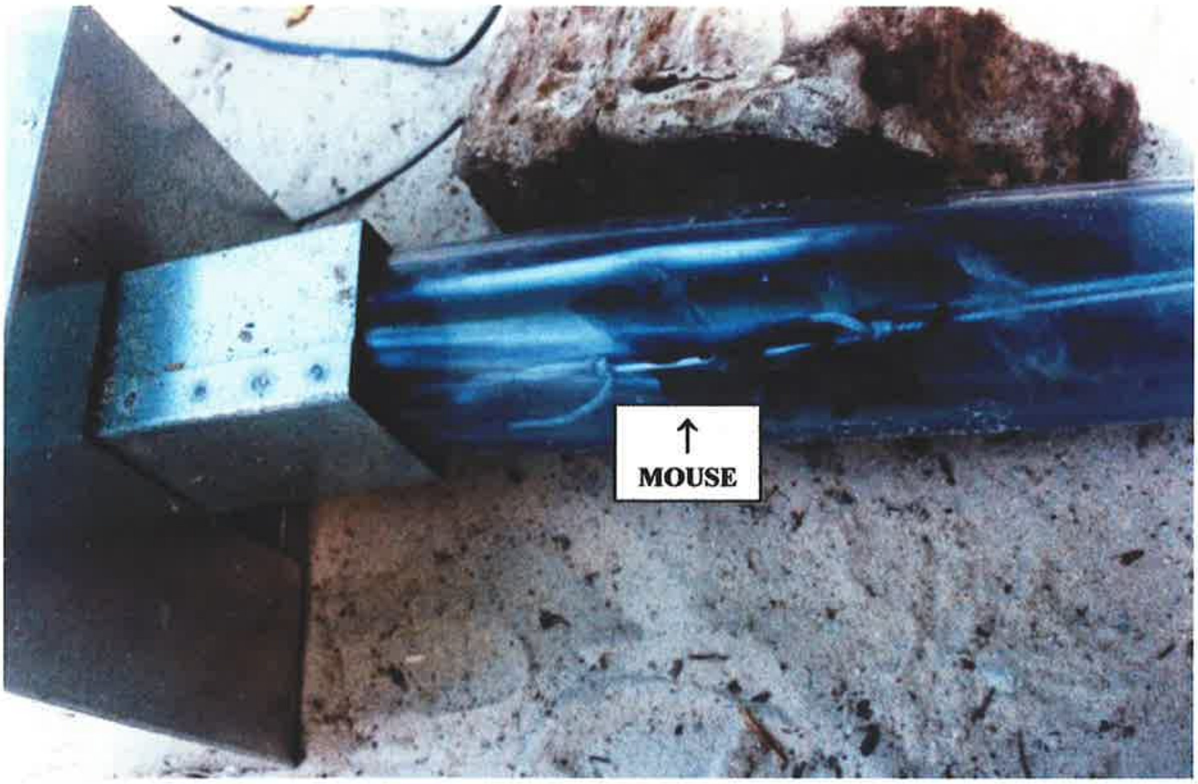


Figure 10.26a. The toy mouse was visible through the flexible "mouse tube".

Figure 10.26b. The seven-meter long "mouse tube".

Figure 10.27a. The "bird" object resembled a pigeon in flight

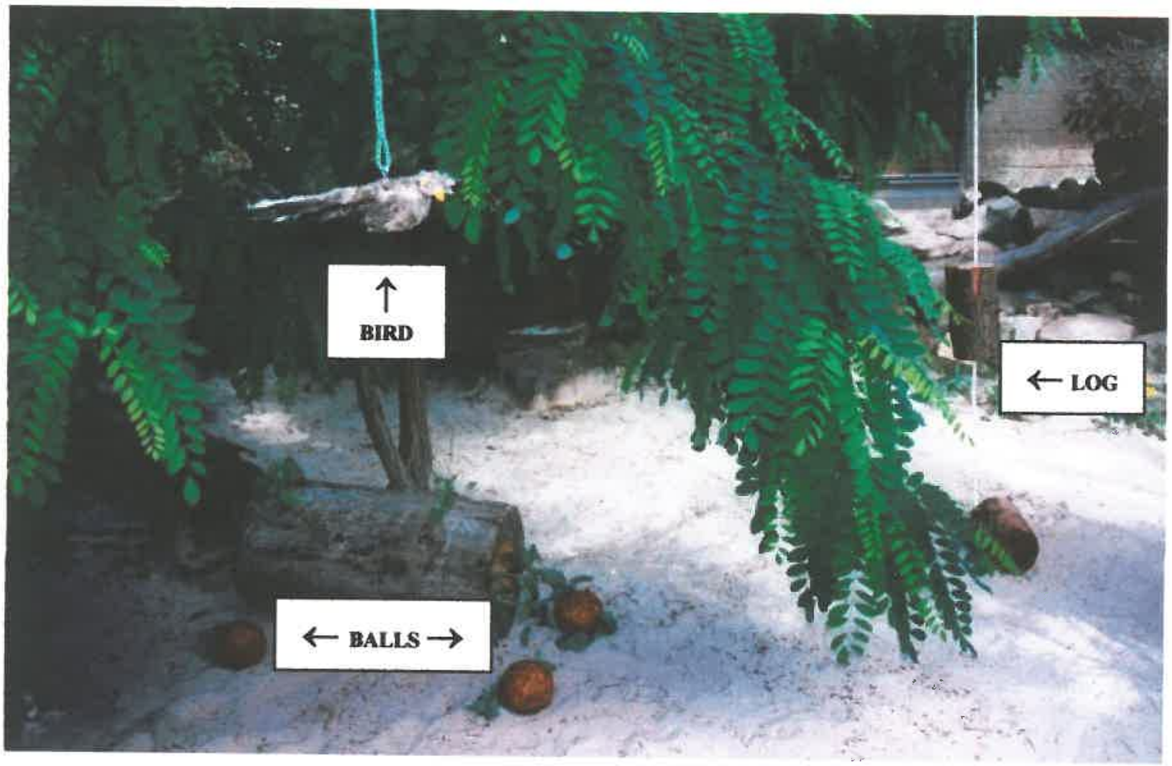


Figure 10.27b. The "bird", cane balls and "hanging log" inside the caracal enclosure

Figure 10.28. Zili chewing one of the "cane balls"

Figure 10.29. The "hanging log"

ZILI

BOOZIE

Figure 10.30. Zili (right) is heavier in build and lighter in colour than Boozie

10.5.3 PROCEDURE

The study was divided into five phases, including three baseline phases and two phases involving the introduction of novel objects. General observations were made over eight weeks, with six observation sessions of one hour's duration taking place every day (i.e., 6 hours per day, for 56 consecutive days). The first baseline was run for three weeks, in order for the caracals to become accustomed to the presence of the observer, and then the non-food-related objects were introduced into the enclosure. Whilst the objects were being fixed into position, ***Zili*** remained at the top of a tree, into which she had retreated prior to the entry of the maintenance staff. ***Boozie*** was locked in the holding enclosure at the back, and then allowed back in once the objects were in place. This phase was run for one week, with the objects remaining in the enclosure at all times.

The non-food-related objects were removed at the end of the fourth week, and general "baseline" observations were made for a week. The fourth phase involved the introduction of the second set of novel stimuli (food-related objects). ***Zili*** had again retreated to the top of a tree, and remained there as the objects were fixed into place. ***Boozie*** also remained in the enclosure, but out of sight. This phase was run for ten days, in order to try a variety of foods and presentation options (to be discussed further subsequently). The final phase was the third baseline, which took place after the food-related objects were removed (for 11 days).

Table 10.3
The experimental design of preliminary Study 5.

Week	Dates	Phase of Study	Object Condition
1 - 3	Mon. 26th Oct 1992 to Sun. 15th Nov 1992	General observations (Baseline 1)	No Objects
4	Mon. 16th Nov 1992 to Sun. 22nd Nov 1992	Presentation of Novel Stimuli	Non-food-related Objects
5	Mon. 23rd Nov 1992 to Sun. 29th Nov 1992	General observations (Baseline 2)	No Objects
6 - 7	Mon. 30th Nov 1992 to Wed. 9th Dec 1992	Presentation of Novel Stimuli	Food-related Objects (in for 10 days)
7 - 8	Thurs. 10th Dec 1992 to Sun. 20th Dec 1992	General observations (Baseline 3)	No Objects

No changes were made to the usual zoo routine. The caracals remained in the outdoor enclosure at all times, even while the enclosure was being cleaned (once daily), although ***Boozie*** sometimes entered the off-limits enclosure located at the back, when the keepers entered to clean the enclosure. The caracals were fed once daily, with keepers scattering the food items (*e.g.*, dead day-old chicks, rats, guinea pigs, hens) around the enclosure, once it had been cleaned. The caracals were not fed on the two "digestive" days per week (an attempt to emulate the "wild" conditions, where not every hunt is successful). There was limited physical interaction between the caracals and their keepers (*i.e.*, the caracals sometimes took food from the keepers' hands).

When the food-objects were in the enclosure, the keepers filled the ***foraging box*** with pieces of meat. An attempt was made to ensure that the caracals received about the same amount of food as they usually received during baseline days. The ***flying-fox*** was only run after the zoo was closed (*i.e.*, after 5.00 p.m.). Pieces of meat, dead day-old chicks and guinea pigs (used only once) were loosely tied to the ***flying-fox*** from outside the enclosure (see Figure 10.37).

Table 10.4
Observation times, feeding times and feeding location for preliminary Study 5.

Observation Times	**Feeding times**	**Feeding Location**	**Zoo Visitors present?**
7.30 a.m. – 8.30 a.m.			No
10.00a.m. – 11.00a.m.			Yes
12.00 p.m. – 1.00 p.m.			Yes
1.30 p.m. – 2.30 p.m.	between 1.00 p.m. & 4.00 p.m.	Near the back gate	Yes
3.00 p.m. – 4.00 p.m.			Yes
4.30 p.m. – 5.30 p.m.			No – after 5.00 p.m.

10.6 PRELIMINARY FINDINGS AND DISCUSSION FOR STUDY 5

10.6.1 GENERAL BEHAVIOURAL OBSERVATIONS (BASELINES)

As with the previous study, this section focuses on a description of aberrant behaviours. Again, however, this should not imply that the caracals did not engage in a wide variety of "normal" or interesting behaviours. Apart from the occasional hiss and ear-flicks, and swipe with the front paws, there was little sign of ***aggression*** throughout the eight-week study, with one notable exception. During Week 3 (Day 4), ***Boozie*** was removed from the enclosure, sedated and had his foot cleaned and bandaged. When he was returned to the enclosure, ***Zili*** was very ***aggressive*** towards him, and they spent most of the last observation session fighting. By the next day, everything had returned to "normal".

Both cats demonstrated typical felid behaviours related to the ***processing*** phase of food acquisition- preparation and ingestion (Lindburg, 1998). They were observed to ***prey play*** with day-old chicks, throwing them up into the air with their mouths, and then batting them around with their paws (Leyhausen, 1979). ***Zili*** and ***Boozie*** plucked feathers from birds and fur from rats or guinea pigs with their teeth, shook prey items around with the mouth, and then ate the food (Leyhausen, 1979).

A number of copulations were observed during two separate periods (Weeks 1 & 2; Weeks 4 & 5). Although some of the copulations took place towards the rear of the enclosure, in areas partially screened from the public viewing areas, just as many took place in full view of the observer. Copulations were recorded on seven different days during the first oestrous period (Days 2,3 & 4 of Week 1; Days 2, 3, 6 & 7 of Week 2), and on three days during the second oestrous period (Day 7 of Week 4; Days 2 & 5 of Week 5).

Free-ranging, radio-collared caracals in Israel, have been observed to mate over a period of five to six days, with females mating with a number of males, with no sign of inter-male ***aggression***, since: "other males stay nearby, awaiting their turn" (Weisbein & Mendelssohn, 1990, p.21). Weisbein and Mendelssohn (1990) found, that one female caracal mated with the same three males, in the same order, during every estrous. These and other males (N=9) were observed to copulate at 42 - 48 hour intervals. Seasonal factors do not appear to influence the reproductive behaviour of free-ranging caracals, since they reproduce throughout the year, with one to three cubs born after a gestation period of about 78 days (Weisbein & Mendelssohn, 1990).

It is not possible to determine whether all the mounts observed occurred with intromission, and many mounts without intromission have been reported in studies of feral domestic cats (Kerby & Macdonald, 1988; Natoli & De Vito, 1988). However, one mount with intromission, accompanied with a copulation cry from ***Zili*** was observed on the last day of mating (27th November). ***Zili*** gave birth to one female offspring (ID = 930064) on the 14th of February, which was 79 days after the last observed mating. Therefore, ***Zili*** was pregnant during the last two weeks of the study.

Boozie and ***Zili*** were observed to ***flick their ears*** at each other on a number of occasions. Ewer (1973) suggests, that these ear movements may serve a social function, having observed: "a pair of these animals exchanging ear twitches - a movement by one evoking an answering twitch by the other" (p.75). He further maintains, that the distinctive caracal ears may serve as a visual means of maintaining social contact. Long-eared species (*e.g.,* servals & caracals) live in warmer climates, where large ears aid in temperature regulation by increasing the animal's heat-radiating surface. Enlarged pinnae may also relate to prey capture involving acute hearing, which is highly directed in nature. Long ears may also reflect "relatively peaceful social relations", since these ears would otherwise "end up in tatters before long" in a species characterised by frequent intra-specific fighting (Ewer, 1973, p.102).

Caracals tend to "greet" other individuals (caracals or human observers) by ***head flagging***: "turning its head from side to side and flickering the ears" (Kingdon, 1977, p.331). He suggests, that this movement provides the most striking view of the caracal's black and white contrasting markings. These head movements appear frequent, highly ritualised, and are accompanied by emphatic and rapid ear movements. Following this behavioural display, which according to Kingdon (1977) may provide information regarding "status" and individual "intentions", the caracals may go their separate ways. ***Head flagging*** was observed on a number of occasions, but it was not clear whether there was a distinction between ***head flagging*** and ***ear flicking*** (without apparent head movements).

10.6.1.1 UNUSUAL BEHAVIOURS

DRAGGING THE FEMALE AROUND BY THE NECK

Although most of the copulations and behaviour prior to and after each copulation were as expected, one aspect appeared unusual. While mounted, ***Boozie*** always held onto the back of ***Zili's*** neck, engaging in the ***nape bite*** seen in many species of felid (Leyhausen, 1979). Typically, males release their hold on the female's nape at the end of copulation. However, during the middle of the first mating period (Day 2 of Week 2), ***Boozie*** began to drag ***Zili*** around the enclosure by the back of the neck. This was quite a feat, since ***Zili*** was larger than him. He walked slowly, dragging ***Zili*** as if she were a particularly large prey item. This behaviour was observed repeatedly during Week 2, and by the end of this week a noticeable section of fur was missing from the back of ***Zili's*** neck (Figure 10.33).

10.6.1.2 ABERRANT BEHAVIOURS

STEREOTYPIC PACING

Bouts of ***stereotypic pacing*** were observed in both caracals, but most often in ***Boozie***. Most of the ***pacing*** took place at a walk, although ***pacing*** at a trot was also observed. Typically, both cats paced in a figure-8 pattern, and in specific areas of the enclosure. ***Boozie*** paced in front of the back door, which is where the keepers entered the enclosure, and both caracals paced along the side fence lines (providing a view of keeper movements along the pathway between the caracal/small carnivore row of enclosures & the big cat row of enclosures), but rarely along the front of the enclosure, where most zoo visitors congregated to observe them. Occasionally the two cats engaged in ***synchronous pacing***. That is, they paced in synchrony with each other: similar speed, pattern and location. ***Pacing*** appeared to peak in the afternoon, typically before presentation of food, and continued if food was not presented (*i.e.*, a "digestive" day). Thus, as Carlstead (1998) suggests, ***pacing*** appeared to be a food-anticipatory stereotypy (similar to schedule-induced terminal activities).

10.6.2 BEHAVIOURS WHEN NON-FOOD-RELATED OBJECTS WERE PRESENT

This section presents a descriptive analysis of some of the behaviours directed at the non-food-related novel stimulus objects, and changes in other behaviours observed prior to the presentation of objects. These three objects were designed purely for play and manipulation. ***Boozie*** largely ignored all three objects, whereas ***Zili*** interacted with the ***bird*** object throughout the week.

10.6.2.1 OBJECT-DIRECTED BEHAVIOURS

BIRD

From the first introduction of the "bird" object, ***Zili*** behaved towards it as if it were a real bird. She engaged in ***teeth chattering***, whenever she looked up at the bird. That is, ***Zili*** made a "chattering" or "smacking" noise, whilst the corners of her mouth were "pulled well back", and her jaws struck "together in spasmodic rhythm" (Leyhausen, 1979, p.38). Throughout the study

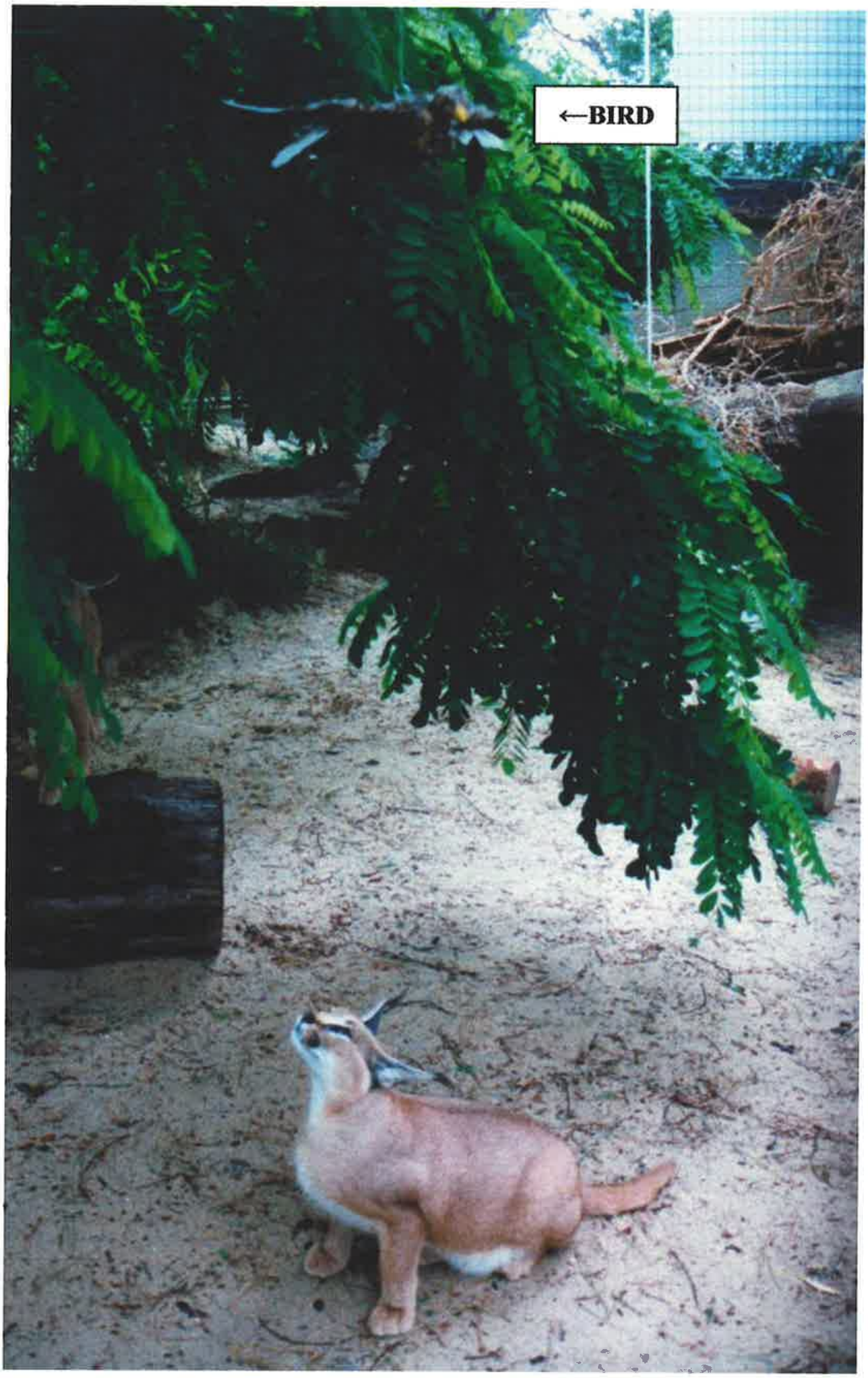


Figure 10.31. Before jumping up at the "bird", Zili typically sat directly underneath it, growling and flicking her ears back-&-forth

Figure 10.32. Zili typically jumped up at the "bird", hooked her claws into it, and then hung onto it (even if it spun around on the cord) while she chewed it

Figure 10.33. Zili was not always successful in "catching" the "bird" (top), but whether she missed or not, the leaps were always spectacular

Zili chattered at birds, and occasionally leapt up at them as they settled in or flew through the enclosure. On one occasion she successfully captured a bird in mid flight, killed it, plucked it, and ate it (Week 2, Day 6). Whenever the ***bird*** object was lowered down from the roof of the enclosure (for observation sessions), ***Zili*** typically sat directly underneath the object, chattered her teeth at it, and then leapt up. Many of the leaps resulted in her "catching" the bird- hanging onto it with both front paws, vigorously chewing it, before letting go and dropping back to the ground (Figures 10.31 – 10.33).

Unlike ***Zili's*** active interactions with the "bird", ***Boozie*** did not leap up at it. It is possible that his foot injury prevented him from engaging in any such vigorous activity, but he did not engage in ***teeth chattering*** or display any other particular interest in this object.

CANE BALLS

Zili sniffed, chewed and batted the cane balls on several occasions on the first day of exposure (Figure 10.28). ***Boozie***, on the other hand, did not interact with these objects during any observation sessions. Every morning, the balls were located in a different position from the last observation session (previous day), suggesting that they had been played with sometime during the evening/night/early morning (outside observation sessions).

HANGING LOGS

Although both caracals sniffed the logs during the week, the logs were never used as a "scratching post", or for any other purpose during the observation sessions. That is, this object was virtually ignored.

10.6.2.2 OTHER BEHAVIOURS

The presence of objects appeared to have little effect on ***Boozie***. It should be noted, his front foot was still bandaged during this week, which may have hindered his activities, particularly the leaping required, in order to interact with the ***bird*** object. ***Zili*** appeared to benefit from the presence of the bird object, engaged in less ***pacing*** during the week. However, she also largely ignored the other objects.

10.6.3 BEHAVIOURS WHEN FOOD-RELATED OBJECTS WERE PRESENT

As with the previous section, this section presents a descriptive analysis of behaviours directed at the novel stimulus objects, and changes in other behaviours observed prior to the presentation of objects. The ***flying fox*** and ***foraging box*** were both used successfully throughout the week, whereas the ***mouse tube*** was virtually ignored by both cats.

10.6.3.1 OBJECT-DIRECTED BEHAVIOURS

FLYING FOX

Every afternoon, just after the zoo closed, the ***flying fox*** was put into use. Small pieces of meat or day-old chicks (*i.e.*, small enough to fit through the wire mesh) were loosely tied to the electrical wire, which was hooked through the wire mesh. The wire and meat were then pushed through the mesh and travelled back-and-forth across the enclosure until a caracal "caught" the meat. Then the wire was hooked back through the mesh and a new piece of meat attached. This continued until all the pieces of meat were gone. After the first few times, the caracals often approached and waited by the mesh while the meat was being attached (Figure 10.37).

Both caracals successfully captured meat from the flying fox every day, although ***Boozie*** made slightly more attempts. No ***aggression*** was observed, and they took turns, each closely watching the other chase and leap at the meat. Sometimes the meat was captured almost as soon as it left the mesh. At other times, it made several trips across the enclosure. On numerous occasions, ***Boozie*** used the tree near the back of the enclosure to springboard up the trunk or to trap the meat against the tree with a leap and hit of the paws (Figure 10.37). The leaps performed by both cats were spectacular (Figures 10.35 – 10.37). Sometimes the caracals leapt and hit at the meat with one paw, and at other times they caught the meat between both paws (Figure 10.35). On one occasion, a dead guinea pig was attached to the wire. However, once captured it did not fall off, and ***Zili*** held and pulled at it (Figure 10.34), which resulted in the motor straining. Such a large prey item was not used again. They caracals did not lose interest in this object. They chased and captured every piece of meat, and rapidly approached every time the flying fox was put into use.

Figure 10.34. Zili pulling at a dead guinea pig suspended from the "flying fox", while Boozie watches on

Figure 10.35. Zili and Boozie both successfully "captured" food from the "flying fox"

Figure 10.36. Boozie (bottom left) and Zili took it in turns to use the "flying fox" apparatus

Figure 10.37. Boozie's leaps were particularly spectacular and he often waited at the mesh while the meat was being attached to the "flying fox" (top left)

FORAGING BOX

As soon as the keeper filled the foraging box with pieces of meat (once daily, in the early afternoon), and left the enclosure, both caracals approached the box. Initially, a black rubber flap covered each of the holes in the box, but these were soon removed. Zili and Boozie pulled at the flaps with their teeth until most of the rubber was torn into shreds (Figure 10.38). Again, there was no ***aggression*** between the caracals, although ***Boozie*** hissed at ***Zili*** on a few occasions (Figure 10.43), and was somewhat territorial over this object, using it more frequently.

Zili's foraging responses were strikingly slow and methodical (Figure 10.39). Typically, she inspected the meat through the clear front window or through a side hole, then gently inserted a paw into the hole, hooked or dragged a piece of meat out, and then consumed it. ***Boozie***'s activities around the box, on the other hand, appeared "frenzied" at times, and included vigorous bouts of ***digging*** on three sides of the box (Figures 10.40a & 10.40b). However, he was equally successful at removing meat from the box. Both cats readily inserted their front paws into the box. ***Boozie*** alternated between his paws, which may have indicted that his right paw was still sore (Figure 10.41), whilst ***Zili*** used her right paw. Dexterity and persistence were required to obtain the last few pieces of meat from the ***foraging box***, since they were sometimes located in the corners and difficult to extract (Figure 10.42). Both cats continued to forage from the box until all the meat was gone.

MOUSE TUBE

This object was almost completely ignored by both caracals. Since no sounds or smells were associated with the toy mouse, the movement alone was not enough to hold the cats' attention. Live rodents produce ultrasonic "squeaks" (Kitchener, 1991) within the hearing range of felid predators. Ultrasound can be used effectively to communicate over short distances in dense habitats, as these sounds do not carry far (Kitchener, 1991). The low intensity of rodent high frequency vocalisations coupled with low frequency rustles of movement have contributed to the development large pinnae in their feline predators. The large ears of the serval aid in detection of rodent prey moving through tall grass (Geertsema, 1985), and similarly the long ears of the sand cat aid in detection of rodent prey in its desert habitat, where faint sounds are absorbed by the hot dry air (Kitchener, 1991). It is likely that caracal ears may also serve a similar function.

Zili investigated the moving mouse and briefly followed it along the tube on one occasion. However, the movement alone was not enough to elicit prey chase. In addition, the caracals were not food-deprived, and magazine training was unable to be attempted.

10.6.3.2 OTHER BEHAVIOURS

Numerous ***play chases***, including ambushes and elaborate leaps at each other, without any sign of ***aggression***, were observed during this week. ***Pacing*** appeared to decrease significantly, and remain at a low level throughout the week. The experimenter/observer became associated with the ***flying fox*** object, and this resulted in approaches towards the observer at various times, particularly upon arrival every morning.

10.6.4 SUMMARY AND CONCLUSIONS

Apart from the ***bird*** object, which was used extensively by ***Zili*** (leaping at it, hanging from it, chewing/biting it), the other non-food-related objects were largely ignored, and appeared to be of little benefit. However, it should be noted that ***Boozie***'s bandaged leg might have prevented him from interacting with the ***bird***, at least.

Presentation of novel food-related objects reduced ***stereotypic pacing***, whilst simultaneously increasing foraging, play and exploration, suggesting that these objects had a beneficial effect upon the caracals. Instead of consuming all the food at once, foraging took place at two different times (early and late afternoon), and required two different foraging skills. To remove meat successfully from the ***foraging box*** required quite accurate paw insertion and manipulation, whereas obtaining meat from the ***flying fox*** involved high leaps and hitting (one paw) or grabbing (two paws) responses. Both of these objects were used constantly until all the food had been obtained, and elicited the appropriate responses every day (*i.e.*, no apparent habituation). The ***mouse tube*** failed to attract interest, and if tested again should incorporate sounds and smells.

The ***flying fox*** appeared to be the most useful of all the objects, since it allowed an active artificial prey-chase. It did not result in excessive hunting behaviour, since it was only in use until all the meat was "captured". A later version of the ***flying fox*** (Mills, 1998) is now a permanent feature of the caracal enclosure (Figure 10.45), but its use is restricted to a few weeks of every year (school holidays).

Figure 10.38. Boozie (top & bottom) and Zili (middle) both tore at the rubber covering the holes of the "foraging box" with their teeth until they had removed most of it

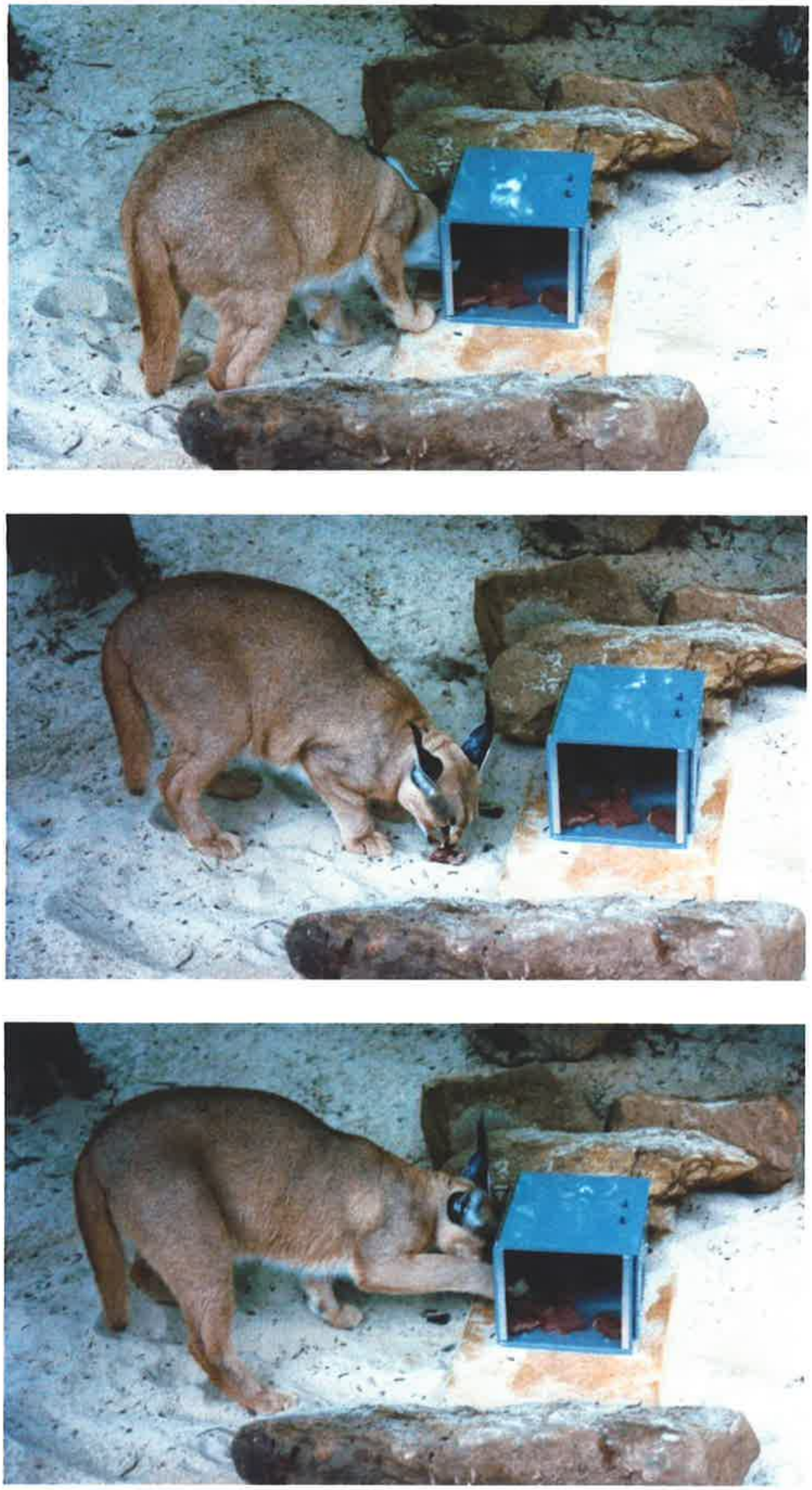


Figure 10.39. Zili slowly and methodically removed meat from the "foraging box" whenever possible

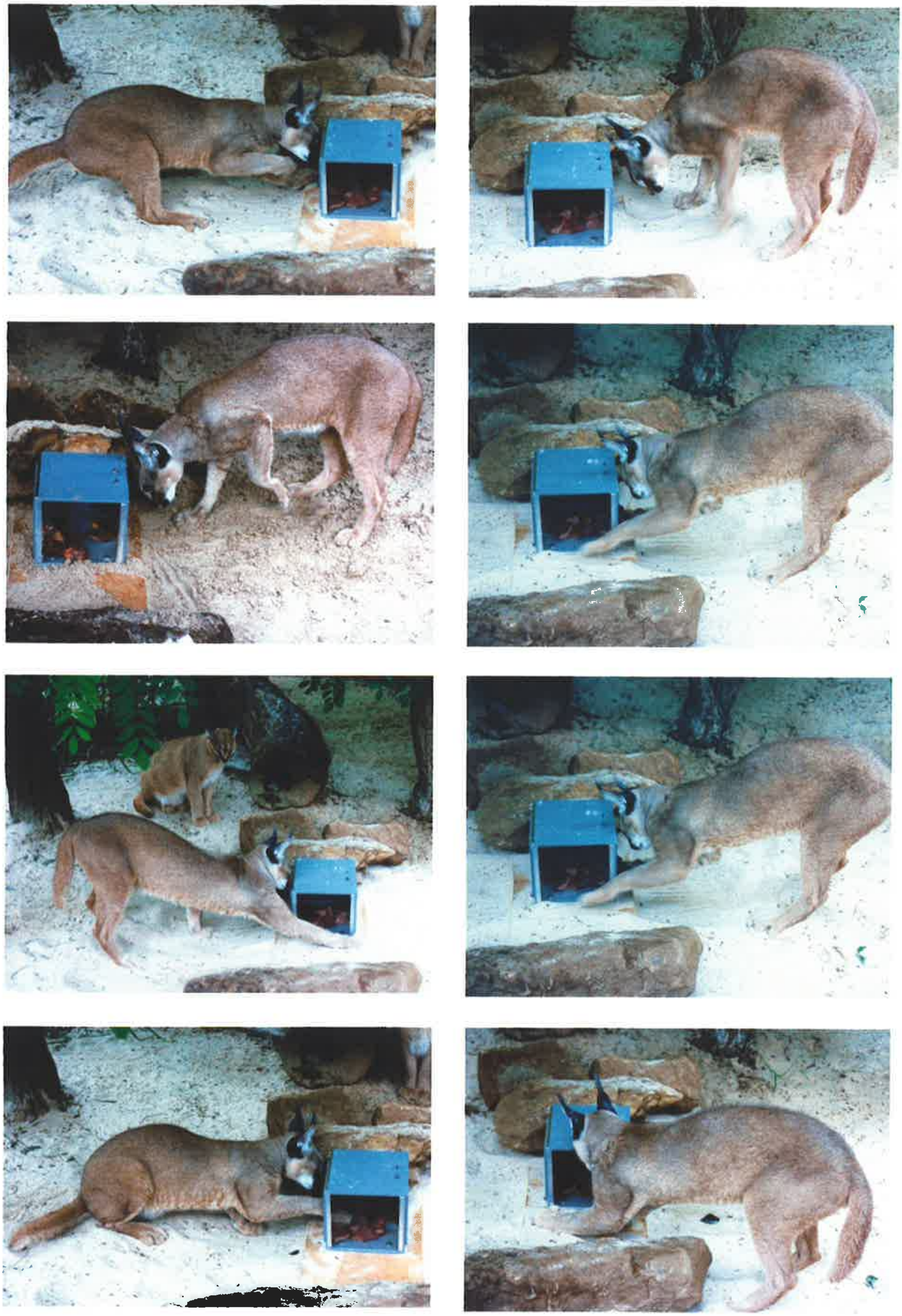


Figure 10.40a. Unlike Zili's unhurried and calm removal of meat from the "foraging box", Boozie's activities around the box appeared "frenzied" at times, and included digging on three sides.

Figure 10.40b. Unlike Zili's unhurried and calm removal of meat from the "foraging box", Boozie's activities around the box appeared "frenzied" at times, and included digging on three sides.

Figure 10.41. Paws were readily inserted into the "foraging box". These photos show Boozie alternating between paws on both sides of the "foraging box".

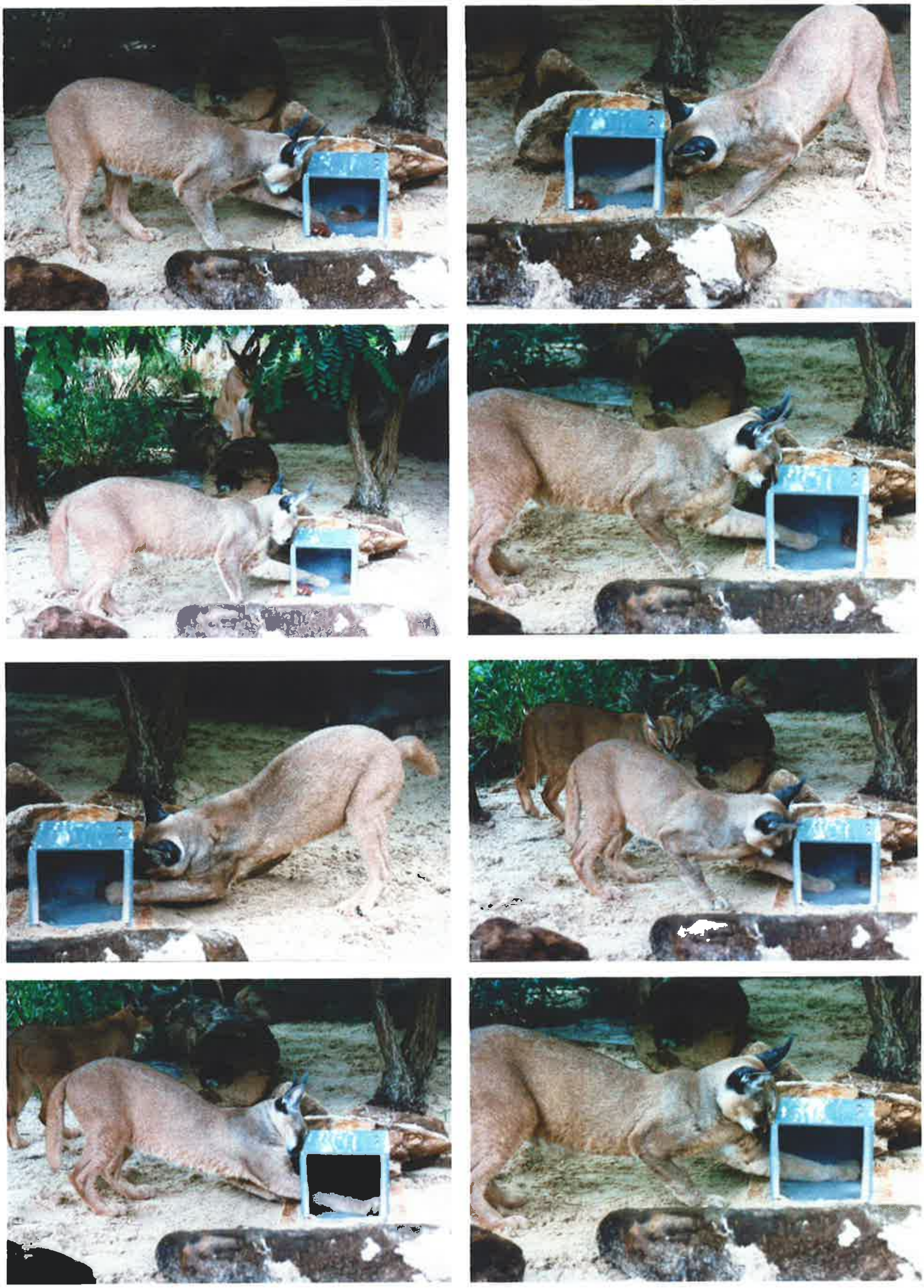


Figure 10.42. Dexterity and some persistence were required in order to obtain the last few pieces of meat from the "foraging box" (all photos are of Boozie)

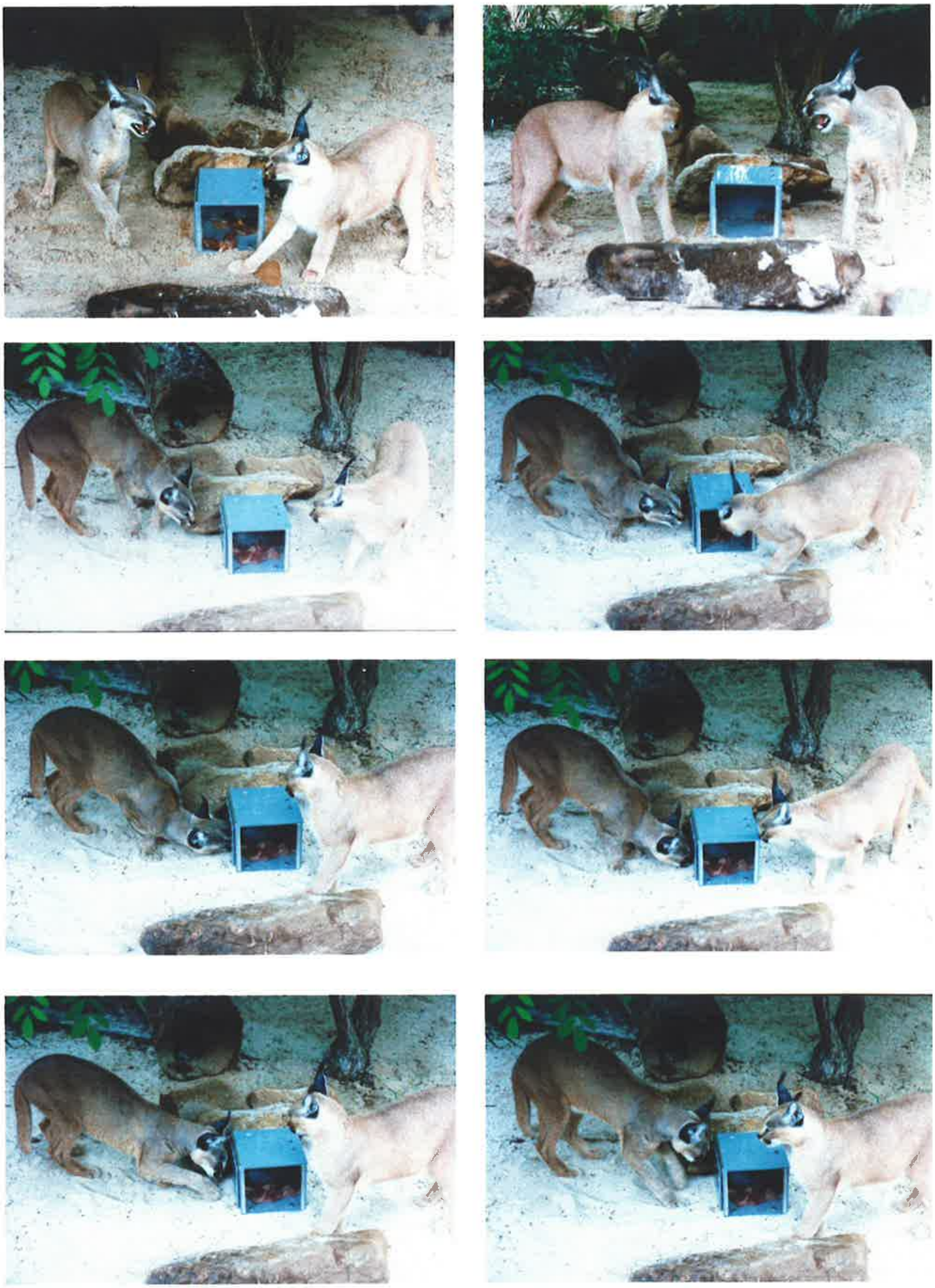


Figure 10.43. Although no fights occurred over any of the objects or feeding devices, Boozie was somewhat territorial over the "foraging box", and hissed at Zili on a few occasions (top).

Figure 10.44. Little interest was shown in the "mouse tube". Zili inspects the stone near the meat feeder/dispenser (top), and then lies down next to it (bottom).

10.7 CONCLUSIONS BASED ON THE FINDINGS OF THE PRELIMINARY STUDIES

> "The animal Psychologist must harbour in his breast not only two souls, but more; he must unite with a thorough training in Physiology, Psychology, and Biology the experience of a Traveller, the practical knowledge of a Director of a Zoological Garden, and the outdoor lore of a Forester, and even then he could not round up his labours satisfactorily unless he were familiar with the trend of modern aesthetics" (Groos, 1898, p.xviii).

Although abnormal or aberrant behaviours are typically associated with captivity and rearing environments that provide inadequate sensory and physical stimulation, not all aberrant behaviours appear to be associated with "reduced psychological well-being in captive chimpanzees" (Nash, Fritz, Alford & Brent, 1999, p.161). For example, ***coprophagy*** and ***self-depilation*** have been found to occur most often in mother-reared chimpanzees. ***Coprophagy*** also appears to be more prevalent in females, and in chimpanzees housed in zoo enclosures rather than laboratories (Nash et al, 1999, p.161). Nash et al (1999) suggest that some aberrant behaviours (*e.g.*, ***coprophagy***) may be culturally transmitted, and therefore chimpanzees housed in a social environment may learn these behaviours. As a result, they cannot be assumed to reflect reduced psychological well-being, particularly since at least one study found an increase in both foraging and ***coprophagy*** as a result of behavioural enrichment (Nash et al, 1999). Chimpanzees occasionally engage in ***coprophagia*** in natural environments, typically picking undigested food remains from the feces with their lips, with only infants handling feces (Goodall, 1986).

Although perhaps not indicative of reduced psychological well-being in captivity, nonetheless, ***coprophagia*** and ***fecal art*** were briefly eliminated in the chimpanzees, and subsequently reduced after presentation of novel food-related stimulus objects in this study. The somewhat disturbing ***insertion of fingers into the rectum*** was similarly briefly eliminated by the introduction of the food-related objects. The caracals exhibited ***stereotypic pacing***, which was also reduced by presentation of food-related objects. For both species, other appropriate activities were elicited: increased foraging, which required manual dexterity and some cognitive skills, increased play and exploratory behaviour, and increased general activity. Thus, the objects based on food provisioning provided opportunities for enrichment for these two very different species.

As Lindburg (1998) points out, it may be futile to attempt to elicit play from adult animals. However, both the caracals and chimpanzees engaged in more play when the food-related objects were in the enclosure. Therefore, feeding enrichment or objects related to prey items (*e.g.*, the ***bird*** object for caracals) rather than the provision of play objects, appears to elicit play in captive adults. Feeding enrichment devices are also less likely rapidly to become ineffective as a result of habituation. Since free-ranging caracals must chase prey and capture it on a daily basis, the ***flying fox*** is likely to be effective in the long-term, but could be interspersed with other artificial prey-chase devices that encourage pouncing or chase along the ground, rather than leaping up into the air (Lindburg, 1998; Markowitz & LaForse, 1987). Such devices allow captive caracals to conserve their natural hunting behaviours, as well as providing thee zoo public with a chance to observe this impressive repertoire of behaviours (Figure 10.46).

Chimpanzees, and the other Great Apes, provide zoo researchers with additional challenges. Whilst feeding enrichment devices are clearly beneficial, few are likely to provide adequate cognitive challenges. The immediate mastery of the ***peanut wheel-maze*** (on the first attempt) used in this study highlights this fact. This study also indicates that it is useful to provide several different food-related objects, allowing different skills to be used, and providing less dominant (or more ***neophobic***) individuals with the opportunity to gain access to at least one object or device. Researchers must become more innovative and continue to test as many enrichment devices as possible.

Figure 10.45. A later version of the "flying fox" (Mills, 1998) is now a permanent feature of the caracal enclosure. These photos show one of Boozie and Zili's offspring chasing (bottom) and leaping at (top) a dead chick attached to the "flying fox".

Figure 10.46. The impressive leaping ability of the caracal is showcased as part of London Zoo's "Animals in Action" display (photos taken in 1995)

CHAPTER 11

OVERVIEW AND CONCLUSIONS

11.1 REVIEW OF PROGRESS

This final chapter presents an overview of the thesis- aims, summary of findings and conclusions. It seeks to determine whether the aims and objectives set out in the early chapters were met. The problems encountered during the experimental phases will be outlined and the lessons learned as a result of conducting research in two different environments, with three different species will be discussed. The theoretical and practical implications of the findings, and the generalisability of the research will be examined. The chapter will culminate with suggestions for future research and brief concluding remarks.

11.1.1 AIMS OF THE PRESENT STUDY

The general aims of this thesis were:

- To investigate exploratory behaviour, particularly in response to the presentation of novel stimulus objects, in two different environments (laboratory & zoo) and with three different species (rats, chimpanzees & caracals).
- To investigate the effect of novel stimulus objects on patterns of aberrant behaviours, in the same two environments, with the same three species.

The following sections will present a summary of findings of the three experiments and two preliminary studies that were conducted in order to meet these two general aims.

11.1.2 EXPLORATION AND OTHER BEHAVIOURS IN LABORATORY RATS

Experiment 1 (Chapter 6) investigated the responses of rats to novel objects (& other behavioural patterns) during ***fixed-interval*** (FI60s), ***variable-interval*** (VI60s) and subsequent ***extinction*** sessions. Experiment 2 (Chapter 7) examined exploration and other behaviours in rats during ***variable-ratio*** (VR30), ***differential reinforcement of low rates*** (DRL15s) and subsequent ***extinction*** sessions. These two experiments completed a set of five simple intermittent schedules of food-reinforcement, which began with Litchfield's (1987) study of exploration and other behaviours during ***fixed-ratio*** (FR30), ***continuous reinforcement***, and ***extinction*** sessions. Chapter 8 presented a summary of the combined findings of the three studies.

The range of behaviors scored for Experiment 1 and Experiment 2 was extensive:

- Behaviour directed at bar and food-trough area (***bar pressing*** & ***bar-related behavior***)
- Behaviour directed at the stimulus objects (***sniff object***, ***sniff & touch object***, & ***chew/bite object***)
- Behaviour directed at the peripheral areas of the box (***propping*** & ***jump at lid***)
- Other behavioral categories (***rearing***, ***displacement***, ***digging/burying***, & ***pica***).

The inclusion of so many categories, allowed a comprehensive analysis of a rat's behaviour (exploratory & other) during various intermittent schedules of food reinforcement to be undertaken.

11.1.2.1 AMOUNT OF BEHAVIOUR OCCURRING DURING PRPs

The results from Experiment 1 and Experiment 2 indicate that more stable PRPs (overall) occurred during the predictable ***fixed-interval*** and ***DRL*** sessions (high proportions of total frequency & duration measures occurred during PRPs). The unpredictable ***variable-interval*** and ***variable-ratio*** sessions lacked stable PRPs (low proportions of total frequency & duration measures occurred during PRPs). That is, the predictions concerning PRP development (or lack of development) on these four different schedules were supported. These results clearly indicate that the larger and more naturalistic open-field environment had little effect on typical ***fixed-interval*** and ***variable-interval*** (Experiment 1) or ***DRL*** and ***variable-ratio*** (Experiment 2) schedule performance, in terms of the PRPs.

Chapter 8, with its summary of results of the five simple intermittent schedules of food-reinforcement, indicates that with respect to the amount of behaviour occurring during the PRPs, the ***variable-ratio*** and ***fixed-interval*** schedules stand apart from the others. That is, the percentages of total behaviours occurring during the PRPs fell at the two extremes, irrespective of whether novel objects were present or not. Very low percentages (frequency & duration) of each of the observed behaviours took place during PRPs on the ***variable-ratio*** schedule. This is not surprising, since non-reinforcement on this schedule is unpredictable, and a predictable PRP is unlikely to develop. As a result, behaviours other than ***bar pressing*** would occur at any time during the inter-reinforcement interval. At the other extreme, very high percentages (frequency & duration) of each of the observed behaviours occurred during PRPs on the ***fixed-interval*** schedule (with the exception of frequency of ***bar-related behaviour***). Again, this is not surprising, since in this instance, the period of non-reinforcement is very predictable. Thus, a predictable PRP is likely to develop, with a number of behaviours other than ***bar pressing*** likely to occur during this period.

11.1.2.2 AMOUNT OF SESSION TIME SPENT ENGAGED IN BEHAVIOURS

The proportion of time spent engaged in the observed behaviours differed for Experiment 1 (Chapter 6) and Experiment 2 (Chapter 7), but a number of behaviours were considered ***excessive*** (*i.e.*, more than 10% of total session time), although not necessarily ***maladaptive***, in both experiments. This was discussed in some detail in Chapter 8 (Section 8.6 & 8.7).

During Experiment 1 (***fixed-interval***, ***variable-interval*** & ***extinction*** sessions), ***behaviour directed at the bar and food-trough area*** was somewhat ***excessive*** during some sessions (especially ***fixed-interval*** sessions). Levels of ***behaviour directed at the peripheral areas of the box*** were ***excessive*** during ***fixed-interval*** and ***variable-interval*** sessions, if objects were absent, and during ***extinction*** for all groups. The levels of ***rearing*** observed during ***extinction*** (in three of the four groups) were considered to be ***excessive***. In summary, the behaviours that occurred to excess during Experiment 1 were those that ***centered at the food source*** (not maladaptive), ***escape-directed behaviour*** or ***visual inspection of the surroundings*** (potentially also linked to seeking an escape).

During Experiment 2 (***DRL***, ***variable-ratio*** & ***extinction*** sessions) high levels of the three ***object-directed behaviours*** (>20% or even 30%) were observed in all sessions, and somewhat excessive amounts of ***behaviour directed at the bar and food-trough area*** (>10% or even 20%) were also observed during some sessions (unlikely to have been maladaptive). Some levels of ***escape-directed behaviour*** (***behaviour directed at the peripheral areas of the box***) and ***visual inspection of the surroundings*** (***rearing***) were also excessive. Only the excessive levels of ***displacement*** (in a number of cases) and ***pica*** (>10% or approaching 10% in a number of cases) could be considered potentially ***maladaptive***, and akin to aberrant behaviours observed in other captive environments (Erwin & Deni, 1979; Shepherdson, 1989).

The 10% of session criterion may appear somewhat arbitrary as an indicator of ***excessive*** behaviour. However, researchers, such as Shepherdson (1989), suggest that if captive animals spend more than 10% of their day engaged in a particular activity, then it should be considered ***excessive*** or ***stereotypic***. Whilst a half-hour experimental session should by no means be considered equivalent to a 24-hour day, nonetheless, the patterns observed might be useful indicators of potentially ***excessive*** behaviour under conditions of intermittent food reinforcement.

Not all ***excessive*** behaviours observed should be considered ***maladaptive***. For example, the excessive levels of ***exploration directed at the stimulus objects*** observed in Experiment 2, might be considered ***adaptive***, since this behaviour could have led to other sources of food & stimulation. It might only have become potentially problematical if it had interfered significantly with obtaining reinforcement. The high levels of ***behaviour centered at the food source*** found in Experiment 1 and Experiment 2 could also be considered ***adaptive***, especially if the food source was unpredictable (*e.g.*, ***variable-ratio*** schedule, where the next response may be rewarded).

The high levels of ***escape-directed behaviour*** (***behaviour directed at the peripheral areas of the box***) and ***visual inspection of the surroundings*** (***rearing***) observed in some cases during both experiments may have indicated how aversive the experimental conditions were. Excessive ***rearing*** may have reflected increased vigilance or it may have been the start of a qualitatively aberrant behaviour (such as ***head tossing***) or a quantitatively aberrant behaviour (such as ***pacing***) observed in some captive animals (Erwin & Deni, 1979).

11.1.2.3 RESISTANCE TO EXTINCTION

Conflicting results (Experiments 1 & 2) were found in terms of predictions concerning ***resistance to extinction***. That is, the ***discrimination hypothesis*** (Church, 1963) appeared to be less relevant for rats run in environments other than the traditional Skinner box or operant chamber. The larger and more naturalistic open-field environment used in these studies clearly extended the repertoire of possible non-operant responses, which in turn appeared to alter the ***resistance to extinction*** of some schedules, making behavioural predictions (of the operant response & other behaviours) more problematic.

In Experiment 1, extinction of ***bar pressing*** did not occur more rapidly in the ***fixed-interval*** groups than in the ***variable-interval*** groups. According to the ***discrimination hypothesis*** (Church, 1963), rats run on the ***fixed-interval*** schedule should have discriminated more readily between the ***schedule*** (FI60-s) and ***extinction*** conditions. A greater ***resistance to extinction*** in the ***variable-interval*** groups was not apparent. In Experiment 2, on the other hand, extinction of ***bar pressing*** did indeed occur more rapidly in the ***DRL*** groups (run on the more predictable schedule), as predicted, with a ***greater resistance to extinction*** apparent for the ***variable-ratio*** groups.

11.1.2.4 SIZE AND COMPLEXITY OF THE EXPERIMENTAL BOX

As already mentioned, the results of Experiment 1 and Experiment 2 indicate that some features of operant responding (or the stimuli present immediately after reinforcement) appeared to be less affected by the increased size or complexity of the experimental environment. For example, the development of PRPs on the predictable FI60-s schedule in Experiment 1 and DRL 15-s schedule in Experiment 2, as expected, suggests that this feature of operant responding was a robust phenomenon. Nevertheless, it should be pointed out, that even when there was a stable PRP, a proportion of every behavioural measure took place outside the PRPs (at other times of non-operant responding throughout the interval). On the other hand, the increased size and complexity of the open-field environment clearly affected ***resistance to extinction***, under some schedule conditions (Experiment 1). It should be noted, that it affected the ***interval*** schedules, rather than the ***ratio*** or rate schedules.

11.1.2.5 EFFECT OF NOVEL OBJECTS ON BEHAVIOURS OBSERVED

The results of Experiment 1 and Experiment 2 indicate that the presence or absence of objects to explore and manipulate (and not just predictability of the schedule) had an effect on some categories of behaviour.

Non-object-directed behaviours during *schedule* sessions

The presence of objects during *schedule* sessions (Experiment 1- *fixed-interval*, & *variable-interval*; Experiment 2- *variable-ratio* & *DRL*) resulted in lower levels (frequency & duration) of most categories of *non-object-directed behaviours* (as expected). However, there were a few measures of behaviour that were more likely to occur in the presence of objects.

With objects in the box during predictable ***fixed-interval*** sessions (Experiment 1), more bouts of ***displacement*** were observed. During predictable ***DRL*** sessions (Experiment 2), the presence of objects also resulted in more ***displacement*** (frequency & duration), but also resulted in a complete absence of ***jump at lid***. If objects were present during unpredictable ***variable-interval*** sessions (Experiment 1), then *pica* did not occur, but more ***digging/burying*** was observed. The presence of objects during unpredictable ***variable-ratio*** sessions (Experiment 2) resulted in an absence of ***jump at lid***.

With respect to the operant response itself (*i.e.*, *bar pressing*), the absence of "distracting" objects resulted in higher rates of ***bar pressing*** for all but the unpredictable ***variable-ratio*** schedule. That is, the presence of objects during this schedule resulted in a doubling of the frequency and duration of *bar pressing*.

Object-directed behaviours during *extinction* sessions

When objects were first encountered had an effect on some ***object-directed behaviours*** during ***extinction***. For Experiment 1, if objects were first encountered during ***extinction***, more ***sniffing and touching*** of objects, or manipulation with the forepaws occurred. By contrast, prior experience with objects resulted in higher rates of ***biting or chewing*** of objects during ***extinction***. For Experiment 2, if objects were first encountered during ***extinction***, more ***sniffing*** or object inspection took place. Prior exposure to objects increased ***exploratory manipulatory responses*** (*i.e.* ***sniffing & touching & chewing/biting***). Thus, for both experiments, the topography of the response during ***extinction*** was affected by prior exposure to objects during ***schedule*** running (when comparing same ***schedule*** counterparts).

If objects were first encountered during ***extinction***, the predictability or unpredictability of the previous schedule (***resistance to extinction***) also had an effect on some ***object-directed behaviours***. In Experiment 1, rats previously run on the unpredictable ***variable-interval*** schedule engaged in less ***sniffing*** and ***chewing/biting*** of objects. However, they spent more time (although not more bouts) ***sniffing*** and ***touching*** the novel objects with the forepaws. For Experiment 2, rats previously run on the unpredictable ***variable-ratio*** schedule engaged in fewer bouts of ***sniffing*** (but more time) and much less ***chewing/biting*** of objects. By contrast, they engaged in much more ***sniffing and touching*** of objects with the forepaws. Thus, for both experiments, if objects were first encountered during ***extinction***, the topography of the response was affected by the predictability or unpredictability of the previous schedule.

Non-object-directed behaviours during *extinction* sessions

When objects were first encountered also had an effect on some ***non-object-directed behaviours*** during ***extinction***. For Experiment 1, if objects were first encountered during ***extinction***, less ***pica*** and ***bar-related behaviour*** occurred, fewer bouts of ***rearing*** and ***displacement***, and less time was spent ***digging/burying*** and ***propping*** (FIOE group). For the VIOE group, less ***pica***, ***digging/burying***, and ***bar-related behaviour*** occurred. For Experiment 2, if objects were first encountered during ***extinction***, no ***jump at lid*** was observed, and there were fewer bouts of ***pica*** and less time was spent ***rearing*** (DRLOE group). For the VROE group, less ***rearing***, ***bar-related behaviour***, and ***jump at lid*** was observed, and less time was spent engaged in ***displacement***.

When objects were first encountered, as well as unpredictability of the previous ***schedule*** (***resistance to extinction***) also had an effect on the operant response itself (*i.e*., ***bar pressing***). In both experiments, if objects were first encountered during ***extinction*** (*i.e.* maximum novelty), less ***bar pressing*** (>60% less for the VROE group) took place if rats were previously run on the unpredictable ***variable-interval*** and ***variable-ratio*** schedules. Thus, rats that had no prior exposure to objects, engaged in far less ***bar pressing*** once objects were present during ***extinction***. Objects with maximal novelty appeared to facilitate the ***extinction*** of the operant response in rats previously run on unpredictable schedules (high *resistance to extinction*).

11.1.3 EFFECT OF NOVEL OBJECTS ON ABERRANT BEHAVIOURS IN LABORATORY RATS

Experiment 3 investigated whether ***polydipsia***, or other excessive behaviours (such as ***aggression*** or ***escape-directed behaviours***) would occur during a ***fixed-interval*** (FI60s) schedule in the more naturalistic open-field Skinner box, when a concurrent water source was available. It was suggested, that the presence of novel objects might reduce or even prevent ***polydipsia*** from occurring.

The range of behaviors scored was again extensive:

- Behaviour directed at bar and food-trough area (***bar pressing*** & ***bar-related behavior***)
- Behaviour directed at the stimulus objects (***sniff object***, ***sniff & touch object***, & ***chew/bite object***)
- Behaviour directed at the water bottle (***drinking***, ***sniff bottle***, ***sniff & touch bottle***, & ***chew/bite bottle***)
- Behaviour directed at the peripheral areas of the box (***propping***)
- Other behavioral categories (***displacement***, ***digging/burying***, & ***resting/sleeping***).

The inclusion of so many categories, allowed a comprehensive analysis of a rat's behaviour (drinking, exploratory & other) during a FI60-s schedule of food reinforcement to be undertaken.

The results of Experiment 3, in conjunction with the findings of Holme (1990), indicate that it is difficult to predict which behaviours will occur excessively in an open-field situation on a ***fixed-interval*** schedule, with a concurrently available water source. The shorter interval (FI60-s), used in Experiment 3, resulted in high levels of ***aggressive behaviour*** (directed towards the stimulus objects & water bottle), but acceptable levels of ***drinking*** and ***escape-directed behaviour***. The longer interval (FI120-s), used by Holme (1990), appeared to evoke ***polydipsia*** and extremely high levels of ***escape-directed behaviour***, but minimal ***aggression***. Since Holme (1990) did not provide her rats with stimulus objects, it is not possible to determine whether the presence of objects to explore would have mediated some of the effects she observed.

Certainly, with respect to Experiment 3, the presence of novel objects did not minimize or prevent excessive ***aggression***. Indeed, some of the objects provided suitable targets, which may have provided further opportunities for aggressive chewing and biting responses. It is not possible to conclude that the presence of these objects prevented ***polydipsia*** from occurring, since excessive ***drinking*** did not appear in the absence of stimulus objects either.

Experiment 3 was designed to create a link between the laboratory open-field environment and the zoo environment. Zoo enclosures provide an excellent opportunity to investigate "open-field" behaviour, with a concurrently available source of water. Animals in zoos are often on a fixed-time schedule of food reinforcement. That is, they tend to be fed at predictable times on predictable days. Even if keepers attempt to vary the feeding times, food still appears at a particular time of day. That is, only some flexibility is possible. The presentation of novel stimulus objects (or other behavioural enrichment techniques) and the opportunity to engage in exploratory behaviour may eliminate or minimise the development of aberrant behaviours. However, based on the findings of Experiment 3, one must conclude that it would be difficult to predict accurately the effect of stimulus objects or schedules of reinforcement in the zoo environment (long inter-food intervals).

The final two preliminary studies attempted to show that the principles of exploratory behaviour, schedules of reinforcement, and patterns of aberrant behaviours that have been largely gleaned from laboratory studies, could be applied to improving captive environments for species other than the laboratory rat (*Rattus norvegicus*).

11.1.4 EFFECT OF NOVEL OBJECTS ON EXPLORATION AND OTHER BEHAVIOURS IN CAPTIVE CHIMPANZEES

Preliminary Study 4 presented a qualitative analysis of exploratory behaviour and other behavioural changes upon presentation of novel stimulus objects (food-related & non-food-related), to a group of six chimpanzees. It was expected that some aberrant behaviours might be observed in the chimpanzees during baseline observations, since captivity tends to pose particular problems for the Great Apes (high cognitive abilities & therefore need extra mental & physical stimulation). This study sought to provide suitable objects that would facilitate exploratory behaviour and play, whilst reducing any aberrant behaviours that were observed.

Without a doubt, the objects, which elicited the greatest amount of exploratory behaviour, were the food-related objects. The ***foraging box*** and ***peanut wheel maze*** attracted all members of the group, but tended to be monopolized by the three adults. Use of the ***seed shaker***, on the other hand, was restricted to the three younger members. Importantly, the introduction of novel objects did not result in aggression, or appear to have any negative side effects. On the contrary, it appeared almost to eliminate ***coprophagia***, ***fecal art*** and ***insertion of fingers into the rectum***- all aberrant behaviours observed during baseline sessions (although they began to reappear towards the end of the week, as they habituated to the objects).

11.1.5 EFFECT OF NOVEL OBJECTS ON EXPLORATION AND OTHER BEHAVIOURS IN CAPTIVE CARACALS

Preliminary Study 5 presented a qualitative analysis of exploratory behaviour and other behavioural changes upon presentation of novel stimulus objects (food-related & non-food-related), to a pair of caracals. It was expected that some aberrant behaviours might be detected in the caracals during baseline observations, since these carnivores were unable to engage in hunting. Again, this study sought to provide suitable objects that would facilitate exploratory behaviour and play, whilst reducing any aberrant behaviours observed.

The object, which stood out as the most effective, was the ***flying fox***. Both caracals used it successfully, during the first attempt. The introduction of both sets of objects did not result in any overtly ***aggressive behaviour***, although ***Boozie*** hissed at ***Zili*** on a few occasions. The ***bird*** object also attracted a lot of attention from ***Zili***, who appeared to behave as if it were a live bird. There appeared to be less ***pacing*** behaviour exhibited during the week in which the ***flying fox*** was used.

11.2 DIFFICULTIES ENCOUNTERED AND LESSONS LEARNED

Fortunately, only two main difficulties were encountered during the research, and neither was unexpected. Indeed, both (in general terms, rather than specific details) were foreseen well in advance of commencement of the final preliminary studies.

11.2.1 COMPROMISES BETWEEN THE IDEAL AND THE PRACTICABLE

> "The special problems of studying behaviour in a natural environment mean that the field worker often has to make compromises between what is ideal and what is practicable...All research involves an element of opportunism, grabbing chances when they are presented. But field work, in particular, requires flexibility and a readiness to change plans when a course of action is frustrated by unexpected difficulties" (Martin & Bateson, 1986, p.101).

Although Adelaide Zoo provided an environment in which a substantial degree of experimental control was possible, nonetheless, a certain number of compromises had to be made between what was considered ideal in the laboratory setting and what was practicable in the zoo setting. Unlike the three experiments conducted in the laboratory, no food-deprivation or feeding schedules were imposed in the zoo studies. Whilst this may have encouraged speculation about the possible schedules of food reinforcement in the zoo environment, it obviously prevented direct comparison with results obtained in the earlier laboratory experiments.

Arguably the greatest challenge posed by the zoo studies, was in terms of designing and constructing novel stimulus objects that were strong, durable, easily cleaned and maintained, complex enough, and aesthetically pleasing. Even more challenging, was the immediate response required from keepers and Steve Tupper (who constructed & installed the objects), if objects were unexpectedly damaged. The chimpanzees (primarily ***Fanny***) succeeded in tearing the cover away from the end of the ***log drum*** (towards the end of Day 1), which exposed the inner sound mechanisms, which in turn may have posed a risk to the chimpanzees (*e.g.*, choking on small parts). The keeper immediately locked the chimpanzees away, and Steve removed the log drum, repaired it (using a stronger metal plate), and reinstalled it the following day. The close co-operation of zoo staff and staff from the Psychology Department, ensured that immediate help was always available when the objects were in the enclosures.

Unexpected injury to ***Boozie*** (a foot puncture wound that became infected), the male caracal, also resulted in a lengthy period of recovery, which required postponement of the study for a number of weeks. Staff rosters resulted in a number of keepers being involved during each of the zoo studies, but they were all supportive and interested in the research. Cleaning and feeding times were not always as predictable as the typical schedule predicted. Although these factors presented no major problem, it did highlight the fact that researchers must be flexible, in terms of time and changes to procedure, when working outside the controlled laboratory environment.

11.2.2 THE USE OF VIDEOTAPE TO RECORD BEHAVIOUR

> "A major problem with film or videotape analysis is that it can be exceedingly time-consuming: behaviour that perhaps lasted only a few minutes may take hours to analyse" (Martin & Bateson, 1986, p.71).

Whilst the videotapes for Experiments 1-3 provided an accurate record of the rats' behaviour, the subsequent event recording was certainly exceedingly time-consuming. The wide-range of behaviours included in the analysis provided a further impediment to quick coding or transcription of the videotapes, since only a few sessions could be scored in any one sitting, in order to maximize intra-observer reliability (*i.e.*, to prevent lapses in concentration or fatigue effects). Some of the resulting computer files provided more than 50,000 lines of data to be analysed. For Experiment 1 and Experiment 2, a total of 96-hours of videotape was scored. For Experiment 3, a further 72-hours worth of videotape was coded. Therefore, this researcher is confident, that a thorough and accurate quantitative analysis of a wide range of behaviours was achieved for the three experiments conducted in the laboratory with rats. Unfortunately, as a result of time constraints and the unrealistic number of hours of observation conducted, only a qualitative analysis of the zoo findings was possible. For each of the zoo studies, a total of 336-hours of observation time took place (*i.e.*, 6 hours per day, 7 days a week, for 8 weeks). A portable event-recorder would be recommended for any replication of these studies.

11.3 THEORETICAL AND PRACTICAL IMPLICATIONS OF THE RESEARCH

The current research has investigated exploratory behaviour in rats, in an open-field environment, during several intermittent schedules of food-reinforcement and subsequent extinction in some detail. It has also examined exploratory behaviour in caracals and chimpanzees in a zoo environment. The current study has focused on responses directed towards novel stimulus objects, and it has also examined the interplay between schedules of reinforcement and "normal" or abberant behaviours. Despite the considerable information gleaned, theoretically, it is beyond the scope of the current series of experiments to present a single adequate theory of exploration. The problems regarding the distinction between play and exploration, as well as differences between the different categories of exploratory behaviour still exist, although in terms of responses directed at novel stimulus objects, the categories used in the present studies were readily distinguished. That is, if the topography of the exploratory responses towards objects is defined in terms of inspection (***sniff object***), manipulation with the forepaws (***sniff & touch object***) or chewing and biting (***chew/bite object***), there appears to be little confusion generated (as reflected in the inter-observer reliability scores).

As other researchers have discovered (*e.g.*, Negrão & Schmidek, 1987), noticeable individual differences in exploration and other behaviours were also observed in the current research (laboratory & zoo environments). This factor alone indicates that larger sample sizes, and further replications are needed before the findings of the laboratory and zoo studies can be considered generalisable across other captive environments. However, based on the qualitative analysis of the zoo findings, it is clearly possible to design and implement objects that can be incorporated into feeding routines. Objects that were novel and reasonably complex, and related to foraging, were clearly the most effective at eliciting exploratory and play responses, and appeared temporarily to reduce aberrant behaviours.

The practical implications of the preliminary studies are that zoos must continue to encourage behavioural research that attempts to discover the possible causes of stereotypic or aberrant behaviours, whilst simultaneously exploring ways of enriching captive environments. That is, behavioural solutions should be found for behavioural problems. The presentation of novel stimulus objects, particularly those that facilitate the use of natural foraging strategies and behaviours, is an effective and cost-effective way of conserving behaviour in a zoo environment. Other research already conducted at Adelaide Zoo has shown that ***ecological learning theory*** can be readily applied to the zoo setting (*e.g.*, Kardos, 1999; Mills, 1998)

11.4 SUGGESTIONS FOR FURTHER RESEARCH

As mentioned in Chapter 1, studies of exploratory behaviour within psychology typically take place within the laboratory, using somewhat arbitrary stimuli. Studies of object manipulation or responses to novel objects in captive chimpanzees, exotic cats or any species other than the laboratory rat, are few in number and the findings are too general to allow a comprehensive analysis of exploratory behaviour. This thesis has expanded the range of species, the experimental setting, and attempted to develop less arbitrary stimuli (particularly those that were food-related). A wide-range of behaviours has been included in the analysis, including aberrant and “normal” behaviours. However, clearly it is not possible to assert that an adequate all-encompassing theory of exploration has been reached, and only further experiments, conducted in a variety of settings will help achieve this goal.

11.4.1 LABORATORY EXPERIMENTS

The different patterns of ***excessive*** behaviours observed in Experiment 3 and Holme’s (1990) study, and the resulting questions raised, can only be resolved by further experimentation. Two experiments, in particular, might provide relevant answers. Experiment 3 could be replicated, but with rats run on a FI120-s schedule. This longer interval might provide results more in line with Holme’s (1990) findings (i.e., ***polydipsia*** & high levels of ***escape-directed behaviour***, but less ***aggressive behaviour***). Similarly, Holme’s (1990) study could be replicated, but with rats run on a FI60-s schedule. Further experiments would also present these rats with novel stimulus objects (one experiment with rats run on a FI120-s schedule & another experiment with rats run on a FI60-s schedule), in order to determine whether the presence of objects to explore would have mediated some of the effects she observed. This is particularly important, since ***polydipsia*** was not observed in Experiment 3, and therefore, it was not possible to state that the presence of novel stimulus objects reduced or eliminated (or perhaps increased) an aberrant adjunctive behaviour such as ***polydipsia***.

11.4.2 ZOO EXPERIMENTS

Quantitative analysis of the preliminary studies conducted at Adelaide Zoo would provide a useful starting point for further studies. More importantly, the objects that were the most effective (*i.e.*, the food-related objects) should be introduced and tested with other chimpanzees and caracals, in other zoos or in other types of enclosures. As mentioned previously, zoo studies are often "confounded by small sample sizes", but this could be overcome with the use of "multiinstitutional" or "interzoo" studies (Mellen, Shepherdson & Hutchins, 1998, p.333). Future studies must continue to invent and test a variety of other suitable objects, that challenge captive animals (physically & mentally) in appropriate ways, and allow them to retain as many species-specific patterns of behaviour as possible.

The opportunity to engage in exploratory behaviour, to allow animals to engage in "information-gathering", to "provide not only complexity but continuing novelty and variability in highly exploratory animals" must be taken into account in the original design of enclosures, and in the continual improvement and maintenance of existing enclosures (Mench, 1998, p.35). Researchers must begin to think beyond traditional two-dimensional designs, and envisage captive environments in a three-dimensional, "theromorphic" or animal-centered way (Timberlake, 1993). Only then is it likely that all the sensory, physical and mental requirements of a particular species will be met, and the goal of behavioural conservation be attained. Even relatively new, multi-million dollar exhibits at some of the leading zoos, present zoo visitors with an inappropriate perception of a species' behavioural repertoire and natural habitat (Figures 11.1 - 11.4). This in turn, suggests that the behavioural needs of the individual captive animals are not being met. Captive provisioning must continue to be an area of prime concern in all zoos, and the effects of allowing staff schedules to determine feeding routines, rather than the style of feeding in natural environments (*e.g.*, continuous browsing & grazing or less regular feeding), must be recognized and addressed (Lindburg, 1998).

11.4.3 FIELD EXPERIMENTS

Field researchers must continue to develop field experiments, which can examine ecologically relevant questions, generate and test appropriate research hypotheses, and then link in with experimental research conducted in laboratory settings. Responses to novel objects or situations encountered in natural environments can be recorded and reported in observational field studies, but many years of observation would be needed to obtain sufficient data. However, as natural environments shrink, and "wild" animals come into contact with humans on a more regular basis, then observations of exploratory behaviour will become more common. Until then, ethical field experiments (*e.g.*, Matsuzawa, 1994) that present "wild" animals with stimuli (objects or sound recordings) will provide further relevant information. However, it must be recognized that any such experiment, which introduces stimuli into the natural environment, will have an effect on the "wild" animals, and an impact on future interactions with humans or objects.

Some field researchers, such as Wrangham (1992), have specifically focused on which aspects of the natural environment are crucial for the appearance of "natural" behaviors (in chimpanzees), and hence should be harnessed or replicated in captivity. Field researchers, particularly those who are aware of captive management issues, are in a unique position to advise zoo researchers on the range of stimuli that are most likely to lead to the expression of a full range of species-specific behaviours.

Zoo researchers must remain up-to-date with field research. Only then may some of the current misperceptions of natural environments and free-ranging individuals be addressed. For example, recent research shows that lowland gorillas are not as terrestrial as their mountain gorilla cousins. That is, they feed high in fig trees (even at the same time as chimpanzees) and build nests in trees, as well as on the ground (Kuroda, Nishihara, Suzuki & Oko, 1996; Yamagiwa, Maruhashi, Yumoto & Mwanza, 1996). This increased terrestriality should be reflected in zoo enclosures, in terms of providing the opportunity to climb. Since all the gorillas in captivity are lowland species, researchers must be careful not to assume that the findings of Dian Fossey, as popularized in the movie "Gorillas in the Mist", represent all gorilla species and groups.

11.5 CONCLUDING REMARKS

To continue to advance an ecologically relevant psychology, which adapts the experimentally rigorous procedures developed in the laboratory to natural situations or ecological questions, the following factors must be facilitated and encouraged:

- The promotion of a continuum of research environments investigating a wide range of species and behaviours
- The promotion of inter- and intra- disciplinary links
- The promotion of behavioural solutions to "real-world" problems.

Fortunately, this is exactly what a number of researchers are doing. Timberlake and his colleagues continue to conduct ecological analyses of laboratory learning (*e.g.*, Pecoraro, Timberlake, & Tinsley, 1999; Timberlake, 1990). Fantino and his colleagues are systematically providing ever more complex analyses of foraging choice (*e.g.*, Fantino & Abarca, 1985; La Fiette & Fantino, 1988; Williams & Fantino, 1996). Since 1977, Zeiler has expanded his analysis of the generality of schedule effects to ever more ecologically relevant scrutiny, assessing the effects of closed or open feeding economies (*e.g.*, Zeiler, 1999a), temporal control (*e.g.*, Zeiler,

Figure 11.1. Although some enclosures may appear naturalistic, if they do not provide adequate "hiding" places for gorillas to escape to, from the constant scrutiny of zoo visitors, then gorillas may retreat to areas that are clearly inappropriate, such as the hard-surfaced dry moat (photos taken by Adam Litchfield at Los Angeles Zoo in Oct. 2000)

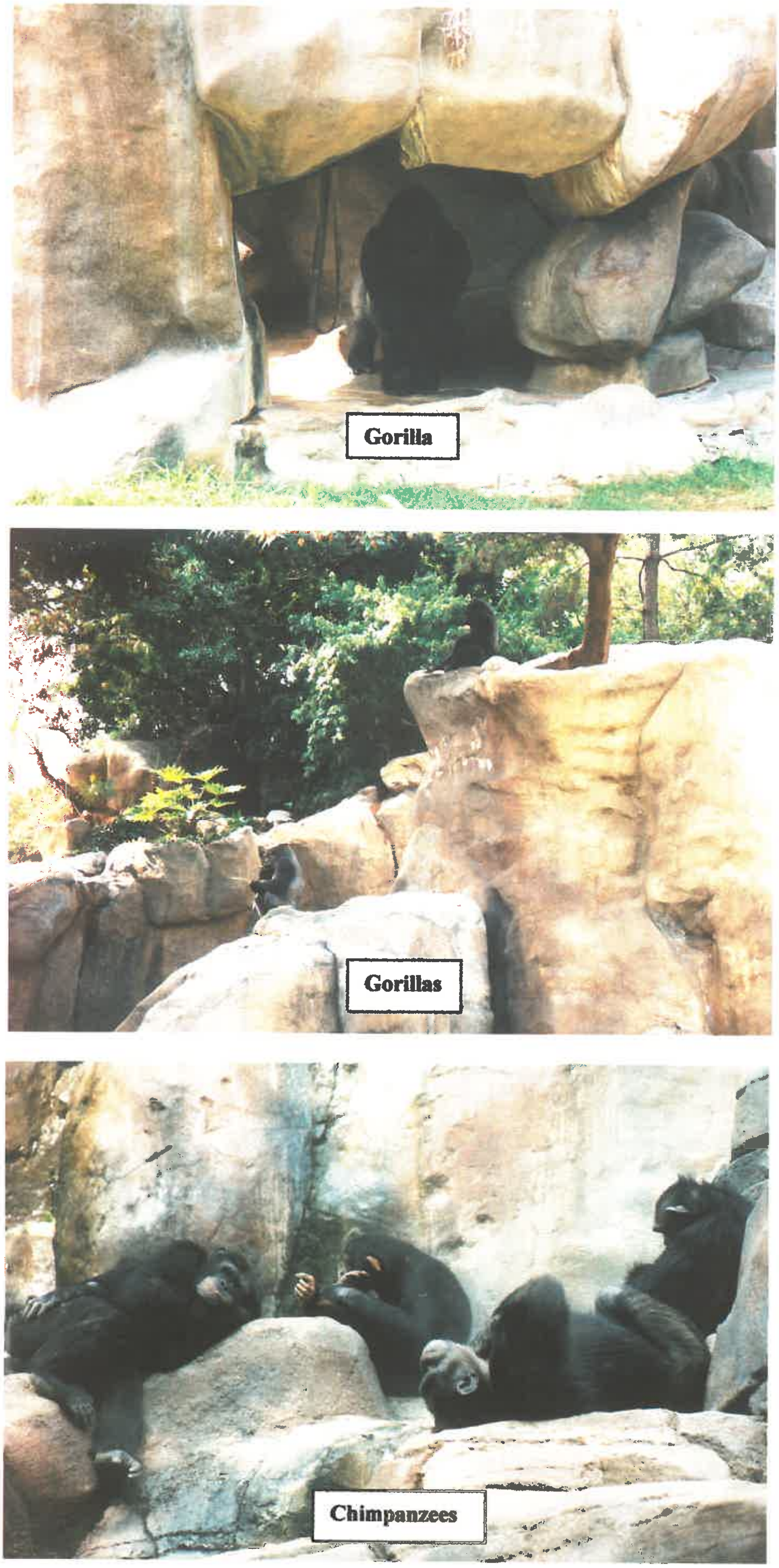


Figure 11.2. Designers of zoo enclosures appear to favour expanses of "mock rock". However, for the Great Apes, it may help perpetuate notions of "cave dwelling", and clearly does not provide the soft and naturalistic elements of a natural environment (photos taken by Adam Litchfield at Los Angeles Zoo in Oct. 2000).

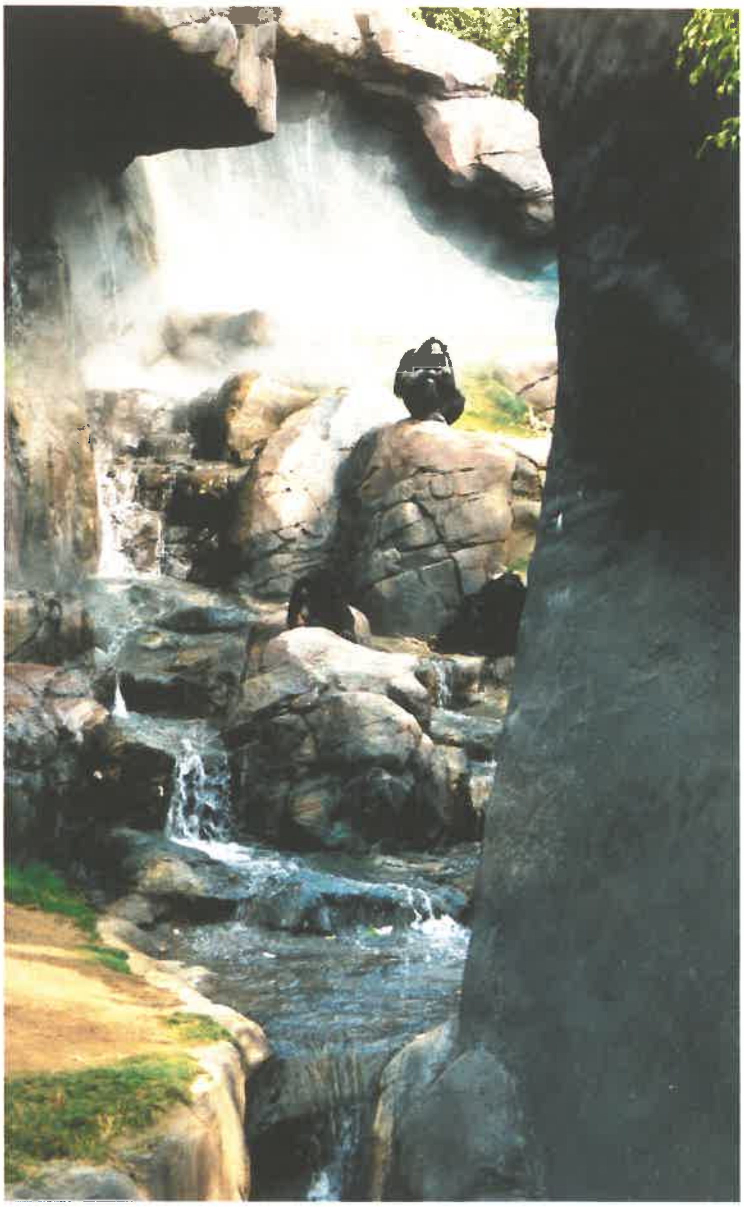


Figure 11.3. Although certainly picturesque, the waterfall and rocks, and limited climbing structures, do not provide these captive chimpanzees with the arboreal elements of a natural environment (photos taken by Adam Litchfield at Los Angeles Zoo in Oct. 2000)

Figure 11.4. This aesthetically pleasing orangutan exhibit does not provide elements of a tall rainforest canopy environment. As a result, orangutans may spend more time on the ground than their free-ranging counterparts (photos taken by Adam Litchfield at Los Angeles Zoo in Oct. 2000)

1999b), searching or waiting for prey (*e.g.*, Zeiler, 1993), and functional analysis (*e.g.*, Zeiler, 1992). The close link between Adelaide Zoo and the University of Adelaide Psychology Department has resulted in a number of studies that have applied ecological learning theory to the conservation of behaviour in the zoo environment (*e.g.*, Kardos, 1999; Landrigan, 1998; Mills, 1998).

This thesis has attempted to adopt a holistic and interdisciplinary approach to the study of exploratory behaviour across environments. Exploratory behaviour provides animals with vital information about the distribution of resources and the location of potential predators or competitors for limited resources. As Kamil and Clements (1990) point out, ecological analyses about the "effects of information about the environment on behavior have not been widely studied" (p.24). The current set of studies has investigated the effect of presentation of novel stimuli on a wide range of behaviours (exploratory, aberrant & other) of rats in an open-field laboratory situation (with or without a concurrent source of water), and on behaviour of chimpanzees and caracals in a zoo situation.

This thesis has also attempted to apply the knowledge gained from studies of exploration in the laboratory to the zoo environment, specifically in the area of behavioural enrichment. It is hoped that future research will continue to seek behavioural solutions to the problems posed by captive environments and ever shrinking natural environments, thus promoting the psychological and physical well-being or welfare of captive and free-ranging species.

LIST OF APPENDICES

APPENDIX A

This section provides the frequency and duration scores for every behavioural category in Experiment 1, for all four groups of rats (for every session & during the PRPs), and for each of the three grouping variables.

The material included in Appendix A consists of a set of three tables per behavioural category scored. The four rats per group are included in the same cell of the table (e.g. the four rats in the FIOS group are lumped together). This set of three tables provides the following information:

(1) frequency and duration of the behaviour for each rat in each session (i.e., raw data), the group mean for each session, the average mean and sum of means for sessions 1-3 and 4-6 (for each group of rats);

(2) frequency and duration of the behaviour during the PRPs for each rat in each ***fixed-interval*** or ***variable-interval*** session (i.e., raw data), the average mean and sum of means for sessions 1-3 (for each group of rats); and

(3) frequency and duration of the behaviour sum of means (over session 1-3), sum of means in PRPs (over sessions 1-3), and percentage of total (for each group of rats).

Only the first table is relevant for the ***bar pressing*** category of behaviour. A table presenting the frequency of reinforcement for each rat in each session is also provided. The behavioural categories are presented in the following order:

(1) ***bar pressing*** (Table A.1);
(2) ***frequency of reinforcement*** (Table A.2);
(3) ***bar-related behaviour*** (Tables A.3 – A.5);
(4) ***sniff object*** (Tables A.6 – A.8);
(5) ***sniff and touch object*** (Tables A.9 – A.11);
(6) ***chew/bite object*** (Tables A.12 – A.14);
(7) ***propping*** (Tables A.15 – A.17);
(8) ***jump at lid*** (Tables A.18 – A.20);
(9) ***displacement*** (Tables A.21 – A.23);
(10) ***digging/burying*** (Tables A.24 – A.26);
(11) ***rearing*** (Tables A.27 – A.29); and
(12) ***pica*** (Tables A.30 – A.32).

Appendix A also provides the:

(1) mean frequency and duration of behaviours for the "object" grouping variable for all sessions (Table A.33) and during the PRPs of ***fixed-interval*** or ***variable-interval*** sessions (Table A.36);

(2) mean frequency and duration of behaviours for the "schedule" grouping variable for all sessions (Table A.34) and during the PRPs of ***fixed-interval*** or ***variable-interval*** sessions (Table A.37); and

(3) mean frequency and duration of behaviours for the "session" grouping variable for all sessions (Table A.35) and during the PRPs of ***fixed-interval*** or ***variable-interval*** sessions (Table A.38).

Table A.1

Frequency and duration of ***bar-pressing*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	455 / 119.4	560 / 110.0	969 / 160.8	654 / 154.4
	494 / 107.7	931 / 166.6	680 / 108.9	570 / 175.7
	831 / 158.9	863 / 144.8	858 / 176.6	947 / 224.7
	686 / 115.1	501 / 97.1	778 / 133.0	801 / 150.2
	mean=616.5/125.28	mea=713.75/129.63	mea=821.25/144.83	mean= 743 / 176.25
SESSION 2	588 / 114.5	1184 / 221.1	966 / 156.7	891 / 167.1
	512 / 96.4	1122 / 197.1	1119 / 153.9	1067 / 210.0
	1065 / 220.6	1174 / 279.2	1600 / 238.5	1772 / 275.9
	932 / 182.6	463 / 95.0	922 / 150.7	840 / 141.5
	mea=774.25/153.53	mean=985.75/198.1	me=1151.75/174.95	mea=1142.5/198.63
SESSION 3	791 / 130.4	1208 / 210.9	1521 / 210.9	793 / 153.9
	565 / 104.0	1209 / 186.6	1396 / 174.5	1414 / 278.6
	1851 / 249.9	1732 / 347.8	1655 / 207.9	1865 / 244.0
	1207 / 239.6	632 / 116.5	1245 / 198.7	1122 / 195.5
	mea=1103.5/180.98	me=1195.25/215.45	mean=1454.25/ 198	mean= 1298.5 / 218
average mean	831.42 / 153.26	964.92 / 181.06	1142.42 / 172.59	1061.33 / 197.63
sum of means	2494.25 / 459.79	2894.75 / 543.18	3427.25 / 517.78	3184 / 592.88
(for sessions 1 to 3)				
SESSION 4	917 / 145.8	1057 / 154.8	1880 / 244.1	473 / 76.5
	775 / 142.8	1084 / 168.0	888 / 104.0	604 / 104.0
	1449 / 198.7	1197 / 217.6	1331 / 168.1	921 / 131.6
	1344 / 206.0	474 / 83.8	1240 / 169.7	690 / 127.4
	me=1121.25/173.33	mean= 953 / 156.05	me=1334.75/171.48	mean= 672 / 109.88
SESSION 5	713 / 121.7	797 / 105.6	1435 / 156.3	467 / 75.9
	541 / 100.0	427 / 69.6	464 / 49.7	790 / 126.4
	768 / 103.2	892 / 151.1	616 / 70.7	789 / 118.2
	543 / 84.5	420 / 71.7	1702 / 181.9	803 / 112.1
	mea=641.25/102.35	mean= 634 / 99.5	me=1054.25/114.65	mea=712.25/108.15
SESSION 6	288 / 50.1	259 / 52.3	1063 / 148.2	269 / 42.7
	124 / 23.4	159 / 29.8	42 / 8.0	429 / 68.6
	457 / 76.8	345 / 74.8	376 / 66.3	203 / 41.8
	44 / 7.2	290 / 54.3	839 / 106.8	87 / 16.6
	mean=228.25/39.38	mean=263.25 / 52.8	mean = 580 / 82.33	mean= 247 / 42.43
average mean	663.58 / 105.02	616.75 / 102.78	989.67 / 122.82	543.75 / 86.82
sum of means	1990.75 / 315.06	1850.25 / 308.35	2969 / 368.46	1631.25 / 260.46
(for sessions 4 to 6)				

Table A.2

Frequency of ***reinforcement*** for each rat in Experiment 1, in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	29	42	30	43
	29	43	30	42
	30	43	30	43
	30	41	30	43
	mean=29.5	mean=42.25	mean=30	mean=42.75
SESSION 2	30	43	28	43
	29	43	29	29
	30	40	30	43
	30	40	29	43
	mean=29.75	mean=41.5	mean=29	mean=39.5
SESSION 3	30	43	30	43
	29	44	29	43
	30	43	30	43
	30	43	29	43
	mean=29.75	mean=43.25	mean=29.5	mean=43
average mean	29.67	42.33	29.5	41.75
sum of means (for sessions 1 to 3)	89	127	88.5	125.25

Table A.3

Frequency and duration of ***bar-related behaviour*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	526 / 260.9 488 / 426.2 384 / 138.9 300 / 86.5 mean=424.5/228.13	208 / 63.3 42 / 12.7 139 / 56.4 169 / 58.3 mean=139.5 / 47.68	522 / 358.6 424 / 188.5 293 / 235.9 395 / 200.6 mean=408.5 / 245.9	388 / 184.9 124 / 46.4 149 / 40.4 697 / 310.2 mean=339.5/145.48
SESSION 2	351 / 153.5 262 / 454.7 309 / 161.0 235 / 144.8 mean=289.25/228.5	409 / 127.9 194 / 37.6 311 / 119.3 462 / 248.5 mean= 344 / 133.33	409 / 340.5 621 / 247.1 689 / 364.0 447 / 198.0 mean=541.5 / 287.4	449 / 191.8 434 / 109.2 154 / 40.6 682 / 341.8 mea=429.75/170.85
SESSION 3	696 / 279.2 384 / 390.2 456 / 171.7 394 / 208.0 mean=482.5/262.28	704 / 272.0 390 / 67.2 261 / 103.9 605 / 240.0 mean= 490 / 170.78	589 / 508.5 618 / 254.0 485 / 306.6 714 / 172.6 mean=601.5/310.43	521 / 217.8 228 / 86.6 229 / 65.4 761 / 339.9 mea=434.75/177.43
average mean sum of means (for sessions 1 to 3)	398.75 / 239.64 1196.25 / 718.91	324.5 / 117.26 973.5 / 351.79	517.17 / 281.24 1551.5 / 843.73	401.33 / 164.59 1204 / 493.76
SESSION 4	753 / 299.8 465 / 261.1 510 / 238.7 442 / 125.5 mean=542.5/231.28	542 / 238.3 271 / 79.8 463 / 204.2 580 / 318.6 mean=464 / 210.23	629 / 233.6 408 / 179.0 377 / 129.2 440 / 121.1 mean=463.5/165.73	206 / 106.3 189 / 48.5 50 / 11.1 413 / 268.3 mean=214.5/108.55
SESSION 5	471 / 371.1 270 / 183.4 389 / 206.7 185 / 72.0 mean=328.75/208.3	373 / 232.0 116 / 21.4 307 / 185.2 440 / 225.9 mean=309 / 166.13	403 / 204.6 137 / 46.4 214 / 90.4 429 / 143.1 mea=295.75/121.13	306 / 200.8 253 / 105.7 43 / 12.4 405 / 245.0 mea=251.75/140.98
SESSION 6	371 / 201.5 182 / 125.3 353 / 288.2 90 / 49.5 mean=249/ 166.13	181 / 103.0 217 / 72.3 220 / 129.3 454 / 334.4 mean=268 / 159.75	490 / 303.7 52 / 39.9 290 / 130.0 316 / 131.3 mean=287 / 151.23	239 / 155.8 291 / 157.8 34 / 11.7 105 / 83.9 mean=167.25/102.3
average mean sum of means (for sessions 4 to 6)	373.42 / 201.90 1120.25 / 605.71	347 / 178.70 1041 / 536.11	348.75 / 146.03 1046.25 / 438.09	211.17 / 117.28 633.5 / 351.83

Table A.4

Frequency and duration of ***bar-related behaviour*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	95 / 61.6 143 / 273.0 79 / 51.0 78 / 35.5 mean=98.75/105.28	55 / 24.0 25 / 9.3 19 / 4.8 55 / 26.5 mean=38.5 / 16.15	123 / 247.7 75 / 88.3 80 / 187.2 117 / 105.0 mean=98.75/157.05	55 / 46.1 26 / 17.0 25 / 9.3 62 / 88.2 mean=42 / 40.15
SESSION 2	68 / 46.4 117 / 386.0 72 / 68.4 112 / 114.2 mean=92.25/153.75	80 / 38.8 23 / 9.4 31 / 21.4 42 / 27.6 mean=44 / 24.3	96 / 245.8 74 / 78.0 74 / 209.6 82 / 92.2 mean=81.5 / 156.4	42 / 33.2 13 / 6.3 16 / 4.8 70 / 80.8 mean=35.25 / 31.28
SESSION 3	95 / 63.1 95 / 262.4 64 / 54.2 123 / 157.4 mean=94.25/134.28	69 / 44.9 25 / 10.8 33 / 27.3 72 / 41.1 mean=49.75 / 31.03	115 / 351.8 79 / 80.8 79 / 174.0 50 / 28.5 mean=80.75/158.78	52 / 44.3 44 / 30.1 46 / 14.8 69 / 79.7 mean=52.75 / 42.23
average mean sum of means (for sessions 1 to 3)	95.08 / 131.10 285.25 / 393.31	44.08 / 23.83 132.25 / 71.48	87 / 157.41 261 / 472.23	43.33 / 37.89 130 / 113.66

Table A.5

Mean frequency and duration of ***bar-related behaviour*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***bar-related behaviour*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FIOS	frequency duration (seconds)	1196.25 718.91	285.25 393.31	23.85 54.71
VIOS	frequency duration (seconds)	973.5 351.79	132.25 71.48	13.59 20.32
FIOE	frequency duration (seconds)	1551.5 843.73	261 472.23	16.82 55.97
VIOE	frequency duration (seconds)	1204 493.76	130 113.66	10.80 23.02

Table A.6

Frequency and duration of ***sniff object*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	215 / 87.6 121 / 75.0 179 / 76.6 119 / 50.7 mean=158.5 / 72.48	157 / 84.2 100 / 30.5 150 / 61.8 171 / 64.5 mean=144.5 / 60.25	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	171 / 65.9 108 / 74.2 134 / 47.3 90 / 41.0 mean=125.75 / 57.1	71 / 40.3 88 / 31.9 152 / 43.2 97 / 34.4 mean= 102 / 37.45	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	92 / 32.4 70 / 36.3 101 / 37.3 75 / 50.8 mean= 84.5 / 39.2	130 / 58.4 112 / 49.8 93 / 29.6 150 / 63.3 mean=121.25/50.28	NO OBJECTS PRESENT	NO OBJECTS PRESENT
average mean sum of means (for sessions 1 to 3)	122.92 / 56.26 368.75 / 168.78	122.58 / 49.33 367.75 / 147.98		
SESSION 4	132 / 56.1 103 / 62.4 113 / 44.4 87 / 52.0 mean=108.75/53.73	129 / 51.3 181 / 54.3 137 / 46.0 117 / 49.8 mean= 141 / 50.35	128 / 57.4 111 / 45.6 115 / 51.9 143 / 72.4 mean=124.25/56.83	131 / 41.9 171 / 60.1 96 / 36.4 125 / 57.8 mean=130.75/49.05
SESSION 5	146 / 58.3 67 / 36.6 80 / 30.1 111 / 62.7 mean= 101 / 46.93	103 / 51.1 202 / 77.9 96 / 39.3 68 / 24.2 mean=117.25/48.13	83 / 34.1 89 / 31.5 74 / 25.4 117 / 53.6 mean=90.75 / 36.15	90 / 34.8 129 / 42.7 52 / 20.9 95 / 31.6 mean= 91.5 / 32.5
SESSION 6	114 / 56.0 87 / 39.2 90 / 31.3 104 / 47.1 mean= 98.75 / 43.4	107 / 50.8 208 / 74.1 107 / 37.6 76 / 29.1 mean= 124.5 / 47.9	98 / 47.9 101 / 29.7 80 / 32.7 142 / 71.5 mean=105.25/45.45	126 / 46.0 116 / 31.6 116 / 41.2 83 / 37.6 mean=110.25 / 39.1
average mean sum of means (for sessions 4 to 6)	102.83 / 48.02 308.5 / 144.06	127.58 / 48.79 382.75 / 146.38	106.75 / 46.14 320.25 / 138.43	110.83 / 40.22 332.5 / 120.65

Table A.7

Frequency and duration of ***sniff object*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	117 / 47.6 70 / 44.6 84 / 43.3 72 / 30.3 mean=85.75 / 41.45	59 / 34.7 31 /11.0 33 / 16.3 30 / 12.6 mean=38.25 / 18.65	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	126 / 50.4 84 / 52.4 54 / 18.6 66 / 26.6 mean=82.5 / 37.0	19 / 11.1 19 / 9.8 42 / 12.7 22 / 8.5 mean=25.5 / 10.53	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	56 / 20.7 41 / 25.2 44 / 18.8 69 / 47.5 mean=52.5 / 28.05	29 / 11.7 29 / 17.3 20 / 8.2 40 / 18.4 mean=29.5 / 13.9	NO OBJECTS PRESENT	NO OBJECTS PRESENT
average mean sum of means (for sessions 1 to 3)	73.58 / 35.5 220.75 / 106.5	31.03 / 14.36 93.25 / 43.08		

Table A.8

Mean frequency and duration of ***sniff object*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***sniff object*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
FIOS	frequency duration (seconds)	368.75 168.78	220.75 106.5	59.86 63.10
VIOS	frequency duration (seconds)	367.75 147.98	93.25 43.08	25.36 29.11
FIOE	frequency duration (seconds)	NO OBJECTS PRESENT		
VIOE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table A.9

Frequency and duration of ***sniff and touch object*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	158 / 306.8 51 / 137.1 111 / 319.4 62 / 116.0 Mean=95.5/ 219.83	60 / 98.1 54 / 31.5 73 / 121.8 113 / 213.6 mean = 75 / 116.25	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	126 / 284.2 52 / 156.5 96 / 198.8 49 / 70.9 mean=80.75/ 177.6	34 / 53.3 49 / 42.7 105 / 165.4 82 / 140.3 mean=67.5/ 100.43	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	130 / 189.3 35 / 59.9 90 / 200.6 43 / 53.6 mean=74.5/ 125.85	41 / 39.1 61 / 54.1 57 / 122.2 71 / 103.3 mean= 57.5 / 79.68	NO OBJECTS PRESENT	NO OBJECTS PRESENT
average mean sum of means (for sessions 1 to 3)	83.58 / 174.43 250.75 / 523.28	66.67 / 98.79 200 / 296.36		
SESSION 4	98 / 139.9 46 / 103.5 80 / 140.5 46 / 102.8 mean=67.5/ 121.68	91 / 155.5 127 / 105.4 93 / 166.9 95 / 170.0 mea=101.5/149.45	81 / 213.2 100 / 325.3 79 / 238.7 85 / 206.2 mea=86.25/245.85	109 / 224.1 123 / 213.8 56 / 142.1 125 / 413.8 me=103.25/248.45
SESSION 5	92 / 164.4 52 / 130.4 47 / 95.9 88 / 163.6 mea=69.75/138.58	72 / 189.5 139 / 218.7 48 / 132.8 77 / 116.0 mean= 84 / 164.25	52 / 113.8 122 / 322.6 71 / 134.5 57 / 153.1 mean= 75.5 / 181	67 / 145.1 96 / 143.7 30 / 52.3 80 / 207.0 mea=68.25/137.03
SESSION 6	84 / 157.6 50 / 87.6 57 / 117.1 90 / 230.3 mea=70.25/148.15	77 / 395.5 155 / 216.8 95 / 401.8 59 / 124.1 mean=96.5/ 284.55	50 / 181.3 101 / 446.8 44 / 49.7 77 / 225.7 mean= 68 / 225.88	78 / 155.0 84 / 112.9 98 / 206.5 104 / 520.7 mean= 91 / 248.78
average mean sum of means (for sessions 4 to 6)	69.17 / 136.14 207.5 / 408.41	94 / 199.42 282 / 598.25	76.58 / 217.58 229.75 / 652.73	87.5 / 211.42 262.5 / 634.26

Table A.10

Frequency and duration of ***sniff and touch object*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	75 / 137.9 31 / 86.4 51 / 130.6 35 / 68.8 mean=48 / 105.93	24 / 34.7 16 / 7.0 13 / 16.6 17 / 27.1 mean=17.5 / 21.35	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	96 / 236.3 42 / 139.2 41 / 103.5 40 / 52.2 mean=54.75 / 132.8	9 / 6.1 5 / 8.3 31 / 49.0 13 / 40.1 mean=14.5 / 25.88	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	84 / 134.9 16 / 38.5 37 / 83.0 39 / 49.2 mean=44 / 76.4	7 / 5.1 15 / 16.3 5 / 10.7 15 / 20.0 mean=10.5 / 13.03	NO OBJECTS PRESENT	NO OBJECTS PRESENT
average mean sum of means (for sessions 1 to 3)	48.92 / 105.04 146.75 / 315.13	14.17 / 20.09 42.5 / 60.26		

Table A.11

Mean frequency and duration of ***sniff and touch object*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***sniff and touch object*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FIOS	frequency duration (seconds)	250.75 523.28	146.75 315.13	58.52 60.22
VIOS	frequency duration (seconds)	200 296.36	42.5 60.26	21.25 20.33
FIOE	frequency duration (seconds)	NO OBJECTS PRESENT		
VIOE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table A.12

Frequency and duration of ***chew/bite object*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	26 / 35.4 4 / 4.0 2 / 1.4 0 / 0 mean= 8 / 10.2	0 / 0 0 / 0 1 / 0.7 1 / 1.2 mean= 0.5 / 1.9	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	13 / 42.6 4 / 7.3 2 / 8.7 0 / 0 mean= 4.75 / 14.65	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	9 / 13.5 0 / 0 5 / 21.5 0 / 0 mean = 3.5 / 8.75	0 / 0 0 / 0 0 / 0 1 / 0.5 mean= 0.25 / 0.13	NO OBJECTS PRESENT	NO OBJECTS PRESENT
average mean sum of means (for sessions 1 to 3)	5.42 / 11.2 16.25 / 33.6	0.25 / 0.68 0.75 / 2.03		
SESSION 4	12 / 60.7 1 / 1.2 7 / 11.3 4 / 19.5 mean= 6 / 23.18	5 / 9.1 6 / 19.5 11 / 16.5 15 / 53.4 mean= 9.25 / 24.63	1 / 0.4 0 / 0 2 / 3.6 2 / 1.7 mean= 1.25 / 1.43	0 / 0 0 / 0 1 / 0.7 19 / 47.3 mean= 5 / 12
SESSION 5	13 / 38.2 0 / 0 0 / 0 7 / 10.6 mean= 5 / 12.2	4 / 30.1 2 / 5.1 0 / 0 3 / 9.5 mean= 2.25 / 11.18	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 4 / 2.9 mean= 1 / 0.73
SESSION 6	11 / 24.4 2 / 3.8 0 / 0 10 / 31.7 mean= 5.75 / 14.98	8 / 27.1 5 / 9.0 13 / 59.0 4 / 5.6 mean= 7.5 / 25.18	0 / 0 15 / 50.1 0 / 0 2 / 5.6 mean= 4.25 / 13.93	5 / 22.8 1 / 0.7 1 / 1.8 5 / 12.4 mean= 3 / 9.43
average mean sum of means (for sessions 4 to 6)	5.58 / 16.79 16.75 / 50.36	6.33 / 20.33 19 / 60.99	1.83 / 5.12 5.5 / 15.36	3 / 7.39 9 / 22.16

Table A.13

Frequency and duration of ***chew/bite object*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	9 / 12.3 4 / 4.0 0 / 0 0 / 0 mean=3.25 / 4.08	0 / 0 0 / 0 0 / 0 1 / 1.2 mean=0.25 / 0.3	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	10 / 27.5 3 / 3.3 1 / 7.5 0 / 0 mean=3.5 / 9.58	0 / 0 0 / 0 0 / 0 0 / 0 mean=0 / 0	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	7 / 8.0 0 / 0 0 / 0 0 / 0 mean=1.75 / 2.0	0 / 0 0 / 0 0 / 0 1 / 0.5 mean=0.25 / 0.13	NO OBJECTS PRESENT	NO OBJECTS PRESENT
average mean sum of means (for sessions 1 to 3)	2.83 / 5.22 8.5 / 15.66	0.17 / 0.14 0.5 / 0.43		

Table A.14

Mean frequency and duration of ***chew/bite object*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***chew/bite object*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FIOS	frequency duration (seconds)	16.25 33.6	8.5 15.66	52.30 46.61
VIOS	frequency duration (seconds)	0.75 2.03	0.5 0.43	66.67 21.18
FIOE	frequency duration (seconds)	NO OBJECTS PRESENT		
VIOE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table A.15

Frequency and duration of ***propping*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	180 / 174.7 25 / 39.1 72 / 56.3 236 / 344.4 mea=128.25/153.63	150 / 205.6 89 / 47.0 112 / 130.2 172 / 119.5 mea=130.75/125.58	136 / 166.0 227 / 394.1 282 / 346.0 323 / 320.3 (mean=242/306.6)	110 / 121.0 532 / 597.6 878 / 408.6 179 / 261.1 mea=424.75/347.08
SESSION 2	200 / 224.3 38 / 80.5 138 / 168.5 223 / 272.9 mea=149.75/186.55	55 / 73.1 40 / 22.1 157 / 185.4 122 / 110.5 (mean=93.5/ 97.78)	123 / 197.7 149 / 217.0 168 / 281.3 209 / 189.9 mea=162.25/221.48	211 / 186.9 317 / 356.5 933 / 611.7 120 / 172.4 mea=395.25/331.88
SESSION 3	195 / 208.6 36 / 65.4 160 / 207.2 231 / 330.2 mean=155.5/202.85	104 / 149.9 20 / 12.4 175 / 234.3 140 / 125.0 mean=109.75/130.4	122 / 140.6 143 / 166.7 227 / 312.9 341 / 272.1 mea=208.25/223.08	152 / 107.7 295 / 405.5 953 / 639.2 104 / 158.5 (mean=376/327.73)
average mean sum of means (for sessions 1 to 3)	144.5 / 181.01 433.5 / 543.03	111.33 / 117.92 334 / 353.76	204.17 / 250.39 612.5 / 751.16	398.67 / 335.56 1196 / 1006.69
SESSION 4	202 / 201.0 65 / 127.4 168 / 232.6 214 / 376.5 mea=162.25/234.38	150 / 195.7 253 / 98.0 151 / 302.2 103 / 102.2 mea=164.25/174.53	160 / 214.9 137 / 213.4 257 / 347.8 263 / 206.8 mea=204.25/245.73	127 / 148.3 424 / 455.9 847 / 766.6 108 / 168.5 mean=376.5/384.83
SESSION 5	209 / 263.1 81 / 133.4 192 / 228.0 193 / 386.0 mea=168.75/252.63	119 / 159.9 147 / 69.6 181 / 340.5 107 / 101.3 mean=138.5/167.83	193 / 293.6 95 / 122.8 112 / 144.1 205 / 165.8 mea=151.25/181.58	125 / 143.4 386 / 435.6 904 / 1043.2 151 / 337.8 (mean=391.5 / 490)
SESSION 6	227 / 272.1 54 / 126.4 225 / 320.5 108 / 312.2 mean=153.5 / 257.8	90 / 186.1 224 / 144.0 150 / 240.8 134 / 133.4 mean=149.5/176.08	171 / 325.2 71 / 128.5 199 / 228.0 258 / 236.5 mea=174.75/229.55	168 / 177.5 494 / 579.8 697 / 740.4 69 / 164.9 mean=357 / 415.65
average mean sum of means (for sessions 4 to 6)	161.5 / 248.27 484.5 / 744.81	150.75 / 172.81 452.25 / 518.44	176.75 / 218.95 530.25 / 656.86	375 / 430.16 1125 / 1290.48

Table A.16

Frequency and duration of ***propping*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	108 / 107.0 14 / 23.9 20 / 17.6 134 / 233.0 mean=69 / 95.38	40 / 73.0 6 / 3.6 32 / 42.4 32 / 23.6 mean=27.5 / 35.65	88 / 119.9 116 / 255.2 86 / 128.9 140 / 189.8 mean=107.5/173.45	15 / 24.0 93 / 114.0 82 / 45.3 2 / 2.3 mean=48 / 46.4
SESSION 2	115 / 140.1 28 / 61.5 53 / 91.8 96 / 156.1 mean=73 / 112.38	8 / 12.4 0 / 0 41 / 52.2 9 / 7.4 mean=14.5 / 18	81 / 134.6 79 / 134.3 64 / 145.8 55 / 73.2 mean=69.75/121.98	48 / 48.0 32 / 51.6 61 / 45.4 2 / 3.5 mean=35.75 / 37.13
SESSION 3	109 / 120.8 6 / 12.6 56 / 107.4 146 / 251.8 mean=79.25/123.15	13 / 22.7 1 / 0.5 64 / 81.9 17 / 15.7 mean=23.75 / 30.2	76 / 92.9 77 / 104.8 103 / 195.7 23 / 28.2 mean=69.75 / 105.4	25 / 26.3 37 / 62.9 105 / 80.5 2 / 1.3 mean=42.25 / 42.75
average mean sum of means (for sessions 1 to 3)	73.75 / 110.30 221.25 / 330.91	21.92 / 27.95 65.75 / 83.85	82.33 / 133.61 247 / 400.83	42 / 42.09 126 / 126.28

Table A.17

Mean frequency and duration of ***propping*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***propping*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
FIOS	frequency	433.5	221.25	51.04
	duration (seconds)	543.03	330.91	60.94
VIOS	frequency	334	65.75	19.69
	duration (seconds)	353.76	83.85	23.70
FIOE	frequency	612.5	247	40.33
	duration (seconds)	751.16	400.83	53.36
VIOE	frequency	1196	126	10.54
	duration (seconds)	1006.69	126.28	12.54

Table A.18

Frequency and duration of ***jump at lid*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 1 / 0.3 92 / 35.3 mean=23.25 / 8.9	0 / 0 48 / 17.2 2 / 0.5 0 / 0 mean=12.5 / 4.43	102 / 31.6 113 / 34.5 0 / 0 16 / 5.1 mean=57.75 / 17.8
SESSION 2	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 13 / 4.2 45 / 15.8 mean=14.5 / 5	0 / 0 52 / 16.5 0 / 0 0 / 0 mean=13 / 4.13	124 / 37.3 60 / 17.0 18 / 4.8 10 / 3.1 mean=53 / 15.55
SESSION 3	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 8 / 2.9 56 / 20.0 mean=16 / 5.73	0 / 0 39 / 11.5 2 / 0.5 0 / 0 mean=10.25 / 3	92 / 26.6 56 / 16.6 6 / 1.5 5 / 1.6 mean=39.75 / 11.58
average mean sum of means (for sessions 1 to 3)	0 / 0 0 / 0	17.92 / 6.54 53.75 / 19.63	11.92 / 3.85 35.75 / 11.56	50.17 / 14.98 150.5 / 44.93
SESSION 4	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 4 / 1.2 28 / 8.6 mean=8 / 2.45	0 / 0 9 / 3.0 0 / 0 2 / 0.5 mean=2.75 / 0.88	23 / 7.1 43 / 11.2 8 / 2.0 0 / 0 mean=18.5 / 5.08
SESSION 5	2 / 0.6 6 / 1.6 0 / 0 0 / 0 mean=2 / 0.55	0 / 0 0 / 0 7 / 2.1 70 / 21.0 mean=19.25 / 5.78	0 / 0 14 / 4.2 0 / 0 0 / 0 mean=3.5 / 1.05	40 / 12.6 46 / 12.4 8 / 1.8 9 / 3.0 mean=25.75 / 7.45
SESSION 6	4 / 1.3 0 / 0 0 / 0 0 / 0 mean=1 / 0.33	0 / 0 0 / 0 10 / 3.0 94 / 31.1 mean=26 / 8.53	0 / 0 12 / 3.7 0 / 0 0 / 0 mean=3 / 0.93	56 / 15.7 39 / 10.5 24 / 6.7 1 / 0.4 mean=30 / 8.33
average mean sum of means (for sessions 4 to 6)	1 / 0.29 3 / 0.88	17.75 / 5.59 53.25 / 16.76	3.08 / 0.95 9.25 / 2.86	24.75 / 6.95 74.25 / 20.86

Table A.19

Frequency and duration of ***jump at lid*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	0 / 0	0 / 0	0 / 0	14 / 4.6
	0 / 0	0 / 0	35 / 12.4	13 / 4.3
	0 / 0	1 / 0.3	0 / 0	0 / 0
	0 / 0	12 / 4.5	0 / 0	0 / 0
	mean=0 / 0	mean=3.25 / 1.2	mean=8.75 / 3.1	mean=6.75 / 2.23
SESSION 2	0 / 0	0 / 0	0 / 0	16 / 4.9
	0 / 0	0 / 0	40 / 12.6	3 / 0.8
	0 / 0	3 / 0.8	0 / 0	1 / 0.2
	0 / 0	1 / 0.3	0 / 0	0 / 0
	mean=0 / 0	mean=1 / 0.28	mean=10 / 3.15	mean=5 / 1.48
SESSION 3	0 / 0	0 / 0	0 / 0	9 / 2.6
	0 / 0	0 / 0	29 / 8.3	2 / 0.6
	0 / 0	4 / 1.3	1 / 0.2	3 / 0.7
	0 / 0	8 / 2.8	0 / 0	0 / 0
	mean=0 / 0	mean=3 / 1.03	mean=7.5 / 2.13	mean=3.5 / 0.98
average mean	0 / 0	2.42 / 0.84	8.75 / 2.79	5.08 / 1.56
sum of means (for sessions 1 to 3)	0 / 0	7.25 / 2.51	26.25 / 8.38	15.25 / 4.69

Table A.20

Mean frequency and duration of ***jump at lid*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***jump at lid*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FIOS	frequency duration (seconds)	No jump at lid	No jump at lid	No jump at lid
VIOS	frequency	53.75	7.25	13.49
	duration (seconds)	19.63	2.51	12.79
FIOE	frequency	35.75	26.25	73.43
	duration (seconds)	11.56	8.38	72.49
VIOE	frequency	150.5	15.25	10.13
	duration (seconds)	44.93	4.69	10.44

Table A.21

Frequency and duration of ***displacement*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	83 / 62.0 27 / 67.9 79 / 47.3 53 / 44.0 (mean= 60.5 / 55.3)	28 / 18.6 8 / 4.5 23 / 19.5 33 / 23.7 (mean= 23 / 16.58)	21 / 59.4 66 / 60.5 53 / 56.2 12 / 22.1 (mean= 38 / 49.55)	74 / 56.5 11 / 5.2 9 / 14.6 90 / 80.9 (mean= 46 / 39.3)
SESSION 2	75 / 49.8 30 / 63.4 85 / 63.2 52 / 60.4 (mean= 60.5 / 59.2)	31 / 29.9 4 / 2.5 39 / 24.6 75 / 70.6 (mean=37.25/ 31.9)	27 / 82.7 53 / 74.8 75 / 71.8 12 / 20.3 (mean=41.75/ 62.4)	94 / 80.4 36 / 14.2 8 / 16.3 93 / 122.7 (mean=57.75/ 58.4)
SESSION 3	82 / 79.0 34 / 61.4 58 / 57.2 57 / 91.5 (mean=57.75/72.28	29 / 25.5 10 / 9.3 42 / 32.8 60 / 50.6 (mean=35.25/29.55	33 / 97.4 66 / 96.3 90 / 136.6 10 / 22.3 (mean=49.75/88.15	91 / 80.9 28 / 13.6 6 / 16.5 101 / 123.9 (mean= 56.5/58.73)
average mean sum of means (for sessions 1 to 3)	59.58 / 62.26 178.75 / 186.78	31.83 / 26.01 95.5 / 78.03	43.17 / 66.7 129.5 / 200.1	53.42 / 52.14 160.25 / 156.43
SESSION 4	51 / 55.6 26 / 37.9 71 / 67.1 55 / 65.8 (mean=50.75/ 56.6)	20 / 23.4 25 / 20.0 71 / 58.6 57 / 66.6 (mean=43.25/42.15	12 / 36.4 68 / 72.5 73 / 85.3 7 / 17.8 (mean= 40 / 53)	70 / 100.0 18 / 10.5 6 / 21.8 85 / 87.7 (mean=44.75 / 55)
SESSION 5	60 / 72.5 28 / 46.9 72 / 71.8 59 / 64.2 (mean=54.75/63.85	28 / 36.7 14 / 31.4 43 / 46.5 61 / 75.1 (mean=36.5/ 47.43)	18 / 66.0 64 / 183.4 88 / 286.6 11 / 35.1 mean=45.25/142.78	66 / 108.7 24 / 35.5 5 / 39.0 96 / 137.2 (mean=47.75/ 80.1)
SESSION 6	56 / 66.2 51 / 105.0 62 / 103.2 54 / 140.2 mean=55.75/103.65	39 / 50.7 20 / 34.7 38 / 59.2 57 / 97.6 (mean=38.5/ 60.55)	12 / 47.0 66 / 297.9 94 / 154.1 19 / 27.6 mean=47.75/131.65	85 / 177.4 23 / 29.8 11 / 42.9 78 / 160.4 mean=49.25/102.63
average mean sum of means (for sessions 4 to 6)	53.75 / 74.7 161.25 / 224.1	39.42 / 50.04 118.25 / 150.13	44.33 / 109.14 133 / 327.43	47.25 / 79.24 141.75 / 237.73

Table A.22

Frequency and duration of ***displacement*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	33 / 30.9 13 / 34.0 28 / 22.2 39 / 35.6 mean=28.25 / 30.68	12 / 6.9 4 / 3.2 4 / 2.3 7 / 8.3 mean=6.75 / 5.18	16 / 41.5 31 / 46.4 22 / 19.3 10 / 18.6 mean=19.75 / 31.45	7 / 2.7 1 / 0.5 3 / 0.8 1 / 0.3 mean=3 / 1.08
SESSION 2	34 / 23.7 23 / 53.1 23 / 26.2 35 / 43.4 mean=28.75 / 36.6	9 / 6.6 0 / 0 10 / 3.3 11 / 16.8 mean=7.5 / 6.68	19 / 69.6 27 / 37.8 37 / 43.8 7 / 4.7 mean=22.5 / 38.98	8 / 21.1 6 / 2.7 1 / 0.3 2 / 1.6 mean=4.25 / 6.43
SESSION 3	31 / 38.0 16 / 23.4 23 / 34.1 50 / 87.3 mean=30 / 45.7	6 / 2.4 1 / 0.2 9 / 4.2 12 / 12.3 mean=7 / 4.78	22 / 70.5 35 / 65.3 40 / 83.3 3 / 5.0 mean=25 / 56.03	9 / 5.2 9 / 6.4 0 / 0 3 / 6.5 mean=5.25 / 4.53
average mean sum of means (for sessions 1 to 3)	29 / 37.66 87 / 112.98	7.08 / 5.55 21.25 / 16.64	22.42 / 42.15 67.25 / 126.46	4.17 / 4.01 12.5 / 12.04

Table A.23

Mean frequency and duration of ***displacement*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***displacement*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
FIOS	frequency	178.75	87	48.67
	duration (seconds)	186.78	112.98	60.49
VIOS	frequency	95.5	21.25	22.25
	duration (seconds)	78.03	16.64	21.33
FIOE	frequency	129.5	67.25	51.93
	duration (seconds)	200.1	126.46	63.20
VIOE	frequency	160.25	12.5	7.8
	duration (seconds)	156.43	12.04	7.7

Table A.24

Frequency and duration of ***digging/burying*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	27 / 27.7 26 / 10.5 7 / 2.3 13 / 8.9 (mean=18.25/12.35	54 / 26.8 18 / 13.4 4 / 0.8 3 / 1.1 (mean=19.75/10.53	3 / 2.3 26 / 42.4 22 / 18.3 68 / 30.0 (mean=29.75/23.25	2 / 0.4 5 / 3.4 0 / 0 3 / 3.5 (mean=2.5 / 1.83)
SESSION 2	11 / 8.4 5 / 2.1 1 / 0.4 10 / 4.4 (mean=6.75 / 3.83)	21 / 12.4 21 / 12.3 12 / 4.9 5 / 1.2 (mean=14.75 / 7.7)	3 / 2.4 14 / 12.0 17 / 9.5 44 / 13.0 (mean=19.5 / 9.23)	9 / 3.9 13 / 10.6 0 / 0 4 / 3.2 (mean=6.5 / 4.43)
SESSION 3	1 / 2.3 15 / 5.3 3 / 1.0 6 / 1.4 (mean=6.25 / 2.5)	23 / 6.3 27 / 17.3 7 / 4.2 21 / 6.6 (mean=19.5 / 8.6)	0 / 0 23 / 33.5 24 / 12.0 12 / 4.7 (mean=14.75/12.55	6 / 5.0 12 / 11.4 0 / 0 2 / 0.4 (mean=5 / 4.2)
average mean sum of means (for sessions 1 to 3)	10.42 / 6.23 31.25 / 18.68	18 / 8.94 54 / 26.83	21.33 / 15.01 64 / 45.03	4.67 / 3.49 14 / 10.46
SESSION 4	2 / 66.0 5 / 1.6 0 / 0 11 / 2.3 (mean=4.5 / 17.48)	29 / 8.4 23 / 4.2 7 / 2.2 15 / 2.5 (mean=18.5 / 4.33)	2 / 0.9 51 / 41.5 32 / 20.4 5 / 0.9 (mean=22.5/15.93)	6 / 1.6 12 / 7.3 1 / 0.1 4 / 1.1 (mean=5.75 / 2.53)
SESSION 5	24 / 17.8 16 / 2.5 2 / 0.8 22 / 5.2 (mean=16 / 6.58)	33 / 7.9 22 / 5.1 21 / 9.5 31 / 5.7 (mean=26.75/ 7.05)	6 / 3.5 14 / 12.3 22 / 12.0 19 / 2.6 (mean=15.25 / 7.6)	6 / 2.4 12 / 6.0 2 / 0.0 7 / 6.0 (mean=6.75 / 3.6)
SESSION 6	37 / 42.3 9 / 8.0 5 / 3.2 32 / 18.9 (mean=20.75/18.1)	34 / 10.7 26 / 12.6 31 / 12.9 13 / 1.8 (mean=26 / 9.5)	5 / 2.5 26 / 13.3 25 / 16.7 39 / 39.0 (mean=23.75/17.88	6 / 2.1 5 / 3.2 4 / 2.3 6 / 1.3 (mean=5.25 / 2.23)
average mean sum of means (for sessions 4 to 6)	13.75 / 14.05 41.25 / 42.16	23.75 / 6.96 71.25 / 20.88	20.5 / 13.8 61.5 / 41.41	5.92 / 2.79 17.75 / 8.36

Table A.25

Frequency and duration of ***digging/burying*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	21 / 23.2 19 / 8.0 0 / 0 11 / 7.8 mean=12.75 / 9.75	13 / 4.5 6 / 3.2 1 / 0.4 0 / 0 mean=5 / 2.03	3 / 2.3 16 / 31.1 9 / 6.6 52 / 25.2 mean=20 / 16.3	0 / 0 0 / 0 0 / 0 0 / 0 mean=0 / 0
SESSION 2	10 / 7.7 4 / 1.5 1 / 0.4 10 / 4.4 mean=6.25 / 3.5	8 / 6.3 6 / 1.8 6 / 2.6 4 / 0.9 mean=6 / 2.9	2 / 0.8 14 / 12.0 12 / 6.9 42 / 12.7 mean=17.5 / 8.1	5 / 2.3 0 / 0 0 / 0 0 / 0 mean=1.25 / 0.58
SESSION 3	11 / 9.6 10 / 3.4 2 / 0.7 5 / 1.0 mean=7 / 3.68	6 / 1.4 9 / 7.5 3 / 2.1 6 / 1.5 mean=6 / 3.13	0 / 0 23 / 33.5 18 / 10.4 2 / 0.7 mean=10.75 / 11.15	3 / 3.4 0 / 0 0 / 0 0 / 0 mean=0.75 / 0.85
average mean sum of means (for sessions 1 to 3)	8.67 / 5.64 26 / 16.93	5.67 / 2.69 17 / 8.06	16.08 / 11.85 48.25 / 35.55	0.67 / 0.48 2 / 1.43

Table A.26

Mean frequency and duration of ***digging/burying*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***digging/burying*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
FIOS	frequency	31.25	26	83.2
	duration (seconds)	18.68	16.93	90.63
VIOS	frequency	54	17	31.48
	duration (seconds)	26.83	8.06	30.04
FIOE	frequency	64	48.25	75.39
	duration (seconds)	45.03	35.55	78.95
VIOE	frequency	14	2	14.29
	duration (seconds)	10.46	1.43	13.67

Table A.27

Frequency and duration of ***rearing*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	28 / 18.4 38 / 57.5 71 / 53.0 71 / 83.9 (mean=52 / 53.2)	18 / 16.1 2 / 1.2 60 / 74.3 43 / 34.0 (mean=30.75/ 31.4)	146 / 199.8 168 / 170.9 127 / 169.7 92 / 77.9 mea=133.25/154.58	374 / 428.8 235 / 176.1 39 / 24.9 113 / 105.0 mean=190.25/183.7
SESSION 2	68 / 49.0 60 / 117.5 143 / 138.7 124 / 170.8 (mean=98.75 / 119)	12 / 15.6 7 / 2.5 126 / 105.2 175 / 234.9 (mean=80 / 89.55)	188 / 404.0 237 / 325.7 124 / 104.0 62 / 77.9 mean=152.75/227.9	322 / 226.3 284 / 241.7 74 / 37.3 96 / 115.4 (mean=194/155.18)
SESSION 3	144 / 120.7 111 / 297.9 115 / 131.8 65 / 104.3 mea=108.75/163.68	21 / 25.1 10 / 4.5 63 / 45.4 164 / 142.0 (mean=64.5/ 54.25)	140 / 268.9 270 / 354.2 105 / 131.3 100 / 112.9 mea=153.75/216.83	409 / 440.9 356 / 292.3 37 / 21.1 90 / 112.0 (mean=223/216.58)
average mean sum of means (for sessions 1 to 3)	86.5 / 111.96 259.5 / 335.88	58.42 / 58.4 175.25 / 175.2	146.58 / 199.77 439.75 / 599.31	202.42 / 185.15 607.25 / 555.46
SESSION 4	166 / 135.2 99 / 235.5 226 / 259.0 55 / 61.9 (mean=136.5/172.9	73 / 103.0 41 / 35.1 76 / 90.7 160 / 189.9 (mean=87.5/104.68	93 / 118.5 197 / 190.8 101 / 87.6 120 / 126.4 mea=127.75/130.83	292 / 420.9 270 / 173.4 136 / 96.3 62 / 54.5 (mean=190/186.28)
SESSION 5	201 / 215.3 141 / 353.1 338 / 548.2 90 / 130.0 mean=192.5/311.65	58 / 100.2 114 / 102.6 176 / 261.5 158 / 220.1 (mean=126.5/171.1	151 / 294.7 253 / 511.2 230 / 451.7 113 / 118.6 mea=186.75/344.05	298 / 527.5 284 / 282.0 91 / 61.7 62 / 42.1 mea=183.75/228.33
SESSION 6	215 / 228.2 148 / 571.7 238 / 289.2 71 / 90.2 (mean=168/294.83)	51 / 53.4 108 / 134.4 106 / 153.2 192 / 339.2 mea=114.25/170.05	174 / 355.2 147 / 379.4 297 / 550.6 88 / 66.2 mean=176.5/337.85	281 / 447.1 308 / 307.0 168 / 162.7 76 / 120.9 mea=208.25/259.43
average mean sum of means (for sessions 4 to 6)	165.67 / 259.79 497 / 779.38	109.42 / 148.61 328.25 / 445.83	163.67 / 270.91 491 / 812.73	194 / 224.68 582 / 674.04

Table A.28

Frequency and duration of ***rearing*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	20 / 13.3 19 / 36.3 27 / 22.8 54 / 65.8 mean=30 / 34.55	6 / 3.6 0 / 0 20 / 18.1 7 / 4.0 mean=8.25 / 6.43	110 / 165.0 74 / 77.2 58 / 84.4 64 / 59.4 mean=76.5 / 96.5	57 / 82.7 38 / 31.5 10 / 8.1 1 / 0.6 mean=26.5 / 30.73
SESSION 2	31 / 24.4 40 / 60.3 42 / 40.6 95 / 140.2 mean=52 / 66.38	7 / 9.8 0 / 0 34 / 21.9 31 / 52.3 mean=18 / 21	138 / 331.3 126 / 186.0 60 / 55.4 27 / 25.1 mean=87.75/149.45	44 / 36.4 21 / 21.1 11 / 5.5 3 / 1.7 mean=19.75 / 16.18
SESSION 3	81 / 67.3 34 / 123.4 49 / 60.4 60 / 90.7 mean=56 / 85.45	1 / 1.2 1 / 0.4 30 / 22.9 30 / 31.2 mean=15.5 / 13.93	88 / 172.9 145 / 206.2 54 / 67.6 24 / 45.8 mean=77.75/123.13	63 / 80.9 42 / 38.8 16 / 10.3 5 / 8.0 mean=31.5 / 34.5
average mean sum of means (for sessions 1 to 3)	46 / 62.13 138 / 186.38	13.92 / 13.79 41.75 / 41.36	80.67 / 123.03 242 / 369.08	25.92 / 27.14 77.75 / 81.41

Table A.29

Mean frequency and duration of ***rearing*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***rearing*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FIOS	frequency	259.5	138	53.18
	duration (seconds)	335.88	186.38	55.49
VIOS	frequency	175.25	41.75	23.82
	duration (seconds)	175.2	41.36	23.61
FIOE	frequency	439.75	242	55.03
	duration (seconds)	599.31	369.08	61.58
VIOE	frequency	607.25	77.75	12.80
	duration (seconds)	555.46	81.41	14.66

Table A.30

Frequency and duration of ***pica*** for each rat in Experiment 1, in each session (sessions 1-3 are ***fixed-interval*** or ***variable-interval*** sessions, and sessions 4-6 are extinction sessions).

	FIOS (A1-A4)	VIOS (B1-B4)	FIOE (C1-C4)	VIOE (D1-D4)
SESSION 1	1 / 5.0 16 / 61.1 0 / 0 2 / 3.0 (mean=4.75 /17.28)	17 / 42.4 10 / 24.8 0 / 0 1 / 10.8 (mean=7 / 19.5)	1 / 9.1 2 / 0.0 0 / 0 16 / 61.1 (mean=4.75 /17.55)	0 / 0 0 / 0 0 / 0 0 / 0 (mean=0 / 0)
SESSION 2	0 / 0 14 / 69.1 0 / 0 3 / 8.0 (mean=4.25 /19.28)	15 / 83.0 6 / 28.2 0 / 0 4 / 25.5 (mean=6.25 /34.18)	0 / 0 1 / 3.9 0 / 0 59 / 193.9 (mean=15 /49.45)	0 / 0 0 / 0 0 / 0 0 / 0 (mean=0 / 0)
SESSION 3	1 / 2.3 16 / 74.3 0 / 0 0 / 0 (mean=4.25 /19.15)	14 / 70.2 14 / 29.5 0 / 0 10 / 45.7 (mean=9.5 /36.35)	0 / 0 0 / 0 0 / 0 23 / 54.9 (mean=5.75 /13.73)	0 / 0 0 / 0 0 / 0 0 / 0 (mean=0 / 0)
average mean sum of means (for sessions 1 to 3)	4.42 / 18.57 13.25 / 55.71	7.58 / 30.01 22.75 / 90.03	8.5 / 26.91 25.5 / 80.73	0 / 0 0 / 0
SESSION 4	2 / 66.0 28 / 227.6 0 / 0 2 / 5.3 (mean=8 /74.73)	32 / 123.4 7 / 50.2 0 / 0 14 / 34.8 (mean=13.25 /52.1)	2 / 13.9 5 / 31.8 0 / 0 17 / 40.4 (mean=6 /21.53)	2 / 14.8 0 / 0 0 / 0 1 / 1.0 (mean=0.75 /3.95)
SESSION 5	12 / 81.9 26 / 261.6 0 / 0 12 / 115.4 (mean=12.5/114.73	29 / 162.1 14 / 106.8 3 / 27.7 7 / 58.1 (mean=13.25/88.68	0 / 0 1 / 19.6 0 / 0 37 / 95.8 (mean=9.5/28.85)	0 / 0 0 / 0 0 / 0 0 / 0 (mean=0 / 0)
SESSION 6	9 / 113.3 26 / 224.8 1 / 3.1 44 / 277.4 (mean=20 /154.65)	56 / 217.1 18 / 191.0 16 / 78.4 5 / 13.8 mean=23.75/125.08	0 / 0 8 / 67.9 0 / 0 42 / 198.2 (mean=12.5/66.53)	4 / 49.0 2 / 0.0 1 / 16.1 31 / 265.9 (mean=9.5/82.75)
average mean sum of means (for sessions 4 to 6)	13.5 / 114.71 40.5 / 344.11	16.75 / 88.62 50.25 / 265.86	9.33 / 38.97 28 / 116.91	3.42 / 28.9 10.25 / 86.7

Table A.31

Frequency and duration of ***pica*** during the PRPs, for each rat in Experiment 1 in each ***fixed-interval*** or ***variable-interval*** session (sessions 1-3).

	FIOS (A1-A4)	**VIOS (B1-B4)**	**FIOE (C1-C4)**	**VIOE (D1-D4)**
SESSION 1	0 / 0 12 / 50.3 0 / 0 2 / 3.0 mean=3.5 / 13.33	5 / 10.0 2 / 3.8 0 / 0 0 / 0 mean=1.75 / 3.45	1 / 9.1 0 / 0 0 / 0 13 / 55.5 mean=3.5 / 16.15	0 / 0 0 / 0 0 / 0 0 / 0 mean=0 / 0
SESSION 2	0 / 0 11 / 47.4 0 / 0 1 / 0.5 mean=3 / 11.98	6 / 49.4 2 / 11.2 0 / 0 0 / 0 mean=2 / 15.15	0 / 0 1 / 3.9 0 / 0 51 / 168.8 mean=13 / 43.18	0 / 0 0 / 0 0 / 0 0 / 0 mean=0 / 0
SESSION 3	0 / 0 16 / 74.3 0 / 0 0 / 0 mean=4 / 18.58	4 / 24.7 5 / 12.5 0 / 0 4 / 14.0 mean=3.25 / 12.8	0 / 0 0 / 0 0 / 0 2 / 11.5 mean=0.5 / 2.88	0 / 0 0 / 0 0 / 0 0 / 0 mean=0 / 0
average mean sum of means (for sessions 1 to 3)	3.5 / 14.63 10.5 / 43.89	2.33 / 10.47 7 / 31.4	5.67 / 20.74 17 / 62.21	0 / 0 0 / 0

Table A.32

Mean frequency and duration of ***pica*** during the PRPs (for all four groups in Experiment 1) summed over the first three sessions (***fixed-interval*** or ***variable-interval***), as a percentage of the total mean frequency and duration of ***pica*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FIOS	frequency duration (seconds)	13.25 55.71	10.5 43.89	79.25 78.79
VIOS	frequency duration (seconds)	22.75 90.03	7 31.4	30.77 34.88
FIOE	frequency duration (seconds)	25.5 80.73	17 62.21	66.67 77.06
VIOE	frequency duration (seconds)	No Pica	No Pica	No Pica

Table A.33

The mean frequency and duration of behaviours for the "object" grouping variable for every session in Experiment 1 ("OS"= objects first present during schedule, *i.e.* FIOS and VIOS groups; "OE"= objects first present during extinction, *i.e.* FIOE and VIOE groups).

BEHAVIOURAL MEASURE	**SESSION 1 OS / OE**	**SESSION 2 OS / OE**	**SESSION 3 OS / OE**	**SESSION 4 OS / OE**	**SESSION 5 OS / OE**	**SESSION 6 OS / OE**
FREQUENCIES						
Digging/Burying	19/ 16.13	10.75/ 13	12.88/ 9.88	11.5/ 14.13	21.38/ 11	23.37/ 14.5
Rearing	41.38/161.75	89.38/173.38	86.63/188.38	112/ 158.88	159.5/185.25	141.13/192.38
Propping	129.5/333.38	121.63/278.75	132.63/292.13	163.25/290.38	153.63/271.38	151.5/265.88
Displacement	41.75/ 42	48.88/ 49.75	46.5/ 53.13	47/ 42.38	45.63/ 46.5	47.13/ 48.5
Bar-related behaviour	282/ 374	316.63/485.63	486.25/518.13	503.25/ 339	318.88/273.75	258.5/ 227.13
Sniff object	151.5/ n/a	113.88/ n/a	102.88/ n/a	124.88/ 127.5	109.13/ 91.13	111.63/107.75
Sniff & Touch object	85.25/ n/a	74.13/ n/a	66/ n/a	84.5/ 94.75	76.88/ 71.88	83.38/ 79.5
Bar-pressing	665.13/782.13	880/ 1147.13	1149.4/1376.4	1037.1/1003.4	637.63/883.25	245.75/ 413.5
DURATIONS (in seconds)						
Digging/Burying	11.44/ 12.54	5.77/ 6.83	5.55/ 8.38	10.91/ 9.23	6.82/ 5.6	13.8/ 10.06
Rearing	42.3/ 169.14	104.28/191.54	108.97/216.71	138.79/158.56	241.38/286.19	232.44/298.64
Propping	139.61/326.84	142.17/276.68	166.63/275.41	204.46/315.28	210.23/335.79	216.94/322.6
Displacement	35.94/ 44.43	45.55/ 60.4	50.92/ 73.44	49.38/ 54	55.64/ 111.44	82.1/ 117.14
Bar-related behaviour	137.91/195.69	180.92/229.13	216.53/243.93	220.76/137.14	187.22/131.06	162.94/126.77
Sniff object	66.37/ n/a	47.28/ n/a	44.74/ n/a	52.04/ 52.94	47.53/ 34.33	45.65/ 42.28
Sniff & Touch object	168.04/ n/a	139.02/ n/a	102.77/ n/a	135.57/247.15	151.42/159.02	216.35/237.33
Bar-pressing	127.46/160.54	175.82/186.79	198.22/ 208	164.69/140.68	100.93/111.4	46.09/ 62.38

Table A.34

The mean frequency and duration of behaviours for the "schedule" grouping variable for every session in Experiment 1 ("FI"= ***fixed-interval*** groups, *i.e.* FIOS and FIOE groups; "VI"= ***variable-interval*** groups, *i.e.* VIOS and VIOE groups).

BEHAVIOURAL MEASURE	**SESSION 1 FI / VI**	**SESSION 2 FI / VI**	**SESSION 3 FI / VI**	**SESSION 4 FI / VI**	**SESSION 5 FI / VI**	**SESSION 6 FI / VI**
FREQUENCIES						
Digging/Burying	24/ 11.13	13.13/ 10.63	10.5/ 12.25	13.5/ 12.13	15.63/ 16.75	22.25/ 15.63
Rearing	92.63/ 110.5	125.75/ 137	131.25/143.75	132.13/138.75	189.63/155.13	172.25/161.25
Propping	185.13/277.75	156/ 244.38	181.88/242.88	183.25/270.38	160/ 265	164.13/253.25
Displacement	49.25/ 34.5	51.13/ 47.5	53.75/ 45.88	45.38/ 44	50/ 42.13	51.75/ 43.88
Bar-related behaviour	416.5/ 239.5	415.38/386.88	542/ 462.38	503/ 339.25	312.25/280.38	268/ 217.63
Sniff object	158.5/ 144.5	125.75/ 102	84.5/ 121.25	116.5/ 135.88	95.88/ 104.38	102/ 117.38
Sniff & Touch object	95.5/ 75	80.75/ 67.5	74.5/ 57.5	76.88/ 102.38	72.63/ 76.13	69.13/ 93.75
Bar-pressing	718.88/728.38	963/ 1064.13	1278.88/1246.88	1228/ 812.5	847.75/673.13	404.13/255.13
DURATIONS (in seconds)						
Digging/Burying	17.8/ 6.18	6.53/ 6.07	7.53/ 6.4	16.71/ 3.43	7.09/ 5.33	17.99/ 5.87
Rearing	103.89/107.55	173.45/122.37	190.26/135.42	151.87/145.48	327.85/199.72	316.34/214.74
Propping	230.12/236.33	204.02/214.83	212.97/229.07	240.06/279.68	217.11/328.92	243.68/295.87
Displacement	52.43/ 27.94	60.8/ 45.15	80.22/ 44.14	54.8/ 48.58	103.32/63.77	117.65/81.59
Bar-related behaviour	237.02/ 96.58	257.95/152.09	286.36/174.11	198.51/159.39	164.72/153.56	158.68/131.03
Sniff object	72.48/ 60.25	57.1/ 37.45	39.2/ 50.28	55.28/ 49.7	41.54/ 40.32	44.43/ 43.5
Sniff & Touch object	219.83/116.25	177.6/ 100.43	125.85/ 79.68	183.77/198.95	159.79/150.64	187.02/266.67
Bar-pressing	135.06/152.94	164.24/198.37	189.49/216.73	172.41/132.97	108.5/ 103.83	60.86/ 47.62

Table A.35
The mean frequency and duration of behaviours for the "session" grouping variable for all groups in Experiment 1.

BEHAVIOURAL MEASURE	**SESSION 1**	**SESSION 2**	**SESSION 3**	**SESSION 4**	**SESSION 5**	**SESSION 6**
FREQUENCIES						
Digging/Burying	17.56	11.88	11.38	12.81	16.19	18.94
Rearing	101.56	131.38	137.5	135.44	172.38	166.75
Propping	231.44	200.19	212.38	226.81	212.5	208.69
Displacement	41.88	49.31	49.81	44.69	46.06	47.81
Bar-related behaviour	328	401.13	502.19	421.13	296.31	242.81
Sniff object	151.5	113.88	102.88	126.19	100.13	109.69
Sniff & Touch object	85.25	74.13	66	89.63	74.38	81.44
Bar-pressing	723.63	1013.56	1262.88	1020.25	760.44	329.63
DURATIONS (in seconds)						
Digging/Burying	11.99	6.3	6.96	10.07	6.21	11.93
Rearing	105.72	147.91	162.84	148.67	263.78	265.54
Propping	233.22	209.42	221.02	259.87	273.01	269.77
Displacement	40.18	52.98	62.18	51.69	83.54	99.62
Bar-related behaviour	166.8	205.02	230.23	178.95	159.14	144.85
Sniff object	66.37	47.28	44.74	52.49	40.93	43.96
Sniff & Touch object	168.04	139.02	102.77	191.36	155.22	226.84
Bar-pressing	144	181.3	203.11	152.69	106.16	54.24

Table A.36
The mean frequency and duration of behaviours during the PRPs for the "object" grouping variable for each ***fixed-interval*** or ***variable-interval*** session in Experiment 1 ("OS"= objects present during schedule, *i.e.* FIOS and VIOS groups; "OE"= objects absent during schedule, *i.e.* FIOE and VIOE groups).

BEHAVIOURAL MEASURE	**SESSION 1 OS / OE**	**SESSION 2 OS / OE**	**SESSION 3 OS / OE**
FREQUENCIES			
Digging/Burying	8.88 / 10	6.13 / 9.38	6.5 / 5.75
Rearing	19.13 / 51.5	35 / 53.75	35.75 / 54.63
Propping	48.25 / 77.75	43.75 / 52.75	51.5 / 56
Displacement	17.5 / 11.38	18.13 / 13.38	18.5 / 15.13
Bar-related behaviour	68.63 / 70.38	68.13 / 58.38	72 / 66.75
Sniff object	62 / n/a	54 / n/a	41 / n/a
Sniff & Touch object	32.75 / n/a	34.63 / n/a	27.25 / n/a
DURATIONS (in seconds)			
Digging/Burying	5.89 / 8.15	3.2 / 4.34	3.41 / 6
Rearing	20.49 / 63.62	43.69 / 82.82	49.69 / 78.82
Propping	65.52 / 109.93	65.19 / 79.56	76.68 / 74.08
Displacement	17.93 / 16.27	21.64 / 22.71	25.24 / 30.28
Bar-related behaviour	60.72 / 98.6	89.03 / 93.84	83.66 / 100.51
Sniff object	30.05 / n/a	23.77 / n/a	20.98 / n/a
Sniff & Touch object	63.64 / n/a	79.34 / n/a	44.72 / n/a

Table A.37

The mean frequency and duration of behaviours during the PRPs for the "schedule" grouping variable for each ***fixed-interval*** or ***variable-interval*** session in Experiment 1 ("FI"= ***fixed-interval*** groups, *i.e.* FIOS and FIOE groups; "VI"= ***variable-interval*** groups, *i.e.* VIOS and VIOE groups).

BEHAVIOURAL MEASURE	SESSION 1 FI / VI	SESSION 2 FI / VI	SESSION 3 FI / VI
FREQUENCIES			
Digging/Burying	16.38 / 2.5	11.88 / 3.63	8.88 / 3.38
Rearing	53.25 / 17.38	69.88 / 18.88	66.88 / 23.5
Propping	88.25 / 37.75	71.38 / 25.13	74.5 / 33
Displacement	24 / 4.88	25.63 / 5.88	27.5 / 6.13
Bar-related behaviour	98.75 / 40.25	86.88 / 39.63	87.5 / 51.25
Sniff object	85.75 / 38.25	82.5 / 25.5	52.5 / 29.5
Sniff & Touch object	48 / 17.5	54.75 / 14.5	44 / 10.5
DURATIONS (in seconds)			
Digging/Burying	13.03 / 1.02	5.8 / 1.74	7.42 / 1.99
Rearing	65.53 / 18.58	107.92 / 18.59	104.29 / 24.22
Propping	134.42 / 41.03	117.18 / 27.57	114.28 / 36.48
Displacement	31.07 / 3.13	37.79 / 6.56	50.87 / 4.66
Bar-related behaviour	131.17 / 28.15	155.08 / 27.79	146.53 / 36.63
Sniff object	41.45 / 18.65	37 / 10.53	28.05 / 13.9
Sniff & Touch object	105.93 / 21.35	132.8 / 25.88	76.4 / 13.03

Table A.38

The mean frequency and duration of behaviours during the PRPs for the "session" grouping variable for all groups in Experiment 1.

BEHAVIOURAL MEASURE	SESSION 1	SESSION 2	SESSION 3
FREQUENCIES			
Digging/Burying	9.44	7.75	6.13
Rearing	35.31	44.38	45.19
Propping	63	48.25	53.75
Displacement	14.44	15.75	16.81
Bar-related behaviour	69.5	63.25	69.38
Sniff object	62	54	41
Sniff & Touch object	32.75	34.63	27.25
DURATIONS (in seconds)			
Digging/Burying	7.02	3.77	4.7
Rearing	42.05	63.25	64.25
Propping	87.72	72.37	75.38
Displacement	17.1	22.17	27.76
Bar-related behaviour	79.66	91.43	91.58
Sniff object	30.05	23.77	20.98
Sniff & Touch object	63.64	79.34	44.72

APPENDIX B

This section provides the frequency and duration scores for every behavioural category in Experiment 2, for all four groups of rats (for every session & during the PRPs), and for each of the three grouping variables.

The material included in Appendix B consists of a set of three tables per behavioural category scored. The four rats per group are included in the same cell of the table (e.g. the four rats in the DRLOS group are lumped together). This set of three tables provides the following information:

(1) frequency and duration of the behaviour for each rat in each session (i.e., raw data), the group mean for each session, the average mean and sum of means for sessions 1-3 and 4-6 (for each group of rats);

(2) frequency and duration of the behaviour during the PRPs for each rat in each ***DRL*** or ***variable-ratio*** session (i.e., raw data), the average mean and sum of means for sessions 1-3 (for each group of rats); and

(3) frequency and duration of the behaviour sum of means (over session 1-3), sum of means in PRPs (over sessions 1-3), and percentage of total (for each group of rats).

Only the first table is relevant for the ***bar pressing*** category of behaviour. A table presenting the frequency of reinforcement for each rat in each session is also provided. The behavioural categories are presented in the following order:

(1) ***bar pressing*** (Table B.1);
(2) ***frequency of reinforcement*** (Table B.2);
(3) ***bar-related behaviour*** (Tables B.3 – B.5);
(4) ***sniff object*** (Tables B.6 – B.8);
(5) ***sniff and touch object*** (Tables B.9 – B.11);
(6) ***chew/bite object*** (Tables B.12 – B.14);
(7) ***propping*** (Tables B.15 – B.17);
(8) ***jump at lid*** (Tables B.18 – B.20);
(9) ***displacement*** (Tables B.21 – B.23);
(10) ***digging/burying*** (Tables B.24 – B.26);
(11) ***rearing*** (Tables B.27 – B.29); and
(12) ***pica*** (Tables B.30 – B.32).

Appendix B also provides the:

(1) mean frequency and duration of behaviours for the "object" grouping variable for all sessions (Table B.33) and during the PRPs of ***DRL*** or ***variable-ratio*** sessions (Table B.36);

(2) mean frequency and duration of behaviours for the "schedule" grouping variable for all sessions (Table B.34) and during the PRPs of ***DRL*** or ***variable-ratio*** sessions (Table B.37); and

(3) mean frequency and duration of behaviours for the "session" grouping variable for all sessions (Table B.35) and during the PRPs of ***DRL*** or ***variable-ratio*** sessions (Table B.38).

Table B.1

Frequency and duration of ***bar-pressing*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	1311 / 211.5 52 / 15.8 23 / 4.7 2026 / 343.2 mean= 853 / 143.8	174 / 33.1 181 / 37.1 166 / 32.9 182 / 39.0 mean=175.75/35.53	265 / 52.6 14 / 2.9 69 / 14.6 549 / 105.2 mean=224.25/43.83	444 / 63.0 210 / 39.8 220 / 43.9 238 / 46.9 mean= 278 / 48.4
SESSION 2	1425 / 241.7 58 / 13.8 17 / 3.5 2158 / 405.8 mean= 914.5/ 166.2	161 / 34.4 166 / 36.6 160 / 37.7 262 / 59.4 mean=187.25/42.03	885 / 172.8 15 / 3.7 77 / 17.4 776 / 156.1 mean=438.25 / 87.5	522 / 74.1 238 / 51.0 272 / 52.7 240 / 47.2 mean= 318 / 56.25
SESSION 3	1924 / 325.6 50 / 13.9 16 / 3.9 2340 / 469.1 mea=1082.5/203.13	170 / 35.5 181 / 40.6 149 / 29.6 301 / 63.7 mean=200.25/42.35	693 / 134.2 24 / 5.8 55 / 13.0 691 / 170.7 mean=365.75/80.93	505 / 73.1 205 / 43.7 222 / 47.9 248 / 53.6 mean= 295 / 54.58
sum of means (for sessions 1 to 3)	2850 / 513.13	563.25 / 119.91	1028.25 / 212.26	891 / 159.23
SESSION 4	1269 / 177.4 80 / 21.2 26 / 5.7 1519 / 283.9 mean=723.5/122.05	173 / 29.0 135 / 29.7 81 / 18.3 208 / 41.3 mean=149.25/29.58	432 / 78.8 29 / 6.4 42 / 9.9 318 / 67.8 mean=205.25/40.73	236 / 35.8 86 / 18.3 126 / 26.7 82 / 17.8 mean=132.5/ 24.65
SESSION 5	779 / 117.1 54 / 11.8 9 / 1.7 1096 / 195.7 mean=484.5 / 81.58	46 / 9.9 63 / 14.1 37 / 7.7 69 / 15.6 mean= 53.75/ 11.83	160 / 35.6 16 / 4.2 29 / 7.0 264 / 59.8 mean=117.25/26.65	117 / 21.9 66 / 15.5 59 / 13.2 90 / 19.3 mean= 83 / 17.48
SESSION 6	436 / 112.0 63 / 14.3 13 / 2.9 178 / 34.0 mean= 172.5 / 40.8	52 / 10.9 64 / 15.1 43 / 9.3 80 / 17.2 mean= 59.75/ 13.13	196 / 43.2 16 / 3.9 36 / 9.6 79 / 18.0 mean= 81.75/ 18.68	61 / 12.0 37 / 8.0 35 / 7.0 36 / 8.0 mean= 42.25 / 8.75
sum of means (for sessions 4 to 6)	1380.5 / 244.43	262.75 / 54.54	404.25 / 86.06	257.75 / 50.88

Table B.2

Frequency of ***reinforcement*** for each rat in Experiment 2, in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	19 1 1 33 mean= 13.5	46 51 41 36 mean= 43.5	7 1 2 17 mean= 6.75	38 35 54 45 mean= 43
SESSION 2	18 1 1 38 mean= 14.5	47 55 47 41 mean= 47.5	12 1 3 20 mean= 9	33 31 49 43 mean= 39
SESSION 3	28 1 1 38 mean= 17	47 49 44 49 mean= 47.25	11 1 2 17 mean= 7.75	31 41 55 54 mean= 45.25
sum of means (for sessions 1 to 3)	45	138.25	23.5	127.25

Table B.3

Frequency and duration of ***bar-related behaviour*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	340 / 136.8 102 / 483.2 41 / 40.6 378 / 161.0 mean=215.25/205.4	235 / 124.4 265 / 236.5 241 / 119.2 195 / 89.8 mean= 234 / 142.48	361 / 574.4 43 / 35.9 158 / 206.4 643 / 635.2 mea=301.25/362.98	301 / 185.6 158 / 73.7 167 / 104.2 200 / 93.6 mean=206.5/114.28
SESSION 2	225 / 108.1 166 / 316.3 36 / 21.0 386 / 149.5 mea=203.25/148.73	174 / 61.1 258 / 151.0 219 / 81.0 201 / 94.9 mean= 213 / 97	515 / 331.1 72 / 65.8 153 / 161.4 730 / 383.7 mean=367.5 / 235.5	328 / 168.3 384 / 205.5 286 / 214.1 260 / 102.7 mean=314.5/172.65
SESSION 3	318 / 96.2 156 / 425.1 26 / 13.0 413 / 128.2 mea=228.25/165.63	208 / 80.6 237 / 153.5 263 / 86.1 338 / 169.9 mean=261.5/122.53	527 / 460.6 87 / 127.8 104 / 224.5 575 / 293.7 mea=323.25/276.65	322 / 233.1 365 / 214.2 252 / 187.1 307 / 128.3 mean=311.5/190.68
sum of means (for sessions 1 to 3)	646.75 / 519.76	708.5 / 362.01	992 / 875.13	832.5 / 477.61
SESSION 4	283 / 102.0 219 / 348.4 49 / 56.7 416 / 190.7 mea=241.75/174.45	135 / 108.8 177 / 262.5 134 / 63.6 172 / 128.9 mean=154.5/140.95	228 / 131.5 81 / 81.7 63 / 107.6 328 / 403.3 mean= 175 / 181.03	154 / 120.0 171 / 174.9 168 / 156.3 123 / 58.9 mean= 154 / 127.53
SESSION 5	325 / 217.5 155 / 495.0 22 / 16.4 395 / 255.6 mea=224.25/246.13	82 / 56.3 106 / 185.8 75 / 52.8 105 / 139.2 mean= 92 / 108.53	141 / 176.5 50 / 57.8 68 / 109.5 264 / 293.2 mea=130.75/159.25	163 / 230.4 240 / 207.7 108 / 206.6 147 / 150.6 mean=164.5/198.83
SESSION 6	215 / 194.3 111 / 484.0 22 / 45.8 151 / 164.2 mea=124.75/222.08	78 / 136.8 95 / 181.4 88 / 76.7 115 / 97.9 mean= 94 / 123.2	201 / 392.2 45 / 87.1 58 / 172.4 104 / 195.3 mean= 102 / 211.75	99 / 131.3 112 / 122.0 81 / 186.9 84 / 88.2 mean= 94 / 132.1
sum of means (for sessions 4 to 6)	590.75 / 642.66	340.5 / 372.68	407.75 / 552.03	412.5 / 458.46

Table B.4

Frequency and duration of ***bar-related behaviour*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	18 / 17.1 3 / 1.8 1 / 0.5 35 / 51.3 mean= 14.25/ 17.68	89 / 42.4 107 / 87.6 72 / 34.1 54 / 23.8 mean= 80.5 / 46.98	6 / 3.7 2 / 1.2 5 / 4.0 16 / 12.5 mean= 7.25 / 5.35	63 / 40.0 27 / 13.3 58 / 33.4 43 / 22.3 mean= 47.75/ 27.25
SESSION 2	20 / 19.4 1 / 0.7 4 / 1.2 35 / 43.0 mean= 15 / 16.08	44 / 16.0 112 / 71.8 65 / 24.7 55 / 19.1 mean= 69 / 32.9	12 / 4.1 3 / 1.1 2 / 1.9 19 / 12.3 mean= 9 / 4.85	65 / 27.4 55 / 40.6 98 / 68.6 52 / 20.7 mean= 67.5 / 39.33
SESSION 3	29 / 13.4 5 / 1.7 1 / 0.2 46 / 25.6 mean= 20.25/ 10.23	73 / 25.8 86 / 54.6 69 / 21.9 104 / 44.8 mean= 83 / 36.78	13 / 5.7 0 / 0 1 / 5.2 20 / 9.3 mean= 8.5 / 5.05	55 / 37.5 84 / 43.3 105 / 51.7 91 / 38.6 mean= 83.75/ 42.78
sum of means (for sessions 1 to 3)	49.5 / 43.99	232.5 / 116.66	24.75 / 15.25	199 / 109.36

Table B.5

Mean frequency and duration of ***bar-related behaviour*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***bar-related behaviour*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
VROS	frequency	646.75	49.5	7.65
	duration (seconds)	519.76	43.99	8.46
DRLOS	frequency	708.5	232.5	32.82
	duration (seconds)	362.01	116.66	32.23
VROE	frequency	992	24.75	2.50
	duration (seconds)	875.13	15.25	1.74
DRLOE	frequency	832.5	199	23.90
	duration (seconds)	477.61	109.36	22.90

Table B.6

Frequency and duration of ***sniff object*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	126 / 81.9 158 / 73.1 125 / 60.3 108 / 68.6 mean=129.25/70.98	268 / 114.7 240 / 103.9 260 / 120.2 239 / 152.0 mean=251.75/122.7	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	81 / 52.0 122 / 73.8 131 / 52.4 71 / 28.1 mean=101.25/51.58	120 / 39.8 141 / 55.5 206 / 63.1 184 / 69.6 mean= 162.75/ 57.0	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	69 / 31.2 127 / 51.0 112 / 34.4 86 / 30.0 mean= 98.5 / 36.65	138 / 39.1 158 / 61.6 231 / 58.1 181 / 62.1 mean= 177 / 55.23	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	329 / 159.21	591.5 / 234.93		
SESSION 4	111 / 61.3 98 / 50.9 118 / 50.5 136 / 60.3 mean=115.75/55.75	142 / 48.9 178 / 82.3 174 / 67.5 137 / 58.0 mean=157.75/64.18	146 / 82.0 233 / 202.0 190 / 146.8 155 / 106.7 mean= 181 / 134.38	189 / 87.2 193 / 119.7 183 / 133.1 193 / 128.0 mean= 189.5/ 117.0
SESSION 5	101 / 49.6 136 / 54.8 82 / 30.9 101 / 57.4 mean= 105 / 48.18	97 / 55.1 125 / 68.7 106 / 38.0 87 / 43.2 mean=103.75/51.25	124 / 78.6 148 / 114.7 123 / 62.5 110 / 58.5 mean=126.25/78.58	93 / 34.4 121 / 57.3 109 / 52.0 141 / 63.3 mean= 116 / 51.75
SESSION 6	86 / 38.7 116 / 56.4 78 / 26.5 119 / 50.0 mean= 99.75 / 42.9	121 / 44.1 116 / 45.5 141 / 58.8 89 / 30.8 mean=116.75 / 44.8	76 / 27.6 157 / 67.8 102 / 45.8 104 / 36.0 mean= 109.75/ 44.3	141 / 40.5 169 / 45.7 136 / 49.1 124 / 38.7 mean= 142.5 / 43.5
sum of means (for sessions 4 to 6)	320.5 / 146.83	378.25 / 160.23	417 / 257.26	448 / 212.25

N.B., an * has been placed next to cases where the duration of **Sniff Object** takes up more than a quarter of the experimental session (that is, more than 450 seconds of the 1800 second session are spent engaged in this object-directed behaviour)

Table B.7

Frequency and duration of ***sniff object*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	15 / 8.5 13 / 6.0 0 / 0 8 / 12.7 mean= 9 / 6.8	103 / 40.5 83 / 32.1 59 / 24.5 60 / 30.6 mean= 76.25/ 31.93	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	0 / 0 0 / 0 13 / 6.6 0 / 0 mean= 3.25 / 1.65	56 / 19.1 62 / 27.3 62 / 19.5 50 / 19.2 mean= 57.5 / 21.28	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	5 / 2.9 9 / 3.4 0 / 0 0 / 0 mean= 3.5 / 1.58	45 / 17.4 48 / 16.8 69 / 18.2 54 / 16.0 mean= 54 / 17.1	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	15.75 / 10.03	187.75 / 70.31		

Table B.8

Mean frequency and duration of ***sniff object*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***sniff object*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
VROS	frequency duration (seconds)	329 159.21	15.75 10.03	4.79 6.30
DRLOS	frequency duration (seconds)	591.5 234.93	187.75 70.31	31.74 29.93
VROE	frequency duration (seconds)	NO OBJECTS PRESENT		
DRLOE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table B.9

Frequency and duration of ***sniff and touch object*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	99 / 397.2 125 / 302.3 156 / 690.9 * 68 / 288.9 mean= 112 / 419.83	186 / 373.7 140 / 386.2 185 / 498.4 * 140 / 383.7 mean=162.75/410.5	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	80 / 303.8 84 / 176.4 142 / 675.9 * 58 / 268.6 mean= 91 / 356.18	125 / 358.2 103 / 297.6 210 / 590.4 * 145 / 389.2 mea=145.75/408.85	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	52 / 241.5 94 / 225.3 118 / 730.4 * 62 / 228.1 mean= 81.5/ 356.33	149 / 433.2 138 / 387.9 201 / 580.3 * 147 / 339.5 mea=158.75/435.23	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	284.5 / 1132.34	467.25 / 1254.58		
SESSION 4	104 / 271.8 106 / 209.6 135 / 461.5 * 103 / 289.2 mean= 112 / 308.03	132 / 320.7 156 / 497.3 * 173 / 633.5 * 125 / 444.4 mea=146.5/473.98*	109 / 526.9 * 95 / 432.8 159 / 645.5 * 95 / 247.8 mea=114.5/463.25*	150 / 526.1 * 140 / 378.7 120 / 403.1 87 / 294.5 mean=124.25/400.6
SESSION 5	82 / 274.5 91 / 178.0 112 / 620.1 * 93 / 371.9 mean= 94.5/ 361.13	112 / 396.4 135 / 384.2 152 / 655.3 * 85 / 434.0 mean=121/ 467.48*	99 / 379.6 113 / 458.1 * 97 / 601.0 * 124 / 321.6 mea=108.25/440.08	114 / 416.6 126 / 457.4 * 98 / 323.6 115 / 315.2 mean=113.25/378.2
SESSION 6	101 / 360.6 122 / 278.3 109 / 518.3 * 144 / 594.9 * mean= 119 / 438.03	141 / 483.7 * 127 / 367.5 154 / 430.5 108 / 461.5 * mean= 132.5/ 435.8	103 / 420.3 125 / 440.1 117 / 644.3 * 130 / 583.0 * me=118.75/521.93*	128 / 708.2 * 177 / 729.2 * 106 / 265.2 107 / 259.9 mea=129.5/490.63*
sum of means (for sessions 4 to 6)	325.5 / 1107.19	400 / 1377.26	341.5 / 1425.26	367 / 1269.43

N.B., an * has been placed next to cases where the duration of **Sniff and Touch Object** takes up more than a quarter of the experimental session (that is, more than 450 seconds of the 1800 second session are spent engaged in this object-directed behaviour)

Table B.10

Frequency and duration of ***sniff and touch object*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	14 / 49.0 12 / 42.4 0 / 0 3 / 9.5 mean= 7.25 / 25.23	61 / 110.4 47 / 105.5 43 / 128.9 41 / 83.9 mean= 48 / 107.18	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	0 / 0 0 / 0 22 / 123.4 0 / 0 mean= 5.5 / 30.85	63 / 177.4 46 / 166.5 60 / 150.8 44 / 133.1 mean=53.25/156.95	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	2 / 6.1 11 / 41.3 0 / 0 0 / 0 mean= 3.25 / 11.85	58 / 218.1 49 / 124.2 57 / 170.3 49 / 123.9 mean=53.25/159.13	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	16 / 67.93	154.5 / 423.26		

Table B.11

Mean frequency and duration of ***sniff and touch object*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***sniff and touch object*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
VROS	frequency duration (seconds)	284.5 1132.34	16 67.93	5.62 6.0
DRLOS	frequency duration (seconds)	467.25 1254.58	154.5 423.26	33.07 33.74
VROE	frequency duration (seconds)	NO OBJECTS PRESENT		
DRLOE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table B.12

Frequency and duration of ***chew/bite object*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	5 / 8.5 7 / 5.1 4 / 3.0 3 / 8.1 mean= 4.75 / 6.18	11 / 10.4 2 / 2.7 14 / 22.2 6 / 9.7 mean= 8.25 / 11.25	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	14 / 21.0 5 / 8.0 4 / 5.2 3 / 3.9 mean= 6.5 / 9.53	6 / 6.0 8 / 14.3 5 / 15.3 5 / 3.7 mean= 6 / 9.83	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	0 / 0 4 / 6.4 7 / 12.8 0 / 0 mean= 2.75 / 4.8	2 / 3.4 21 / 102.7 6 / 13.4 2 / 2.0 mean= 7.75 / 30.38	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	14 / 20.51	22 / 51.46		
SESSION 4	25 / 155.1 33 / 161.9 16 / 75.2 15 / 23.5 mean=22.25/103.93	26 / 66.7 47 / 157.9 28 / 86.7 24 / 50.8 mean= 31.25/ 90.53	8 / 17.2 5 / 9.9 14 / 20.0 11 / 19.6 mean= 9.5 / 16.68	9 / 9.6 16 / 46.2 6 / 8.8 6 / 19.3 mean= 9.25 / 20.98
SESSION 5	15 / 51.3 12 / 76.3 26 / 90.4 18 / 46.4 mean= 17.75 / 66.1	25 / 89.9 45 / 280.5 26 / 143.2 7 / 14.3 mean=25.75/131.98	8 / 8.0 4 / 5.1 5 / 15.2 30 / 114.4 mean=11.75 / 35.68	13 / 24.8 7 / 8.0 11 / 12.2 17 / 27.0 mean= 12 / 18.0
SESSION 6	22 / 137.7 36 / 118.4 27 / 157.3 40 / 187.2 mean=31.25/150.15	26 / 48.6 127 / 367.5 16 / 99.7 14 / 112.3 mean=45.75/157.03	12 / 23.3 3 / 3.2 13 / 27.1 19 / 21.6 mean= 11.75 / 18.8	5 / 11.4 7 / 5.3 3 / 1.8 20 / 60.1 mean= 8.75 / 19.65
sum of means (for sessions 4 to 6)	71.25 / 320.18	102.75 / 379.54	33 / 71.16	30 / 58.63

Table B.13

Frequency and duration of ***chew/bite object*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	2 / 4.9 0 / 0 0 / 0 0 / 0 mean= 0.5 / 1.23	0 / 0 1 / 2.4 2 / 2.2 1 / 0.6 mean= 1 / 1.3	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	0 / 0 0 / 0 1 / 1.8 0 / 0 mean= 0.25 / 0.45	4 / 5.1 6 / 12.9 0 / 0 2 / 1.6 mean= 3 / 4.9	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	0 / 0 2 / 1.7 0 / 0 0 / 0 mean= 0.5 / 0.43	0 / 0 10 / 62.1 3 / 6.9 0 / 0 mean= 3.25 / 17.25	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	1.25 / 2.11	7.25 / 23.45		

Table B.14

Mean frequency and duration of ***chew/bite object*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***chew/bite object*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
VROS	frequency duration (seconds)	14 20.51	1.25 2.11	8.93 10.29
DRLOS	frequency duration (seconds)	22 51.46	7.25 23.45	32.96 45.57
VROE	frequency duration (seconds)	NO OBJECTS PRESENT		
DRLOE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table B.15

Frequency and duration of ***propping*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	59 / 69.6	157 / 474.5	112 / 409.3	261 / 555.6
	120 / 380.6	132 / 314.2	98 / 254.4	141 / 229.2
	93 / 193.9	23 / 24.2	122 / 287.4	124 / 260.7
	73 / 85.1	81 / 84.2	152 / 417.9	155 / 275.5
	mean= 86.25/ 182.3	mean=98.25/224.28	mean= 121 / 342.25	mea=170.25/330.25
SESSION 2	74 / 71.5	137 / 474.0	92 / 175.1	222 / 385.7
	103 / 311.8	98 / 272.7	97 / 264.6	136 / 212.9
	49 / 121.6	26 / 40.1	177 / 368.2	104 / 267.3
	60 / 78.8	85 / 122.1	174 / 438.3	145 / 247.6
	mean= 71.5/ 145.93	mean= 86.5/ 227.23	mean= 135 / 311.55	mea=151.75/278.38
SESSION 3	55 / 88.6	135 / 438.1	142 / 286.5	182 / 377.3
	110 / 342.7	68 / 225.2	146 / 338.0	119 / 256.2
	40 / 71.6	26 / 60.4	69 / 266.0	85 / 254.8
	59 / 75.1	114 / 131.1	159 / 463.2	167 / 356.6
	mean= 66 / 144.5	mean= 85.75/ 213.7	mean=129 / 338.43	mea=138.25/311.23
sum of means (for sessions 1 to 3)	223.75 / 472.73	270.5 / 665.21	385 / 992.23	460.25 / 919.86
SESSION 4	64 / 84.4	145 / 573.5	82 / 243.2	81 / 241.5
	140 / 320.5	59 / 192.8	70 / 190.5	80 / 151.6
	68 / 169.3	29 / 24.4	49 / 103.1	75 / 225.4
	60 / 102.0	99 / 150.5	100 / 384.7	142 / 437.7
	mean= 83 / 169.05	mean= 83 / 235.3	mean=75.25/230.38	mean= 94.5/ 264.05
SESSION 5	62 / 80.6	111 / 689.2	74 / 174.8	68 / 196.9
	126 / 339.6	50 / 207.1	75 / 240.0	81 / 171.7
	25 / 47.4	32 / 94.7	50 / 116.2	53 / 199.8
	68 / 87.7	146 / 346.8	99 / 406.6	158 / 566.6
	mean=70.25/138.83	mean=84.75/334.45	mean= 74.5 / 234.4	mean= 90 / 283.75
SESSION 6	50 / 130.3	107 / 460.4	87 / 228.1	85 / 301.1
	74 / 170.6	83 / 307.1	88 / 372.2	72 / 151.7
	39 / 113.1	65 / 126.5	48 / 195.1	76 / 240.3
	75 / 166.0	91 / 233.3	88 / 341.0	164 / 694.6
	mean= 59.5 / 145	mean= 86.5/ 281.83	mean= 77.75/ 284.1	mean=99.25/346.93
sum of means (for sessions 4 to 6)	212.75 / 452.88	254.25 / 851.58	227.5 / 748.88	283.75 / 894.73

Table B.16

Frequency and duration of ***propping*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	1 / 0.6 7 / 11.8 0 / 0 0 / 0 mean= 2 / 3.1	65 / 256.6 53 / 110.9 9 / 8.3 26 / 27.2 mean=38.25/100.75	0 / 0 3 / 5.1 0 / 0 0 / 0 mean= 0 / 0	45 / 113.1 12 / 12.2 65 / 145.3 49 / 70.5 mean= 42.75/ 85.28
SESSION 2	0 / 0 0 / 0 3 / 7.9 0 / 0 mean= 0.75 / 1.98	57 / 161.3 44 / 129.0 10 / 17.2 25 / 26.5 mean= 34 / 83.5	0 / 0 6 / 6.7 0 / 0 0 / 0 mean= 1.5 / 1.68	30 / 48.5 7 / 11.0 43 / 107.8 37 / 61.6 mean= 29.25/ 57.23
SESSION 3	2 / 1.8 3 / 6.7 0 / 0 0 / 0 mean= 1.25 / 2.13	46 / 138.0 22 / 77.5 11 / 28.7 47 / 58.4 mean= 31.5 / 75.65	1 / 0.7 0 / 0 0 / 0 1 / 2.7 mean= 0.5 / 0.85	9 / 26.8 12 / 28.8 39 / 97.0 75 / 180.9 mean= 33.75/ 83.38
sum of means (for sessions 1 to 3)	4 / 7.21	103.75 / 259.9	2.75 / 3.81	105.75 / 225.89

Table B.17

Mean frequency and duration of ***propping*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***propping*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
VROS	frequency duration (seconds)	223.75 472.73	4 7.21	1.79 1.53
DRLOS	frequency duration (seconds)	270.5 665.21	103.75 259.9	38.35 39.07
VROE	frequency duration (seconds)	385 992.23	2.75 3.81	0.71 0.38
DRLOE	frequency duration (seconds)	460.25 919.86	105.75 225.89	22.98 24.56

Table B.18

Frequency and duration of ***jump at lid*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 3 / 0.9 0 / 0 mean= 0.75 / 0.23	0 / 0 2 / 0.5 1 / 0.2 0 / 0 mean= 0.75 / 0.18
SESSION 2	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	1 / 0 0 / 0 4 / 1.2 0 / 0 mean= 1.25 / 0.3	1 / 0.4 0 / 0 1 / 0.0 2 / 0.7 mean= 1 / 0.28
SESSION 3	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	4 / 1.1 0 / 0 0 / 0 0 / 0 mean= 1 / 0.28	1 / 0.3 3 / 0.8 1 / 0.2 5 / 1.4 mean= 2.5 / 0.68
sum of means (for sessions 1 to 3)	0 / 0	0 / 0	3 / 0.81	4.25 / 1.14
SESSION 4	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
SESSION 5	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	1 / 0.4 0 / 0 0 / 0 0 / 0 mean= 0.25 / 0.1	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
SESSION 6	1 / 3.2 0 / 0 0 / 0 2 / 0.6 mean= 0.75 / 0.95	1 / 0.3 0 / 0 0 / 0 1 / 0.3 mean= 0.5 / 0.15	1 / 0.3 0 / 0 0 / 0 0 / 0 mean= 0.25 / 0.08	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
sum of means (for sessions 4 to 6)	0.75 / 0.95	0.5 / 0.15	0.5 / 0.18	0 / 0

Table B.19

Frequency and duration of ***jump at lid*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 1 / 0.2 0 / 0 mean= 0.25 / 0.05
SESSION 2	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
SESSION 3	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 1 / 0.2 1 / 0.3 mean= 0.5 / 0.13
sum of means (for sessions 1 to 3)	0 / 0	0 / 0	0 / 0	0.75 / 0.18

Table B.20

Mean frequency and duration of ***jump at lid*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***jump at lid*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
VROS	frequency	0	0	
	duration (seconds)	0	0	
DRLOS	frequency	0	0	
	duration (seconds)	0	0	
VROE	frequency	3	0	0
	duration (seconds)	0.81	0	0
DRLOE	frequency	4.25	0.75	17.65
	duration (seconds)	1.14	0.18	15.79

Table B.21

Frequency and duration of ***displacement*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	38 / 68.9 8 / 60.3 27 / 160.0 10 / 25.0 mean= 20.75/ 78.55	30 / 80.2 57 / 104.6 20 / 60.3 37 / 134.1 mean= 36 / 94.8	22 / 45.4 38 / 216.7 20 / 82.1 64 / 107.8 mean= 36 / 113	15 / 58.5 25 / 80.7 62 / 151.9 20 / 72.0 mean= 30.5 / 90.78
SESSION 2	50 / 174.7 6 / 36.0 31 / 292.6 14 / 38.0 mean=25.25/135.33	33 / 126.1 64 / 177.9 37 / 188.4 48 / 176.1 mean= 45.5/ 167.13	26 / 62.4 16 / 84.4 17 / 70.8 105 / 161.4 mean= 41 / 94.75	22 / 60.7 28 / 100.5 46 / 120.3 21 / 65.7 mean= 29.25 / 86.8
SESSION 3	68 / 142.1 10 / 60.4 26 / 225.7 5 / 25.7 mean=27.25/113.48	39 / 118.9 65 / 151.2 28 / 74.5 40 / 82.5 mean= 43 / 106.78	24 / 60.2 23 / 109.9 20 / 163.7 111 / 199.3 mean= 44.5/ 133.28	17 / 25.1 12 / 58.7 59 / 220.9 33 / 113.1 mean=30.25/104.45
sum of means (for sessions 1 to 3)	73.25 / 327.36	124.5 / 368.71	121.5 / 341.03	90 / 282.03
SESSION 4	23 / 147.5 10 / 81.1 31 / 174.6 16 / 28.6 mean= 20 / 107.95	18 / 76.2 26 / 60.7 27 / 272.1 21 / 90.5 mean= 23 / 124.88	30 / 61.6 21 / 66.7 20 / 128.9 48 / 126.6 mean= 29.75/ 95.95	29 / 196.0 28 / 75.6 38 / 162.4 42 / 83.2 mean= 34.25/ 129.3
SESSION 5	67 / 269.5 30 / 124.2 19 / 334.7 26 / 124.1 mean= 35.5/ 213.13	15 / 84.8 36 / 116.4 29 / 218.8 32 / 131.5 mean= 28 / 137.88	24 / 90.0 19 / 91.7 19 / 112.7 53 / 122.0 mean= 28.75/ 104.1	39 / 444.1 22 / 97.5 36 / 262.1 30 / 101.2 mean=31.75/226.23
SESSION 6	45 / 194.1 27 / 226.5 22 / 207.9 21 / 50.0 mean=28.75/169.63	34 / 125.3 65 / 187.3 32 / 311.2 41 / 344.5 mean= 43 / 242,08	45 / 175.4 23 / 219.3 28 / 130.3 42 / 296.3 mean= 34.5/ 205.33	16 / 184.2 20 / 126.0 54 / 368.6 41 / 135.2 mean=32.75 / 203.5
sum of means (for sessions 4 to 6)	84.25 / 490.71	94 / 504.84	93 / 405.38	98.75 / 559.03

Table B.22

Frequency and duration of ***displacement*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	0 / 0 0 / 0 0 / 0 1 / 13.2 mean= 0.25 / 3.3	13 / 33.9 21 / 40.6 3 / 1.7 4 / 7.8 mean= 10.25 / 21	0 / 0 2 / 0.7 0 / 0 0 / 0 mean= 0.5 / 0.18	3 / 11.5 4 / 6.4 33 / 54.3 5 / 3.2 mean= 11.25/ 18.85
SESSION 2	0 / 0 0 / 0 10 / 48.8 0 / 0 mean= 2.5 / 12.2	11 / 48.2 22 / 52.7 12 / 31.5 14 / 53.1 mean=14.75 / 46.38	0 / 0 1 / 2.3 0 / 0 0 / 0 mean= 0.25 / 0.58	1 / 0.9 6 / 8.5 20 / 47.0 5 / 11.6 mean= 8 / 17.0
SESSION 3	0 / 0 1 / 7.3 0 / 0 0 / 0 mean= 0.25 / 1.83	9 / 12.1 22 / 44.6 4 / 3.6 7 / 16.0 mean= 10.5 / 19.08	0 / 0 0 / 0 0 / 0 1 / 0.5 mean= 0.25 / 0.13	3 / 2.6 2 / 4.4 32 / 110.3 6 / 10.3 mean= 10.75 / 31.9
sum of means (for sessions 1 to 3)	3 / 17.33	35.5 / 86.46	1 / 0.89	30 / 67.75

Table B.23

Mean frequency and duration of ***displacement*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***displacement*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
VROS	frequency	73.25	3	4.10
	duration (seconds)	327.36	17.33	5.29
DRLOS	frequency	124.5	35.5	28.51
	duration (seconds)	368.71	86.46	23.45
VROE	frequency	121.5	1	0.82
	duration (seconds)	341.03	0.89	0.26
DRLOE	frequency	90	30	33.33
	duration (seconds)	282.03	67.75	24.02

Table B.24

Frequency and duration of ***digging/burying*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	2 / 0.6 11 / 3.1 2 / 0.4 0 / 0 mean= 3.75 / 1.03	10 / 5.4 34 / 12.9 43 / 9.5 5 / 1.2 mean= 23 / 7.25	3 / 0.6 12 / 3.6 16 / 2.8 4 / 3.6 mean= 8.75 / 2.65	24 / 9.6 2 / 0.9 49 / 20.4 40 / 7.6 mean= 28.75 / 9.63
SESSION 2	6 / 2.2 29 / 8.2 5 / 2.3 2 / 1.8 mean= 10.5 / 3.63	9 / 1.7 19 / 9.4 19 / 7.8 10 / 3.1 mean= 14.25 / 5.5	4 / 1.5 9 / 2.8 8 / 2.8 2 / 0.2 mean= 5.75 / 1.83	38 / 13.0 10 / 2.1 70 / 26.2 92 / 16.6 mean= 52.5 / 14.48
SESSION 3	4 / 0.9 13 / 4.5 10 / 2.5 2 / 0.6 mean= 7.25 / 2.13	5 / 6.2 38 / 20.1 52 / 11.9 17 / 3.2 mean= 28 / 10.35	21 / 4.2 9 / 2.2 35 / 11.0 0 / 0 mean= 16.25 / 4.35	48 / 11.0 7 / 2.2 54 / 24.6 22 / 3.0 mean= 32.75 / 10.2
sum of means (for sessions 1 to 3)	21.5 / 6.79	65.25 / 23.1	30.75 / 8.83	114 / 34.31
SESSION 4	9 / 1.8 1 / 0.4 1 / 0.3 6 / 1.0 mean= 4.25 / 0.88	9 / 2.9 22 / 4.1 25 / 4.5 12 / 2.3 mean= 17 / 3.45	24 / 10.0 18 / 5.5 13 / 2.8 3 / 2.5 mean= 14.5 / 5.2	16 / 3.9 12 / 2.9 23 / 10.3 20 / 5.5 mean= 17.75 / 6.35
SESSION 5	11 / 1.9 7 / 1.6 1 / 0.2 9 / 1.6 mean= 7 / 1.33	2 / 2.7 12 / 2.8 18 / 6.9 13 / 2.2 mean= 11.25 / 3.65	19 / 6.7 9 / 1.7 21 / 4.9 6 / 1.2 mean= 13.75 / 3.63	16 / 3.9 2 / 0.4 73 / 25.9 17 / 4.3 mean= 27 / 8.63
SESSION 6	20 / 3.9 27 / 5.5 7 / 1.0 26 / 8.4 mean= 20 / 4.7	14 / 2.9 10 / 2.6 17 / 2.3 10 / 1.3 mean= 12.75 / 2.28	14 / 5.0 15 / 3.0 9 / 1.4 3 / 0.8 mean= 10.25 / 2.55	9 / 1.6 7 / 1.2 42 / 15.0 9 / 1.1 mean= 16.75 / 4.73
sum of means (for sessions 4 to 6)	31.25 / 6.91	41 / 9.38	38.5 / 11.38	61.5 / 19.71

Table B.25

Frequency and duration of ***digging/burying*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	3 / 1.1 12 / 4.4 8 / 1.6 2 / 0.7 mean= 6.25 / 1.95	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 17 / 4.9 12 / 2.2 mean= 7.25 / 1.78
SESSION 2	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	1 / 0.1 11 / 6.6 7 / 1.3 3 / 1.5 mean= 5.5 / 2.38	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	6 / 1.4 1 / 0.1 25 / 9.3 23 / 4.0 mean= 13.75 / 3.7
SESSION 3	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 12 / 9.2 17 / 4.7 6 / 1.9 mean= 8.75 / 3.95	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	10 / 2.2 4 / 0.6 26 / 13.4 7 / 1.2 mean= 11.75 / 4.35
sum of means (for sessions 1 to 3)	0 / 0	20.5 / 8.28	0 / 0	32.75 / 9.83

Table B.26

Mean frequency and duration of ***digging/burying*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***digging/burying*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
VROS	frequency duration (seconds)	21.5 6.79	0 0	0 0
DRLOS	frequency duration (seconds)	65.25 23.1	20.5 8.28	31.42 35.84
VROE	frequency duration (seconds)	30.75 8.83	0 0	0 0
DRLOE	frequency duration (seconds)	114 34.31	32.75 9.83	28.73 28.65

Table B.27

Frequency and duration of ***rearing*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	39 / 51.2	77 / 83.3	47 / 78.6	149 / 199.1
	74 / 71.7	74 / 72.7	133 / 260.4	219 / 257.6
	69 / 80.1	32 / 69.7	174 / 299.5	161 / 194.6
	20 / 14.5	211 / 225.4	59 / 57.1	128 / 151.6
	mean= 50.5 / 54.38	mean= 98.5/ 112.78	mean=103.25/173.9	mea=164.25/200.73
SESSION 2	31 / 32.2	91 / 192.0	50 / 75.7	156 / 288.1
	92 / 255.9	90 / 141.0	134 / 298.8	182 / 157.1
	55 / 71.7	9 / 8.9	270 / 453.3	127 / 175.0
	23 / 14.3	109 / 116.6	61 / 46.9	148 / 192.3
	mean= 50.25/ 93.53	mean=74.75/114.63	mea=128.75/218.68	mea=153.25/203.13
SESSION 3	43 / 86.9	88 / 120.1	79 / 79.4	142 / 219.3
	74 / 147.3	55 / 81.2	165 / 230.4	172 / 152.3
	25 / 22.2	35 / 49.5	99 / 178.3	99 / 98.7
	19 / 23.0	167 / 254.8	63 / 55.5	164 / 213.8
	mean= 40.25/ 69.85	mean= 86.25/ 126.4	mean= 101.5/ 135.9	mea=144.25/171.03
sum of means (for sessions 1 to 3)	141 / 217.76	259.5 / 353.81	333.5 / 528.48	461.75 / 574.89
SESSION 4	64 / 84.4	91 / 167.8	17 / 11.4	52 / 84.2
	99 / 144.4	34 / 41.7	51 / 44.5	56 / 56.9
	105 / 93.3	29 / 24.4	44 / 46.4	47 / 62.4
	66 / 76.1	116 / 247.4	31 / 36.0	72 / 103.0
	mean= 83.5 / 99.55	mean= 67.5/ 120.33	mean= 35.75/ 34.58	mean= 56.75/ 76.63
SESSION 5	65 / 95.2	51 / 101.3	18 / 24.7	27 / 30.1
	81 / 103.7	28 / 35.2	39 / 47.4	91 / 93.4
	38 / 49.4	40 / 95.7	37 / 60.7	37 / 51.3
	32 / 34.7	120 / 182.0	49 / 76.8	97 / 113.7
	mean= 54 / 70.75	mean=59.75/103.55	mean= 35.75 / 52.4	mean= 63 / 72.13
SESSION 6	60 / 89.4	43 / 39.0	22 / 26.7	56 / 91.2
	46 / 118.4	63 / 67.6	52 / 48.3	92 / 130.4
	33 / 24.2	67 / 78.9	30 / 33.6	39 / 57.2
	55 / 42.9	83 / 124.7	37 / 32.4	109 / 112.9
	mean= 48.5 / 68.73	mean= 64 / 77.55	mean= 35.25/ 35.25	mean= 74 / 97.93
sum of means (for sessions 4 to 6)	186 / 239.03	191.25 / 301.43	106.75 / 122.23	193.75 / 246.69

Table B.28

Frequency and duration of ***rearing*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	0.34 / 0.29	31.6 / 30.05	0.33 / 0.12	38.47 / 39.51
	0.74 / 0.43	29.6 / 31.2	1.06 / 0.46	50.64 / 85.29
	0.48 / 0.52	18.8 / 26.9	1.22 / 0.89	47.31 / 54.45
	0.16 / 0.09	86.4 / 86.8	0.41 / 0.18	34.27 / 45.6
	mean=0.43 / 0.33	mean= 41.6 / 43.7	mean= 0.76 / 0.41	mean= 42.67/56.21
SESSION 2	0.23 / 0.29	34.2 / 76.7	0.35 / 0.23	34.86 / 73.55
	0.72 / 1.1	39.3 / 59.4	1.01 / 0.67	54.75 / 45.66
	0.56 / 0.34	6.4 / 3.6	1.87 / 1.02	22.48 / 52.57
	0.18 / 0.12	51.01 / 47.6	0.54 / 0.21	42.93 / 61.3
	mean= 0.42 / 0.46	mean= 32.7 / 46.8	mean= 0.94 / 0.53	mean= 38.76/58.27
SESSION 3	0.54 / 0.42	38.4 / 48.1	0.67 / 0.18	32.33 / 63.89
	0.59 / 0.68	19.8 / 27.8	1.34 / 0.57	49.07 / 38.0
	0.3 / 0.08	21.3 / 22.3	0.81 / 0.41	28.4 / 29.66
	0.17 / 0.09	65.4 / 105.6	0.38 / 0.13	47.51 / 59.86
	mean= 0.4 / 0.32	mean= 36.2 / 50.96	mean= 0.8 / 0.32	mean=39.32/47.85
sum of means (for sessions 1-3)	1.25 / 1.11	110.5 / 141.46	2.5 / 1.26	120.75 / 162.33

Table B.29

Mean frequency and duration of ***rearing*** during the PRPs (for all groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***rearing*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
VROS	frequency	141	1.25	0.89
	duration (seconds)	217.76	1.11	0.51
DRLOS	frequency	259.5	110.5	42.58
	duration (seconds)	353.81	141.46	39.98
VROE	frequency	333.5	2.5	0.75
	duration (seconds)	528.48	1.26	0.24
DRLOE	frequency	461.75	120.75	26.15
	duration (seconds)	574.89	162.33	28.24

Table B.30
Frequency and duration of ***pica*** for each rat in Experiment 2, in each session (sessions 1-3 are ***DRL*** or ***variable-ratio*** sessions, and sessions 4-6 are extinction sessions).

	VROS (A1-A4)	**DRLOS (B1-B4)**	**VROE (C1-C4)**	**DRLOE (D1-D4)**
SESSION 1	10 / 117.6 10 / 132.3 10 / 152.2 6 / 41.5 mean= 9 / 110.9	6 / 12.0 4 / 10.3 42 / 259.5 7 / 16.4 mean= 14.75/ 74.55	16 / 55.6 24 / 216.5 23 / 142.3 0 / 0 mean=15.75/138.13	7 / 32.6 30 / 108.0 15 / 75.5 47 / 188.5 mean=24.75/101.15
SESSION 2	23 / 115.2 20 / 124.1 8 / 77.9 1 / 2.0 mean= 13 / 79.8	4 / 6.6 5 / 21.9 44 / 213.1 13 / 55.5 mean= 16.5 / 74.28	13 / 76.6 24 / 241.5 7 / 67.9 0 / 0 mean= 11 / 96.5	23 / 111.8 21 / 92.4 27 / 197.7 71 / 300.4 mean=35.5/175.58
SESSION 3	9 / 98.4 10 / 157.6 7 / 107.0 1 / 1.0 mean= 6.75 / 91	9 / 30.1 3 / 6.0 51 / 188.2 28 / 122.2 mean= 22.75/ 86.63	10 / 61.6 24 / 264.9 36 / 330.0 3 / 7.4 mean=18.25/165.98	33 / 148.4 37 / 150.6 25 / 193.1 43 / 175.2 mean=34.5/166.83
sum of means (for sessions 1 to 3)	28.75 / 281.7	54 / 235.46	45 / 400.61	94.75 / 443.56
SESSION 4	26 / 116.5 3 / 5.9 7 / 66.1 9 / 80.1 mean= 11.25/ 67.15	7 / 14.7 20 / 67.4 51 / 194.2 35 / 160.8 mean=28.25/109.28	15 / 115.1 25 / 167.1 25 / 194.0 6 / 30.9 mean=17.75/126.78	21 / 127.0 28 / 173.2 21 / 123.6 32 / 167.0 mean= 25.5 / 147.7
SESSION 5	21 / 144.4 5 / 71.5 7 / 31.0 15 / 150.2 mean= 12 / 99.28	13 / 66.9 31 / 157.7 26 / 162.7 26 / 172.9 mean= 24 / 140.05	51 / 336.9 29 / 347.2 38 / 325.5 6 / 40.5 mean= 31 / 262.53	15 / 133.5 22 / 107.6 32 / 262.8 23 / 74.0 mean= 23 / 144.48
SESSION 6	18 / 108.1 15 / 49.2 8 / 19.6 24 / 196.2 mean= 16.25/ 93.28	27 / 128.8 23 / 101.5 40 / 229.6 17 / 118.1 mean= 26.75/ 144.5	29 / 139.8 19 / 181.9 26 / 227.1 6 / 83.2 mean= 20 / 158	13 / 102.1 23 / 116.7 25 / 205.9 19 / 106.1 mean= 20 / 132.7
sum of means (for sessions 4 to 6)	39.5 / 259.71	79 / 393.83	68.75 / 547.31	68.5 / 424.88

Table B.31

Frequency and duration of ***pica*** during the PRPs, for each rat in Experiment 2 in each ***DRL*** or ***variable-ratio*** session (sessions 1-3).

	VROS (A1-A4)	DRLOS (B1-B4)	VROE (C1-C4)	DRLOE (D1-D4)
SESSION 1	1 / 5.2	1 / 0.8	0 / 0	1 / 8.0
	0 / 0	1 / 0.5	0 / 0	5 / 18.0
	0 / 0	14 / 90.4	0 / 0	5 / 24.7
	0 / 0	1 / 3.5	0 / 0	17 / 64.6
	mean= 0.25 / 1.3	mean= 4.25 / 23.8	mean= 0 / 0	mean= 7 / 28.83
SESSION 2	0 / 0	1 / 1.5	0 / 0	4 / 24.4
	0 / 0	1 / 9.9	0 / 0	3 / 12.7
	0 / 0	12 / 64.4	0 / 0	12 / 105.0
	0 / 0	0 / 0	0 / 0	26 / 137.6
	mean= 0 / 0	mean= 3.5 / 18.95	mean= 0 / 0	mean= 11.25/ 69.93
SESSION 3	0 / 0	4 / 16.4	0 / 0	8 / 49.5
	0 / 0	1 / 1.0	0 / 0	14 / 75.6
	0 / 0	16 / 76.9	0 / 0	12 / 107.0
	0 / 0	8 / 45.6	0 / 0	14 / 71.9
	mean= 0 / 0	mean= 7.25 / 34.98	mean= 0 / 0	mean= 12 / 76
sum of means (for sessions 1 to 3)	0.25 / 1.3	15 / 77.73	0 / 0	30.25 / 174.76

Table B.32

Mean frequency and duration of ***pica*** during the PRPs (for all four groups in Experiment 2) summed over the first three sessions (***DRL*** or ***variable-ratio***), as a percentage of the total mean frequency and duration of ***pica*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
VROS	frequency	28.75	0.25	0.87
	duration (seconds)	281.7	1.3	0.46
DRLOS	frequency	54	15	27.78
	duration (seconds)	235.46	77.73	33.01
VROE	frequency	45	0	0
	duration (seconds)	400.61	0	0
DRLOE	frequency	94.75	30.25	31.93
	duration (seconds)	443.56	174.76	39.40

Table B.33

The mean frequency and duration of behaviours for the "object" grouping variable for every session in Experiment 2 ("OS"= objects first present during schedule, *i.e.* DRLOS and VROS groups; "OE"= objects first present during extinction, *i.e.* DRLOE and VROE groups).

BEHAVIOURAL MEASURE	**SESSION 1 OS / OE**	**SESSION 2 OS / OE**	**SESSION 3 OS / OE**	**SESSION 4 OS / OE**	**SESSION 5 OS / OE**	**SESSION 6 OS / OE**
FREQUENCIES						
Pica	11.88 / 20.25	14.75 / 23.25	14.75 / 26.38	19.75 / 21.63	18 / 27	21.5 / 20
Digging/Burying	13.38 / 18.75	12.38 / 29.13	17.63 / 24.5	10.63 / 16.13	9.13 / 20.38	16.38 / 13.5
Rearing	74.5 / 133.75	62.5 / 141	63.25 / 122.88	75.5 / 46.25	56.88 / 49.38	56.25 / 54.63
Propping	92.25 / 145.63	79 / 143.38	75.88 / 133.63	83 / 84.88	77.5 / 82.25	73 / 88.5
Displacement	28.38 / 33.25	35.38 / 35.13	35.13 / 37.38	21.5 / 32	31.75 / 30.25	35.88 / 33.63
Bar-related behaviour	224.63/253.88	208.13 / 341	244.88/317.38	198.13 / 164.5	158.13/147.63	109.38 / 98
Sniff object	190.5 / n/a	132 / n/a	137.75 / n/a	136.75/185.25	104.38/121.13	108.25/126.13
Sniff & Touch object	137.38 / n/a	118.38 / n/a	120.13 / n/a	129.25/119.38	107.75/110.75	125.75/124.13
Chew/Bite object	6.5 / n/a	6.25 / n/a	5.25 / n/a	26.75 / 9.38	21.75 / 11.88	38.5 / 10.25
Bar-pressing	514.38/251.13	550.88/378.13	641.38/330.38	436.38/168.88	269.13/100.13	116.13 / 62
DURATIONS (in seconds)						
Pica	92.73 / 119.64	77.04 / 136.04	88.82 / 166.41	88.22 / 137.24	119.67/203.51	118.89/145.35
Digging/Burying	4.14 / 6.14	4.57 / 8.16	6.24 / 7.28	2.17 / 5.78	2.49 / 6.13	3.49 / 3.64
Rearing	83.58 / 187.32	104.08/210.91	98.13 / 153.47	109.94 / 55.61	87.15 / 49.38	73.14 / 66.59
Propping	203.29/336.25	186.58/294.97	179.1 / 324.83	202.18/247.22	236.64/259.08	213.42/315.52
Displacement	86.68 / 101.89	151.23 / 90.78	110.13/118.87	116.42/112.63	175.51/165.17	205.86/204.42
Bar-related behaviour	173.94/238.63	122.87/204.08	144.08/233.67	157.7 / 154.28	177.33/179.04	172.64/171.93
Sniff object	96.84 / n/a	54.29 / n/a	45.94 / n/a	59.97 / 125.69	49.72 / 65.17	43.85 / 43.9
Sniff & Touch object	415.17/ n/a	382.52 / n/a	395.78 / n/a	391.01/431.93	414.31/409.14	436.92/506.28
Chew/Bite object	8.72 / n/a	9.68 / n/a	17.59 / n/a	97.23 / 18.83	99.04 / 26.84	153.59/19.23
Bar-pressing	89.67 / 46.12	104.12 / 71.88	122.74 / 67.76	75.82 / 32.69	46.71 / 22.07	26.97 / 13.72

Table B.34

The mean frequency and duration of behaviours for the "schedule" grouping variable for every session in Experiment 2 ("DRL"= ***Differential Reinforcement of Low Rates*** groups, *i.e.* DRLOS and DRLOE groups; "VR"= ***variable-ratio*** groups, *i.e.* VROS and VROE groups).

BEHAVIOURAL MEASURE	**SESSION 1 DRL / VR**	**SESSION 2 DRL / VR**	**SESSION 3 DRL / VR**	**SESSION 4 DRL / VR**	**SESSION 5 DRL / VR**	**SESSION 6 DRL / VR**
FREQUENCIES						
Pica	19.75 / 12.38	26 / 12	28.63 / 12.5	26.88 / 14.5	23.5 / 21.5	23.38 / 18.13
Digging/Burying	25.88 / 6.25	33.38 / 8.13	30.38 / 11.75	17.38 / 9.38	19.13 / 10.38	14.75 / 15.13
Rearing	131.38 / 76.88	114 / 89.5	115.25 / 70.88	62.13 / 59.63	61.38 / 44.88	69 / 41.88
Propping	134.25/103.63	119.13/103.25	112 / 97.5	88.75 / 79.13	87.38 / 72.38	92.88 / 68.63
Displacement	33.25 / 28.38	37.38 / 33.13	36.63 / 35.88	28.63 / 24.88	29.88 / 32.13	37.88 / 31.63
Bar-related behaviour	220.25/258.25	263.75/285.38	286.5 / 275.75	154.25/208.38	128.25 / 177.5	94 / 113.38
Sniff object	251.75/129.25	162.75/101.25	177 / 98.5	173.63/148.38	109.88/115.63	129.63/104.75
Sniff & Touch object	162.75/ 112	145.75/ 91	158.75/ 81.5	135.38/113.25	117.13/101.38	131 / 118.88
Chew/Bite object	8.25 / 4.75	6 / 6.5	7.75 / 2.75	20.25 / 15.88	18.88 / 14.75	27.25 / 21.5
Bar-pressing	226.88/538.63	252.63/676.38	247.63/724.13	140.88/464.38	68.38 / 300.88	51 / 127.13
DURATIONS (in seconds)						
Pica	87.85 / 124.52	124.93 / 88.15	126.73/128.49	128.49 / 96.97	142.27/180.91	138.6 / 125.64
Digging/Burying	8.44 / 1.84	9.99 / 2.73	10.28 / 3.24	4.9 / 3.04	6.14 / 2.48	3.51 / 3.63
Rearing	156.76/114.14	158.88/156.11	148.72/102.88	98.48 / 67.07	87.84 / 61.58	87.74 / 51.99
Propping	277.27/262.28	252.81/228.74	262.47/241.47	249.68/199.72	309.1/186.62	314.38/214.55
Displacement	92.78 / 95.78	126.97/115.04	105.62/123.38	127.09/101.95	182.06/158.62	222.79/187.48
Bar-related behaviour	128.38/284.19	134.83/192.12	156.61/221.14	134.24/177.74	153.68/202.69	127.65/216.92
Sniff object	122.7 / 70.98	57 / 51.58	55.23 / 36.65	90.59 / 95.07	51.5 / 63.38	44.15 / 43.6
Sniff & Touch object	410.5/ 419.83	408.85/356.18	435.23/ 356.33	437.29/385.64	422.84/400.61	463.22/479.98
Chew/Bite object	11.25 / 6.18	9.83 / 9.53	30.38 / 4.8	55.76 / 60.31	74.99 / 50.89	88.34 / 84.48
Bar-pressing	41.97 / 93.82	49.14 / 126.85	48.47 / 142.03	27.12 / 81.39	14.66 / 54.12	10.94 / 29.74

Table B.35

The mean frequency and duration of behaviours for the "session" grouping variable for all groups in Experiment 2.

BEHAVIOURAL MEASURE	SESSION 1	SESSION 2	SESSION 3	SESSION 4	SESSION 5	SESSION 6
FREQUENCIES						
Pica	16.06	19	20.56	20.69	22.5	20.75
Digging/Burying	16.06	20.75	21.06	13.38	14.75	14.94
Rearing	104.13	101.75	93.06	60.88	53.13	55.44
Propping	118.94	111.19	104.75	83.94	79.88	80.75
Displacement	30.81	35.25	36.25	26.75	31	34.75
Bar-related behaviour	239.25	274.56	281.13	181.31	152.88	103.69
Sniff object	190.5	132	137.75	161	112.75	117.19
Sniff & Touch object	137.38	118.38	120.13	124.31	109.25	124.94
Chew/Bite object	6.5	6.25	5.25	18.06	16.81	24.38
Bar-pressing	382.75	464.5	485.88	302.63	184.63	89.06
DURATIONS (in seconds)						
Pica	106.18	106.54	127.61	112.73	161.59	132.12
Digging/Burying	5.14	6.36	6.76	3.97	4.31	3.57
Rearing	135.45	157.49	125.8	82.77	74.71	69.87
Propping	269.77	240.77	251.97	224.7	247.86	264.47
Displacement	94.28	121	114.5	114.52	170.34	205.14
Bar-related behaviour	206.29	163.47	188.87	155.99	178.19	172.28
Sniff object	96.84	54.29	45.94	92.83	57.44	43.88
Sniff & Touch object	415.17	382.52	395.78	411.47	411.72	471.6
Chew/Bite obkect	8.72	9.68	17.59	58.03	62.94	86.41
Bar-pressing	67.89	88	95.25	54.25	34.39	20.34

Table B.36

The mean frequency and duration of behaviours during the PRPs for the "object" grouping variable for each ***DRL*** or ***variable-ratio*** session in Experiment 2 ("OS"= objects present during schedule, *i.e.* DRLOS and VROS groups; "OE"= objects absent during schedule, *i.e.* DRLOE and VROE groups).

BEHAVIOURAL MEASURE	SESSION 1 OS / OE	SESSION 2 OS / OE	SESSION 3 OS / OE
FREQUENCIES			
Pica	2.25 / 3.5	1.75 / 5.63	3.63 / 6
Digging/Burying	3.13 / 3.63	2.75 / 6.88	4.38 / 5.88
Rearing	21.02 / 21.72	16.56 / 19.85	18.3 / 20.06
Propping	20.13 / 21.38	17.38 / 15.38	16.38 / 17.13
Displacement	5.25 / 5.88	8.63 / 4.13	5.38 / 5.5
Bar-related behaviour	47.38 / 27.5	42 / 38.25	51.63 / 46.13
Sniff object	42.63 / n/a	30.38 / n/a	28.75 / n/a
Sniff & Touch object	27.63 / n/a	29.38 / n/a	28.25 / n/a
DURATIONS (in seconds)			
Pica	12.55 / 14.42	9.48 / 34.97	17.49 / 38
Digging/Burying	0.98 / 0.89	1.19 / 1.85	1.98 / 2.18
Rearing	22.02 / 28.31	23.63 / 29.4	25.64 / 24.09
Propping	51.93 / 42.64	42.74 / 29.46	38.89 / 42.12
Displacement	12.15 / 9.52	29.29 / 8.79	10.46 / 16.02
Bar-related behaviour	32.33 / 16.3	24.49 / 22.09	23.51 / 23.92
Sniff object	19.37 / n/a	11.47 / n/a	9.34 / n/a
Sniff & Touch object	66.21 / n/a	93.9 / n/a	85.49 / n/a

Table B.37

The mean frequency and duration of behaviours during the PRPs for the "schedule" grouping variable for each ***DRL*** or ***variable-ratio*** session in Experiment 2 ("DRL"= ***differential reinforcement of low rates*** groups, *i.e.* DRLOS and DRLOE groups; "VR"= ***variable-ratio*** groups, *i.e.* VROS and VROE groups).

BEHAVIOURAL MEASURE	**SESSION 1 DRL / VR**	**SESSION 2 DRL / VR**	**SESSION 3 DRL / VR**
FREQUENCIES			
Pica	5.63 / 0.13	7.38 / 0	9.63 / 0
Digging/Burying	6.75 / 0	9.63 / 0	10.25 / 0
Rearing	42.14 / 0.6	35.73 / 0.68	37.76 / 0.6
Propping	40.5 / 1	31.63 / 1.13	32.63 / 0.88
Displacement	10.75 / 0.38	11.38 / 1.38	10.63 / 0.25
Bar-related behaviour	64.13 / 10.75	68.25 / 12	83.38 / 14.38
Sniff object	76.25 / 9	57.5 / 3.25	54 / 3.5
Sniff & Touch object	48 / 7.25	53.25 / 5.5	53.25 / 3.25
DURATIONS (in seconds)			
Pica	26.32 / 0.65	44.44 / 0	55.49 / 0
Digging/Burying	1.87 / 0	3.04 / 0	4.15 / 0
Rearing	49.96 / 0.37	52.54 / 0.5	49.41 / 0.32
Propping	93.02 / 1.55	70.37 / 1.83	79.52 / 1.49
Displacement	19.93 / 1.74	31.69 / 6.39	25.49 / 0.98
Bar-related behaviour	37.12 / 11.52	36.12 / 10.47	39.78 / 7.64
Sniff object	31.93 / 6.8	21.28 / 1.65	17.1 / 1.58
Sniff & Touch object	107.18 / 25.23	156.95 / 30.85	159.13 / 11.85

Table B.38

The mean frequency and duration of behaviours during the PRPs for the "session" grouping variable for all groups in Experiment 2.

BEHAVIOURAL MEASURE	**SESSION 1**	**SESSION 2**	**SESSION 3**
FREQUENCIES			
Pica	2.88	3.69	4.81
Digging/Burying	3.38	4.81	5.13
Rearing	21.37	18.21	19.18
Propping	20.75	16.38	16.75
Displacement	5.56	6.38	5.44
Bar-related behaviour	37.44	40.13	48.88
Sniff object	42.63	30.38	28.75
Sniff & Touch object	27.63	29.38	28.25
DURATIONS (in seconds)			
Pica	13.48	22.22	27.75
Digging/Burying	0.93	1.52	2.08
Rearing	25.16	26.52	24.86
Propping	47.28	36.1	40.5
Displacement	10.83	19.04	13.24
Bar-related behaviour	24.32	23.29	23.71
Sniff object	19.37	11.47	9.34
Sniff & Touch object	66.21	93.9	85.49

APPENDIX C

This section provides the frequency and duration scores for every behavioural category in Experiment 3, for both groups of rats (for every session & during the PRPs), and for each of the three grouping variables.

The material included in Appendix C consists of a set of three tables per behavioural category scored. The four rats per group are included in the same cell of the table (e.g. the four rats in the FIOS group are lumped together). This set of three tables provides the following information:

(1) frequency and duration of the behaviour for each rat for each part of session (i.e., raw data), the group mean for each session, the average mean and sum of means for sessions 1-3 and 4-6 (for each group of rats);
(2) frequency and duration of the behaviour during the PRPs for each rat in each ***fixed-interval*** session (i.e., raw data), the group mean for each session, the average mean and sum of means for sessions 1-3 (for each group of rats); and
(3) frequency and duration of the behaviour sum of means (over session 1-3), sum of means in PRPs (over sessions 1-3), and percentage of total (for each group of rats).

Only the first table is relevant for the ***bar pressing*** and ***push lid with snout*** categories of behaviour. A table presenting the frequency of reinforcement for each rat in each session is also provided. The behavioural categories are presented in the following order:

(1) ***bar pressing*** (Table C.1);
(2) ***frequency of reinforcement*** (Table C.2);
(3) ***bar-related behaviour*** (Tables C.3 – C.5);
(4) ***sniff object*** (Tables C.6 – C.8);
(5) ***sniff and touch object*** (Tables C.9 – C.11);
(6) ***chew/bite object*** (Tables C.12 – C.14);
(7) ***propping*** (Tables C.15 – C.17);
(8) ***displacement*** (Tables C.18 – C.20);
(9) ***digging/burying*** (Tables C.21 – C.23);
(10) ***sniff bottle*** (Tables C.24 – C.26);
(11) ***sniff and touch bottle*** (Tables C.27 – C.29);
(12) ***chew/bite bottle*** (Tables C.30 – C.32);
(13) ***drinking*** (Tables C.33 – C.35);
(14) ***resting/sleeping*** (Tables C.36 – C.38); and
(15) ***push lid with snout*** (Table C.39).

Appendix C also provides the:

(1) mean frequency and duration of behaviours for the "object" grouping variable for all parts of every session (Table C.40) and during the PRPs of ***fixed-interval*** sessions (Table C.43);
(2) mean frequency and duration of behaviours for the "part of session" grouping variable for the ***fixed-interval*** (Table C.41a) and ***extinction*** (Table C.41b) sessions and during the PRPs of ***fixed-interval*** sessions (Table C.44); and
(3) mean frequency and duration of behaviours for the "session" grouping variable for all parts of every session (Table C.42) and during the PRPs of ***DRL*** or ***variable-ratio*** sessions (Table C.45).

Table C.1

Frequency and duration of ***bar-pressing*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	group FIOE	group FIOS
session 1; 1st 30 mins	444/ 132.6; 211/ 63.2; 407/ 103.4; 165 / 39.8 (mean = 306.75/ 84.75)	300/ 74.6; 502/ 695.9*; 136/ 39.1; 330 / 76.5 (mean = 317 / 221.53)
mid 30 mins	475/ 131.3; 185/ 58.4; 241/ 66.1; 148 / 33.9 (mean = 262.25/ 72.43)	259/ 67.6; 514/ 115.7; 311/ 86.0; 183 / 44.9 (mean = 316.75/ 78.55)
last 30 mins	266/ 72.0; 169/ 50.2; 220/ 59.9; 227 / 56.1 (mean = 220.5 / 59.55)	140/ 37.6; 582/ 115.1; 594/ 135.0; 223 / 48.2 (mean = 384.75/ 83.98)
	session 1 av. mean = 263.17/ 72.24	session 1 av. mean = 339.5/ 128.02
session 2; 1st 30 mins	463/ 126.2; 246/ 74.1; 414/ 117.2; 173 / 39.5 (mean = 324 / 89.25)	331/ 79.4; 505/ 101.4; 418/ 88.7; 407 / 92.2 (mean = 415.25/ 90.43)
mid 30 mins	584/ 164.7; 250/ 60.8; 494/ 142.8; 53 / 13.3 (mean = 345.25 / 95.4)	345/ 82.3; 551/ 115.5; 725/ 141.5; 272 / 63.1 (mean = 473.25/ 100.6)
last 30 mins	650/ 188.5; 221/ 62.0; 322/ 86.1; 54 / 14.8 (mean = 311.75 / 87.85)	239/ 70.7; 534/ 112.7; 724/ 139.4; 323 / 69.2 (mean = 455 / 98.0)
	session 2 av. mean = 327 / 90.83	session 2 av. mean = 447.83/ 96.34
session 3; 1st 30 mins	608/ 155.1; 235/ 69.0; 427/ 122.7; 218 / 46.4 (mean = 372 / 98.3)	173/ 40.9; 463/ 100.3; 459/ 102.2; 414 / 89.9 (mean = 377.25/ 83.33)
mid 30 mins	442/ 124.5; 151/ 53.3; 413/ 118.2; 181 / 39.6 (mean = 296.75 / 83.9)	208/ 54.2; 517/ 109.4; 512/ 111.8; 303 / 67.0 (mean = 385 / 85.6)
last 30 mins	513/ 133.6; 217/ 67.9; 360/ 95.9; 41 / 11.0 (mean = 282.75 / 77.1)	272/ 75.5; 569/ 114.0; 272/ 61.7; 243 / 49.9 (mean = 339 / 75.28)
	session 3 av. mean = 317.17/ 259.3	session 3 av. mean = 367.08/ 81.40
sum of means -1st 30 minutes	1002.75 / 272.3	1109.5 / 395.29
(sessions 1 to 3) - mid 30 minutes	904.25/251.73 (sum of av. means)	1175/ 264.75 (sum of av. means)
- last 30 minutes	815 / 224.5 (= 907.34/422.37)	1178.75/257.26 (=1154.41/305.76)
session 4; 1st 30 mins	143 / 43.8; 40 / 13.2; 153 / 39.4; 54 / 12.5 (mean = 97.5 / 27.23)	98 / 25.3; 223 / 52.1; 131 / 29.1; 180 / 35.1 (mean = 158 / 35.4)
mid 30 mins	20 / 7.5; 3 / 1.1; 9 / 2.5; 4 / 1.2 (mean = 9 / 3.08)	6 / 1.5; 49 / 17.8; 13 / 3.8; 11 / 2.6 (mean = 19.75 / 6.43)
last 30 mins	18 / 6.1; 5 / 1.7; 14 / 3.7; 21 / 5.5 (mean = 14.5 / 4.25)	8 / 2.0; 22 / 11.7; 9 / 2.7; 10 / 2.2 (mean = 12.25 / 4.65)
	session 4 av. mean = 40.33 / 11.52	session 4 av. mean = 63.33 / 15.49
session 5; 1st 30 mins	40 / 11.9; 9 / 3.0; 18 / 4.9; 33 / 7.9 (mean = 25 / 6.93)	25 / 6.0; 24 / 10.8; 16 / 4.8; 27 / 5.9 (mean = 23 / 6.88)
mid 30 mins	36 / 11.0; 5 / 13.7; 22 / 6.1; 5 / 1.3 (mean = 17 / 8.03)	9 / 2.5; 9 / 2.8; 12 / 3.9; 10 / 2.4 (mean = 10 / 2.9)
last 30 mins	27 / 9.6; 3 / 1.3; 13 / 4.0; 7 / 1.9 (mean = 12.5 / 4.2)	9 / 2.3; 13 / 4.6; 9 / 2.8; 6 / 1.6 (mean = 9 / 2.83)
	session 5 av. mean = 18.17 / 6.39	session 5 av. mean = 14 / 4.20
session 6; 1st 30 mins	13 / 4.6; 6 / 1.9; 12 / 3.3; 20 / 5.6 (mean = 12.75 / 3.85)	13 / 3.5; 6 / 2.6; 19 / 5.5; 12 / 2.7 (mean = 12.5 / 3.58)
mid 30 mins	30 / 9.9; 0 / 0; 16 / 4.5; 2 / 0.7 (mean = 12 / 3.78)	8 / 2.9; 1 / 0.6; 14 / 4.4; 13 / 3.1 (mean = 9 / 2.75)
last 30 mins	23 / 8.5; 3 / 1.0; 14 / 3.8; 17 / 4.5 (mean = 14.25 / 4.45)	7 / 1.9; 2 / 0.8; 10 / 3.3; 7 / 1.8 (mean = 6.5 / 1.95)
	session 6 av. mean = 13 / 4.03	session 6 av. mean = 9.33 / 2.76
sum of means - 1st 30 minutes	135.25 / 38.01	193.5 / 45.86
(sessions 4 to 6) - mid 30 minutes	38 / 14.89 (sum of av. means)	38.75 / 12.08 (sum of av. means)
- last 30 minutes	41.25 / 12.9 (= 71.5 / 21.94)	27.75 / 9.43 (= 86.66 / 22.45)

Table C.2

Frequency of ***reinforcement*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	29 ; 28 ; 27 ; 27 (mean = 27.75)	27 ; 28 ; 23 ; 27 (mean = 26.25)
mid 30 mins	29 ; 28 ; 26 ; 26 (mean = 27.25)	29 ; 29 ; 25 ; 28 (mean = 27.75)
last 30 mins	28 ; 28 ; 25 ; 27 (mean = 27)	20 ; 30 ; 30 ; 29 (mean = 27.25)
	session 1 av. mean = 27.33	session 1 av. mean = 27.08
session 2; 1st 30 mins	29 ; 29 ; 29 ; 26 (mean = 28.25)	28 ; 29 ; 29 ; 29 (mean = 28.75)
mid 30 mins	29 ; 30 ; 30 ; 20 (mean = 27.25)	28 ; 30 ; 30 ; 29 (mean = 29.25)
last 30 mins	30 ; 26 ; 28 ; 19 (mean = 25.75)	27 ; 30 ; 30 ; 29 (mean = 29)
	session 2 av. mean = 27.08	session 2 av. mean = 29
session 3; 1st 30 mins	30 ; 28 ; 28 ; 26 (mean = 28)	27 ; 30 ; 29 ; 30 (mean = 29)
mid 30 mins	30 ; 27 ; 29 ; 25 (mean = 27.75)	26 ; 29 ; 31 ; 30 (mean = 29)
last 30 mins	29 ; 29 ; 29 ; 18 (mean = 26.25)	28 ; 30 ; 26 ; 29 (mean = 28.25)
	session 3 av. mean = 27.33	session 3 av. mean = 28.75
sum of means -1st 30 minutes	84	84
(sessions 1 to 3) - mid 30 minutes	82.25	86
- last 30 minutes	79 (sum of av. means = 81.74)	84.5 (sum of av. means = 84.83)

Table C.3

Frequency and duration of ***bar-related behaviour*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	282/ 205.8; 175/ 160.5; 287/ 175.6; 273 / 221.5 (mean=254.25/190.85)	363/ 261.5; 48/ 116.9; 159/ 109.8; 330 / 258.0 (mean = 225 / 186.55)
mid 30 mins	311/ 211.9; 182/ 145.3; 176/ 140.4; 315 / 416.8 (mean = 246 / 228.6)	296/ 245.2; 18 / 7.2; 209/ 130.7; 291 / 222.2 (mean = 203.5/151.33)
last 30 mins	397/462.7*; 195/ 142.0; 144 / 71.4; 365 / 342.2 (mean=275.25/254.58)	84/ 45.9; 26/ 20.4; 188/ 75.4; 244 / 168.6 (mean = 135.5/ 77.58)
	session 1 av. mean = 258.5/ 224.68	session 1 av. mean = 188 / 138.49
session 2; 1st 30 mins	223/ 136.4; 247/ 187.8; 221/ 139.4; 299 / 310.5 (mean =247.5/193.53)	168/ 97.9; 16/ 13.8; 105/ 41.2; 479 / 347.6 (mean = 192 / 125.13)
mid 30 mins	169/ 110.2; 187/ 118.9; 156/ 97.0; 137 / 161.9 (mean =162.25/122.0)	148/ 62.1; 52/ 34.9; 95/ 106.9; 327 / 233.8 (mean =155.5/109.43)
last 30 mins	168/ 129.5; 130/ 62.1; 234/ 160.5; 129 / 109.9 (mean =165.25/115.5)	111 / 69.8; 7 / 2.8; 79 / 41.0; 219 / 100.8 (mean = 104 / 53.6)
	session 2 av. mean =191.67/143.68	session 2 av. mean = 150.5 / 96.05
session 3; 1st 30 mins	183/ 144.7; 237/ 158.4; 146/ 69.7; 297 / 232.3 (mean=215.75/151.28)	67 / 29.1; 47 / 68.2; 131 / 59.9; 345 / 166.9 (mean = 147.5/ 81.03)
mid 30 mins	244/ 233.7; 169/ 116.7; 231/ 178.0; 268 / 166.2 (mean = 228 / 173.65)	89 / 34.2; 20 / 15.5; 126 / 67.5; 252 / 128.1 (mean =121.75/61.33)
last 30 mins	302/ 312.8; 177/ 105.7; 158/ 99.1; 54 / 37.9 (mean = 172.75/ 138.88)	121 / 52.2; 13 / 5.6; 156 / 106.1; 224 / 92.0 (mean = 128.5 / 63.98)
	session 3 av. mean = 205.5/ 154.60	session 3 av. mean =132.58 / 68.78
sum of means -1st 30 minutes	717.5 / 535.66	564.5 / 392.71
(sessions 1 to 3) - mid 30 minutes	636.25 / 524.25 (sum of av. means)	480.75 / 322.09 (sum of av. means)
- last 30 minutes	613.25 / 508.96 (= 655.67/522.96)	368 / 195.16 (= 471.08/303.32)
session 4; 1st 30 mins	133 / 114.2; 76 / 69.2; 84 / 54.9; 102 / 61.1 (mean = 98.75 / 74.85)	113 / 47.7; 51 / 61.1; 128 / 77.9; 190 / 159.5 (mean = 120.5/ 86.55)
mid 30 mins	138 / 519.1*; 25 / 40.6; 33 / 23.2; 136 / 353.9 (mean = 83 / 234.2)	20 / 9.4; 58 / 117.1; 54 / 51.7; 59 / 64.5 (mean = 47.75 / 60.68)
last 30 mins	142 / 398.1; 36 / 40.3; 33 / 32.5; 161 / 237.3 (mean = 93 / 177.05)	67 / 93.1; 148/ 538.2*; 57 / 56.9; 41 / 47.0 (mean = 78.25 / 183.8)
	session 4 av. mean = 91.58/ 162.03	session 4 av. mean = 82.17/ 110.34
session 5; 1st 30 mins	112 / 116.8; 36 / 30.5; 53 / 104.3; 82 / 42.7 (mean = 70.75 / 73.58)	45 / 19.3; 48 / 59.4; 58 / 45.7; 58 / 37.0 (mean = 52.25 / 40.35)
mid 30 mins	119 / 178.2; 39 / 97.4; 80 / 62.8; 17 / 39.4 (mean = 63.75 / 94.45)	19 / 10.5; 53 / 91.8; 56 / 55.2; 66 / 60.0 (mean = 48.5 / 54.38)
last 30 mins	65 / 112.2; 18 / 20.7; 57 / 66.9; 159 / 357.0 (mean = 74.75/ 139.2)	56 / 51.3; 40 / 31.7; 43 / 59.1; 28 / 25.1 (mean = 41.75 / 41.8)
	session 5 av. mean = 69.75/ 102.41	session 5 av. mean = 47.5 / 45.51
session 6; 1st 30 mins	48 / 61.6; 27 / 58.5; 31 / 31.9; 52 / 96.2 (mean = 39.5 / 62.05)	40 / 20.8; 24 / 18.6; 70 / 60.9; 35 / 47.2 (mean = 42.25 / 36.88)
mid 30 mins	79 / 102.7; 7 / 9.5; 44 / 32.9; 32 / 20.7 (mean = 40.5 / 41.45)	60 / 60.6; 7 / 8.2; 72 / 56.8; 36 / 41.6 (mean = 43.75 / 41.8)
last 30 mins	67 / 611.6*; 18 / 40.2; 37 / 43.1; 125 / 337.6 (mean =61.75/258.13)	37 / 67.7; 42 / 82.9; 37 / 45.4; 41 / 47.6 (mean = 39.25 / 60.9)
	session 6 av. mean = 47.25/ 120.54	session 6 av. mean = 41.75 / 46.53
sum of means - 1st 30 minutes	209 / 210.48	215 / 163.78
(sessions 4 to 6) - mid 30 minutes	187.25 / 370.1 (sum of av. means)	140 / 156.86 (sum of av. means)
- last 30 minutes	229.5 / 574.38 (= 208.58/ 384.98)	159.25 / 286.5 (= 171.42/ 202.38)

Table C.4

Frequency and duration of ***bar-related behaviour*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	71 / 92.71; 31 / 38.88; 123/ 88.65; 84 / 87.08 (mean = 77.25 / 76.83)	66 / 53.41; 20 / 80.33; 24 / 26.67; 94 / 102.08 (mean = 51 / 65.62)
mid 30 mins	100/ 104.33; 53/ 57.99; 98/ 96.28; 138/ 193.0 (mean = 97.25/ 112.9)	136/ 127.87; 10 / 4.0; 18 / 23.02; 137 / 124.11 (75.25 / 69.75)
last 30 mins	153/ 244.36; 48/ 49.48; 37/29.48; 110/ 110.57 (mean = 87 / 108.47)	31 / 21.35; 13 / 14.12; 53 / 49.41; 114 / 79.03 (mean = 52.75/ 40.98)
	session 1 av. mean = 87.17 / 99.4	session 1 av. mean = 59.67 / 58.78
session 2; 1st 30 mins	67/ 73.34; 41/ 34.81; 92/ 75.39; 84 / 76.23 (mean = 71 / 64.94)	51 / 45.01; 11 / 12.74; 37 / 23.17; 120 / 112.84 (mean =54.75/48.44)
mid 30 mins	111/ 82.28; 53/ 53.95; 83/ 69.18; 74 / 66.92 (mean = 80.25 / 68.08)	49 / 24.85; 50 / 34.07; 58 / 54.73; 105 / 115.22 (mean = 65.5/ 57.22)
last 30 mins	87/ 73.67; 31/ 20.77; 89/ 57.84; 61 / 63.78 (mean = 67 / 54.02)	29 / 15.19; 7 / 2.84; 37 / 20.97; 59 / 33.34 (33 / 18.09)
	session 2 av. mean = 72.75 / 62.35	session 2 av. mean = 51.08 / 41.25
session 3; 1st 30 mins	67/ 81.25; 44/ 31.48; 72/ 42.0; 62 / 30.25 (mean = 61.25 / 46.25)	25 / 11.12; 30 / 34.37; 35 / 21.16; 82 / 43.03 (mean = 43 / 27.42)
mid 30 mins	73/120.13; 49/64.42; 108/116.05; 78 / 35.64 (mean = 77 / 84.06)	41 / 16.68; 11 / 6.65; 47 / 32.93; 85 / 60.75 (mean = 46 / 29.25)
last 30 mins	154/ 242.29; 63/ 59.63; 75/ 62.55; 37 / 20.17 (mean = 82.25 / 96.16)	33 / 14.85; 7 / 3.36; 55 / 46.63; 91 / 45.60 (mean = 46.5 / 27.61)
	session 3 av. mean = 73.5 / 75.49	session 3 av. mean = 45.17 / 28.09
sum of means -1st 30 minutes	209.5 / 188.02	148.75 / 141.48
(sessions 1 to 3) - mid 30 minutes	254.5 / 265.04 (sum of av. means)	186.75 / 156.22 (sum of av. means)
- last 30 minutes	236.25 / 258.65 (= 233.42/237.24)	132.25 / 86.68 (= 155.92/ 128.12)

Table C.5

Mean frequency and duration of ***bar-related behaviour*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***bar-related behaviour*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	717.5	209.5	29.20
- dur.	535.66	188.02	35.10
mid 30 mins- freq.	636.25	254.5	40.0
- dur.	524.25	265.04	50.56
last 30 mins- freq.	613.25	236.25	38.52
- dur.	508.96	258.65	50.82
FIOS 1st 30 mins - freq.	564.5	148.75	26.35
- dur.	392.71	141.48	36.03
mid 30 mins- freq.	480.75	186.75	38.85
- dur.	322.09	156.22	48.50
last 30 mins- freq.	368	132.25	35.94
- dur.	195.16	86.68	44.42

Table C.6

Frequency and duration of ***sniff object*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	NO OBJECTS PRESENT	165 / 194.8; 133 / 350.5; 99 / 92.6 163 / 164.7 (mean = 140 / 200.65)
mid 30 mins		43 / 61.1; 51 / 21.0; 82 / 60.5; 80 / 87.7 (mean = 64 / 57.58)
last 30 mins		29 / 20.9; 18 / 7.2; 52 / 50.9; 86 / 65.9 (mean = 46.25 / 36.23) session 1 av. mean = 83.42 / 98.15
session 2; 1st 30 mins	NO OBJECTS PRESENT	106 / 105.5; 62 / 21.6; 74 / 54.7; 79 / 47.1 (mean = 80.25 / 57.23)
mid 30 mins		58 / 33.6; 23 / 8.6; 62 / 38.9; 94 / 80.0 (mean = 59.25 / 40.28)
last 30 mins		50 / 36.7; 40 / 11.1; 40 / 45.7; 91 / 81.5 (mean = 55.25 / 43.75) session 2 av. mean = 64.92 / 47.09
session 3; 1st 30 mins	NO OBJECTS PRESENT	64 / 36.6; 65 / 23.7; 68 / 51.2; 96 / 57.0 (mean = 73.25 / 42.13)
mid 30 mins		60 / 30.8; 41 / 10.0; 83 / 71.1; 81 / 79.4 (mean = 66.25 / 47.83)
last 30 mins		82 / 61.1; 30 / 6.4; 82 / 53.5; 91 / 67.0 (mean = 71.25 / 47.0) session 3 av. mean = 70.25 / 45.65
sum of means -1st 30 minutes		293.5 / 300.01
(sessions 1 to 3) - mid 30 minutes		189.5 / 145.69 (sum of av. means)
- last 30 minutes		172.75 / 126.98 (= 218.59/190.89)
session 4; 1st 30 mins	150/ 228.5; 127/ 121.2; 138/ 135.2; 153 / 166.6 (mean = 142 / 162.88)	121 / 67.9; 69 / 26.4; 112 / 92.6; 98 / 62.4 (mean = 100 / 62.33)
mid 30 mins	39 / 70.4; 81 / 122.3; 46 / 23.6; 36 / 45.1 (mean = 50.5 / 65.35)	18 / 17.8; 24 / 16.0; 66 / 81.9; 69 / 75.2 (mean = 44.25 / 47.73)
last 30 mins	26 / 58.4; 68 / 68.1; 66 / 63.0; 79 / 98.3 (mean = 59.75 / 71.95) session 4 av. mean = 84.08/ 100.06	18 / 10.7; 35 / 47.9; 79 / 131.1; 63 / 104.1 (mean = 48.75 / 73.45) session 4 av. mean = 64.33 / 61.17
session 5; 1st 30 mins	118 / 152.6; 124 / 99.6; 72 / 53.3; 91 / 77.5 (mean = 101.25 / 95.75)	100 / 86.7; 79 / 43.2; 56 / 45.8; 95 / 98.6 (mean = 82.5 / 68.58)
mid 30 mins	44 / 48.8; 59 / 566.7*; 74 / 96.9; 3 / 1.0 (mean = 45 / 178.35)	42 / 47.2; 35 / 20.8; 49 / 48.2; 78 / 113.9 (mean = 51 / 57.53)
last 30 mins	34 / 34.5; 71 / 88.9; 35 / 47.5; 25 / 16.3 (mean = 41.25 / 46.8) session 5 av. mean = 62.5 / 106.97	60 / 63.5; 17 / 5.9; 55 / 40.7; 62 / 70.3 (mean = 48.5 / 45.1) session 5 av. mean = 60.67 / 57.07
session 6; 1st 30 mins	63 / 123.6; 82 / 94.1; 69 / 45.7; 82 / 58.8 (mean = 74 / 80.55)	80 / 54.7; 79 / 57.0; 62 / 62.1; 58 / 40.2 (mean = 69.75 / 53.5)
mid 30 mins	34 / 49.3; 38 / 73.8; 46 / 47.5; 20 / 20.6 (mean = 34.5 / 47.8)	52 / 37.5; 26 / 23.2; 58 / 57.4; 108 / 92.6 (mean = 61 / 52.68)
last 30 mins	11 / 17.4; 63 / 62.8; 54 / 53.3; 36 / 39.8 (mean = 41 / 43.33) session 6 av. mean = 49.83 / 57.23	7 / 15.2; 28 / 14.2; 41 / 54.3; 55 / 37.0 (mean = 32.75 / 30.18) session 6 av. mean = 54.5 / 45.45
sum of means - 1st 30 minutes	317.25 / 339.18	252.25 / 184.41
(sessions 4 to 6) - mid 30 minutes	130 / 291.5 (sum of av. means)	156.25 / 157.94 (sum of av. means)
- last 30 minutes	142 / 162.08 (= 196.41/ 264.26)	130 / 148.73 (= 179.5 / 163.69)

Table C.7

Frequency and duration of ***sniff object*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	group FIOE	group FIOS
session 1; 1st 30 mins	NO OBJECTS PRESENT	78 / 71.54; 35/ 110.91; 31 / 26.64; 74 / 64.05 (mean = 54.5 / 68.29)
mid 30 mins		35 / 54.57; 34 / 13.54; 16 / 6.99; 66 / 65.32 (mean = 37.75 / 35.11)
last 30 mins		25 / 16.86; 8 / 2.34; 43 / 43.73; 81 / 64.19 (mean = 39.25 / 31.78)
		session 1 av. mean = 43.83 / 45.06
session 2; 1st 30 mins	NO OBJECTS PRESENT	60 / 61.59; 14 / 6.44; 41 / 36.39; 52 / 29.78 (mean = 41.75 / 33.55)
mid 30 mins		48 / 26.32; 19 / 7.41; 57 / 36.75; 78 / 64.17 (mean = 50.5 / 33.66)
last 30 mins		44 / 30.51; 21 / 6.62; 27 / 34.45; 76 / 71.31 (mean = 42 / 35.72)
		session 2 av. mean = 44.75 / 34.31
session 3; 1st 30 mins	NO OBJECTS PRESENT	37 / 19.26; 34 / 13.98; 25 / 17.12; 64 / 34.99 (mean = 40 / 21.34)
mid 30 mins		57 / 29.60; 29 / 7.01; 65 / 56.58; 72 / 68.04 (mean = 55.75 / 40.31)
last 30 mins		66 / 51.85; 19 / 4.24; 69 / 46.96; 78 / 56.18 (mean = 58 / 39.81)
		session 3 av. mean = 51.25 / 33.82
sum of means -1st 30 minutes		136.25 / 123.18
(sessions 1 to 3) - mid 30 minutes		144 / 109.08 (sum of av. means)
- last 30 minutes		139.25 / 107.31(= 139.83/ 113.19)

Table C.8

Mean frequency and duration of ***sniff object*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***sniff object*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	NO OBJECTS PRESENT	-	-
- dur.			
mid 30 mins- freq.			
- dur.			
last 30 mins- freq.			
- dur.			
FIOS 1st 30 mins - freq.	293.5	136.25	46.42
- dur.	300.01	123.18	41.06
mid 30 mins- freq.	189.5	144	75.99
- dur.	145.69	109.08	74.87
last 30 mins- freq.	172.75	139.25	80.61
- dur.	126.98	107.31	84.51

Table C.9

Frequency and duration of ***sniff and touch object*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	NO OBJECTS PRESENT	78 / 162.1; 80 / 143.3; 41 / 84.8; 77 / 184.7 (mean = 69 / 143.73)
mid 30 mins		22 / 66.3; 35 / 74.7; 22 / 48.8; 23 / 63.7 (mean = 25.5 / 63.38)
last 30 mins		21 / 33.2; 6 / 17.3; 12 / 12.1; 32 / 59.7 (mean = 17.75 / 30.58)
		session 1 av. mean = 37.42 / 79.23
session 2; 1st 30 mins	NO OBJECTS PRESENT	57 / 106.3; 46 / 115.1; 25 / 26.5; 45 / 69.1 (mean = 43.25 / 79.25)
mid 30 mins		41 / 51.2; 14 / 26.3; 15 / 35.1; 34 / 118.5 (mean = 26 / 57.78)
last 30 mins		39 / 40.8; 29 / 61.7; 14 / 48.0; 33 / 78.7 (mean = 28.75 / 57.3)
		session 2 av. mean = 32.67 / 64.78
session 3; 1st 30 mins	NO OBJECTS PRESENT	72 / 68.4; 43 / 64.8; 23 / 36.1; 50 / 95.4 (mean = 47 / 66.18)
mid 30 mins		41 / 46.3; 26 / 30.0; 30 / 52.7; 24 / 62.1 (mean = 30.25 / 47.78)
last 30 mins		43 / 42.0; 13 / 23.1; 55 / 140.1; 37 / 179.9 (mean = 37 / 96.28)
		session 3 av. mean = 38.08 / 70.08
sum of means -1st 30 minutes		159.25 / 289.16
(sessions 1 to 3) - mid 30 minutes		81.75 / 168.94 (sum of av. means)
- last 30 minutes		83.5 / 184.16 (= 108.17/ 214.09)
session 4; 1st 30 mins	65 / 168.1; 84 / 196.6; 102 / 280.9; 109 / 292.5 (mean = 90 / 234.53)	81 / 179.6; 70 / 137.9; 79 / 165.5; 92 / 195.0 (mean = 80.5 / 169.5)
mid 30 mins	21 / 116.6; 45 / 479.8*; 47 / 133.2; 17 / 57.3 (mean = 32.5 / 196.73)	15 / 39.9; 18 / 64.4; 36 / 148.7; 33 / 122.9 (mean = 25.5 / 93.98)
last 30 mins	17 / 108.5; 56 / 417.1; 36 / 243.4; 31 / 130.2 (mean = 35 / 224.8)	19 / 91.0; 18 / 63.9; 35 / 108.1; 15 / 59.5 (mean = 21.75 / 80.63)
	session 4 av. mean = 52.5 / 218.69	session 4 av. mean = 42.58/ 114.70
session 5; 1st 30 mins	51 / 116.8; 69 / 165.8; 52 / 162.4; 79 / 279.8 (mean = 62.75 / 181.2)	85 / 280.6; 70 / 189.0; 42 / 76.3; 75 / 152.6 (mean = 68 / 174.63)
mid 30 mins	34 / 126.8; 39 / 419.6; 45 / 251.1; 10 / 86.2 (mean = 32 / 220.93)	33 / 98.0; 17 / 30.9; 32 / 90.2; 29 / 130.0 (mean = 27.75 / 87.28)
last 30 mins	25 / 128.3; 38 / 233.2; 12 / 132.5; 18 / 626.9* (mean = 23.25/280.23)	39 / 108.3; 25 / 136.0; 29 / 184.7; 41 / 243.6 (mean = 33.5 / 168.15)
	session 5 av. mean = 39.33/ 227.45	session 5 av. mean = 43.08/ 143.35
session 6; 1st 30 mins	36 / 126.8; 41 / 119.1; 58 / 216.8; 60 / 262.3 (mean = 48.75/ 181.25)	52 / 164.1; 59 / 253.8; 63 / 164.3; 56 / 121.4 (mean = 57.5 / 175.9)
mid 30 mins	16 / 53.8; 33 / 330.3; 29 / 773.0; 24 / 162.3 (mean = 25.5/ 329.85*)	32 / 150.3; 29 / 174.3; 44 / 107.0; 77 / 348.7 (mean = 45.5 / 195.08)
last 30 mins	21 / 222.2; 42 / 399.9; 24 / 142.4; 33 / 86.0 (mean = 30 / 212.63)	2 / 13.4; 50 / 153.6; 22 / 186.8; 43 / 287.5 (mean = 29.25/ 160.33)
	session 6 av. mean = 34.75/ 241.24	session 6 av. mean = 44.08/ 177.10
sum of means - 1st 30 minutes	201.5 / 596.98	206 / 520.03
(sessions 4 to 6) - mid 30 minutes	90 / 747.51 (sum of av. means)	98.75 / 376.34 (sum of av. means)
- last 30 minutes	88.25 / 717.66 (= 126.58/ 687.38)	84.5 / 409.11 (= 129.74/ 435.15)

Table C.10

Frequency and duration of ***sniff and touch object*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	NO OBJECTS PRESENT	36 / 69.90; 18 / 30.08; 14 / 25.58; 24 / 46.90 (mean = 23 / 43.12)
mid 30 mins		18 / 58.86; 24 /41.08; 8 / 14.50; 21 / 54.32 (mean = 17.75 / 42.19)
last 30 mins		18 / 32.02; 3 / 5.57; 11 / 11.71; 29 / 58.08 (mean = 15.25 / 26.85)
		session 1 av. mean = 18.67 / 37.39
session 2; 1st 30 mins	NO OBJECTS PRESENT	27 / 56.34; 10 / 31.38; 17 / 17.40; 31 / 45.57 (mean = 21.25 / 37.67)
mid 30 mins		36 / 46.39; 11 / 24.91; 15 / 35.12; 28 / 106.40 (mean = 22.5 / 53.21)
last 30 mins		36 / 37.45; 16 / 40.75; 11 / 44.23; 25 / 68.47 (mean = 22 / 47.73)
		session 2 av. mean = 21.92 / 46.20
session 3; 1st 30 mins	NO OBJECTS PRESENT	47 / 38.85; 23 / 34.04; 10 / 14.01; 29 / 53.57 (mean = 27.25 / 35.12)
mid 30 mins		39 / 40.0; 17 / 20.21; 24 / 46.79; 21 / 52.66 (mean = 25.25 / 39.92)
last 30 mins		38 / 38.59; 9 / 18.38; 47 / 119.42; 28 / 135.63 (mean = 30.5 / 78.01)
		session 3 av. mean = 27.67 / 51.02
sum of means -1st 30 minutes		71.5 / 115.91
(sessions 1 to 3) - mid 30 minutes		65.5 / 135.32 (sum of av. means)
- last 30 minutes		67.75 / 152.59 (= 68.26 / 134.61)

Table C.11

Mean frequency and duration of ***sniff and touch object*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***sniff and touch object*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	NO OBJECTS PRESENT	-	-
- dur.			
mid 30 mins- freq.			
- dur.			
last 30 mins- freq.			
- dur.			
FIOS 1st 30 mins - freq.	159.25	71.5	44.90
- dur.	289.16	115.91	40.09
mid 30 mins- freq.	81.75	65.5	80.12
- dur.	168.94	135.32	80.10
last 30 mins- freq.	83.5	67.75	81.14
- dur.	184.16	152.59	82.86

Table C.12

Frequency and duration of ***chew/bite object*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins mid 30 mins last 30 mins	NO OBJECTS PRESENT	9 / 30.5; 0 / 0; 3 / 7.7; 10 / 14.2 (mean = 5.5 / 13.1) 3 / 7.9; 0 / 0; 0 / 0; 1 / 1.0 (mean = 1 / 2.23) 6 / 136.1; 0 / 0; 0 / 0; 5 / 80.9 (mean = 2.75 / 54.25) session 1 av. mean = 3.08 / 23.19
session 2; 1st 30 mins mid 30 mins last 30 mins	NO OBJECTS PRESENT	21 / 289.9; 0 / 0; 1 / 1.4; 7 / 20.9 (mean = 7.25 / 78.05) 19 / 449.6; 0 / 0; 1 / 0.5; 2 / 4.7 (mean = 5.5 / 113.7) 31 / 911.5*; 0 / 0; 0 / 0; 1 / 10.7 (mean = 8 / 230.55) session 2 av. mean = 6.92 / 140.77
session 3; 1st 30 mins mid 30 mins last 30 mins	NO OBJECTS PRESENT	33 / 992.1*; 0 / 0; 0 / 0; 4 / 9.0 (mean = 9.25 / 250.28) 19 / 852.7*; 0 / 0; 2 / 4.9; 1 / 24.2 (mean = 5.5 / 220.45) 23 / 514.5*; 0 / 0; 1 / 0.3; 0 / 0 (mean = 6 / 128.7) session 3 av. mean = 6.92 / 199.81
sum of means -1st 30 minutes **(sessions 1 to 3) - mid 30 minutes** **- last 30 minutes**		22 / 341.43 12 / 336.38 (sum of av. means) 16.75 / 413.5 (= 16.92 / 363.77)
session 4; 1st 30 mins mid 30 mins last 30 mins	2 / 2.2; 4 / 13.9; 18 / 164.5; 24 / 341.1 (mean = 12 / 130.43) 1 / 3.0; 0 / 0; 5 / 73.9; 1 / 0.8 (mean = 1.75 / 19.43) 3 / 16.1; 1 / 1.5; 0 / 0; 0 / 0 (mean = 1 / 4.4) session 4 av. mean = 4.92 / 51.42	11 / 148.1; 21 / 175.0; 33 / 471.4*; 30 / 161.4 (mean = 23.75/ 238.98) 2 / 3.4; 0 / 0; 4 / 12.7; 6 / 70.0 (mean = 3 / 21.53) 0 / 0; 0 / 0; 4 / 5.7; 0 / 0 (mean = 1 / 1.43) session 4 av. mean = 9.25 / 87.31
session 5; 1st 30 mins mid 30 mins last 30 mins	2 / 2.3; 2 / 1.8; 1 / 2.5; 9 / 52.8 (mean = 3.5 / 14.85) 0 / 0; 0 / 0; 1 / 0.6; 0 / 0 (mean = 0.25 / 0.15) 0 / 0; 1 / 4.0; 0 / 0; 0 / 0 (mean = 0.25 / 1.0) session 5 av. mean = 1.33 / 5.33	24 / 176.4; 12 / 33.7; 12 / 120.0; 14 / 78.0 (mean = 15.5 / 102.03) 10 / 74.9; 1 / 3.8; 0 / 0; 1 / 3.1 (mean = 3 / 20.45) 2 / 21.1; 0 / 0; 0 / 0; 4 / 13.7 (mean = 1.5 / 8.7) session 5 av. mean = 6.67 / 43.73
session 6; 1st 30 mins mid 30 mins last 30 mins	0 / 0; 0 / 0; 6 / 336.1; 7 / 46.2 (mean = 3.25 / 95.58) 0 / 0; 1 / 5.7; 0 / 0; 0 / 0 (mean = 0.25 / 1.43) 0 / 0; 0 / 0; 0 / 0; 0 / 0 (mean = 0 / 0) session 6 av. mean = 1.17 / 32.34	7 / 26.8; 9 / 34.1; 24 / 325.5; 24 / 427.1 (mean = 16 / 203.38) 0 / 0; 2 / 4.3; 4 / 137.9; 2 / 4.6 (mean = 2 / 36.7) 0 / 0; 0 / 0; 0 / 0; 0 / 0 (mean = 0 / 0) session 6 av. mean = 6 / 80.03
sum of means - 1st 30 minutes **(sessions 4 to 6) - mid 30 minutes** **- last 30 minutes**	18.75 / 240.86 2.25 / 21.01 (sum of av. means) 1.25 / 5.4 (= 7.42 / 89.09)	55.25 / 544.39 8 / 78.68 (sum of av. means) 2.5 / 10.13 (= 21.92 / 211.07)

Table C.13

Frequency and duration of ***chew/bite object*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	group FIOE	group FIOS
session 1; 1st 30 mins	NO OBJECTS PRESENT	6 / 26.60; 0 / 0; 0 / 0; 1 / 2.65 (mean = 1.75 / 7.31)
mid 30 mins		3 / 7.88; 0 / 0; 0 / 0; 1 / 0.97 (mean = 1 / 2.21)
last 30 mins		4 / 99.84; 0 / 0; 0 / 0; 4 / 70.69 (mean = 2 / 42.63)
		session 1 av. mean = 1.58 / 17.38
session 2; 1st 30 mins	NO OBJECTS PRESENT	12 / 242.82; 0 / 0; 0 / 0; 6 / 19.29 (mean = 4.5 / 65.53)
mid 30 mins		17 / 399.02; 0 / 0; 1 / 0.47; 2 / 4.68 (mean = 5 / 101.04)
last 30 mins		28 / 861.20;* 0 / 0; 0 / 0; 1 / 10.71 (7.25 / 217.98)
		session 2 av. mean = 5.58 / 128.18
session 3; 1st 30 mins	NO OBJECTS PRESENT	26 / 879.55;* 0 / 0; 0 / 0; 3 / 8.20 (mean = 7.25 / 221.94)
mid 30 mins		18 / 749.72;* 0 / 0; 2 / 4.88; 1 / 24.22 (mean = 5.25 / 194.71)
last 30 mins		23 / 514.54;* 0 / 0; 1 / 0.34; 0 / 0 (mean = 6 / 128.72)
		session 3 av. mean = 6.17 / 181.79)
sum of means -1st 30 minutes		13.5 / 294.78
(sessions 1 to 3) - mid 30 minutes		11.25 / 297.96 (sum of av. means)
- last 30 minutes		15.25 / 389.33 (= 13.33 / 327.35)

Table C.14

Mean frequency and duration of ***chew/bite object*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***chew/bite object*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	NO OBJECTS PRESENT	-	-
- dur.			
mid 30 mins- freq.			
- dur.			
last 30 mins- freq.			
- dur.			
FIOS 1st 30 mins - freq.	22	13.5	61.36
- dur.	341.43	294.78	86.34
mid 30 mins- freq.	12	11.25	93.75
- dur.	336.38	297.96	88.58
last 30 mins- freq.	16.75	15.25	91.05
- dur.	413.5	389.33	94.16

Table C.15

Frequency and duration of ***propping*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	43 / 63.5; 30 / 55.8; 31 / 93.1; 39 / 87.2 (mean = 35.75 / 74.9)	24 / 41.5; 58 / 114.6; 31 / 59.6; 15 / 44.9 (mean = 32 / 65.15)
mid 30 mins	71 / 164.2; 37 / 129.0; 17 / 75.4; 9 / 40.5 (mean = 33.5 / 102.28)	4 / 14.4; 73 / 141.9; 106 / 317.3; 19 / 43.8 (mean = 50.5 / 129.35)
last 30 mins	18 / 61.5; 22 / 72.1; 23 / 103.6; 26 / 69.4 (mean = 22.25 / 76.65) session 1 av. mean = 30.5 / 84.61	7 / 41.3; 23 / 52.6; 45 / 191.3; 14 / 34.0 (mean = 22.25 / 79.8) session 1 av. mean = 34.92 / 91.43
session 2; 1st 30 mins	77 / 155.3; 43 / 166.9; 27 / 75.4; 29 / 68.9 (mean = 44 / 116.63)	13 / 33.7; 36 / 61.7; 36 / 76.4; 28 / 98.6 (mean = 28.25 / 67.6)
mid 30 mins	25 / 79.1; 8 / 33.8; 16 / 70.8; 2 / 4.5 (mean = 12.75 / 47.05)	6 / 17.9; 45 / 108.9; 45 / 96.6; 14 / 59.4 (mean = 27.5 / 70.7)
last 30 mins	23 / 69.1; 44 / 219.6; 15 / 69.0; 9 / 34.2 (mean = 22.75 / 97.98) session 2 av. mean = 26.5 / 87.22	2 / 2.8; 74 / 119.6; 12 / 50.6; 12 / 47.0 (mean = 25 / 55.0) session 2 av. mean = 26.92 / 64.43
session 3; 1st 30 mins	51 / 110.7; 22 / 54.4; 35 / 106.3; 47 / 118.0 (mean = 38.75 / 97.35)	6 / 11.4; 46 / 92.2; 25 / 51.0; 33 / 142.9 (mean = 27.5 / 74.38)
mid 30 mins	25 / 77.3; 10 / 26.8; 13 / 73.3; 12 / 44.9 (mean = 15 / 55.58)	8 / 17.7; 104 / 367.5; 17 / 47.8; 12 / 42.5 (mean = 35.25 / 118.88)
last 30 mins	13 / 24.4; 13 / 47.6; 13 / 66.3; 0 / 0 (mean = 9.75 / 34.58), session 3 av. mean = 21.17 / 62.50	1 / 1.0; 101 / 296.9; 67 / 191.0; 9 / 17.9 (mean = 44.5 / 126.7) session 3 av. mean = 35.75/ 106.65
sum of means -1st 30 minutes	118.5 / 288.88	87.75 / 207.13
(sessions 1 to 3) - mid 30 minutes	61.25 / 204.91 (sum of av. means)	113.25 / 318.93 (sum of av. means)
- last 30 minutes	54.75 / 209.21 (= 78.17 / 234.33)	91.75 / 261.5 (= 97.59 / 262.51)
session 4; 1st 30 mins	25 / 56.7; 16 / 39.1; 33 / 95.9; 15 / 32.9 (mean = 22.25 / 56.15)	12 / 23.2; 50 / 76.0; 24 / 93.9; 32 / 105.5 (mean = 29.5 / 74.65)
mid 30 mins	14 / 48.3; 11 / 52.5; 23 / 67.2; 6 / 16.8 (mean = 13.5 / 46.2)	10 / 37.5; 43 / 135.8; 31 / 123.5; 22 / 107.4 (mean = 26.5 / 101.05)
last 30 mins	15 / 48.3; 23 / 100.9; 20 / 92.2; 22 / 83.0 (mean = 20 / 81.1) session 4 av. mean = 18.58 / 61.15	5 / 17.0; 58 / 176.4; 15 / 93.0; 15 / 89.8 (mean = 23.25 / 94.05) session 4 av. mean = 26.42 / 89.92
session 5; 1st 30 mins	41 / 98.2; 50 / 150.2; 28 / 93.0; 51 / 157.5 (mean = 42.5 / 124.73)	22 / 79.1; 125 / 298.2; 35 / 120.3; 38 / 171.7 (mean = 55 / 167.33)
mid 30 mins	27 / 137.8; 32 / 109.3; 16 / 64.8; 5 / 16.9 (mean = 20 / 82.2)	10 / 31.6; 62 / 253.4; 28 / 108.9; 18 / 86.6 (mean = 29.5 / 120.13)
last 30 mins	21 / 79.8; 38 / 160.6; 12 / 76.9; 15 / 63.4 (mean = 21.5 / 95.18) session 5 av. mean = 28 / 100.70	18 / 75.2; 60 / 160.9; 43 / 174.1; 14 / 67.2 (mean = 33.75 / 119.35) session 5 av. mean = 39.42/ 135.60
session 6; 1st 30 mins	42 / 125.5; 26 / 74.3; 35 / 117.8; 41 / 167.1 (mean = 36 / 121.18)	21 / 82.9; 55 / 135.9; 36 / 123.6; 39 / 159.2 (mean = 37.75 / 125.4)
mid 30 mins	43 / 161.2; 4 / 19.4; 39 / 162.0; 21 / 133.2 (mean = 26.75/ 118.95)	19 / 67.8; 18 / 71.4; 61 / 287.2; 57 / 278.8 (mean = 38.75 / 176.3)
last 30 mins	13 / 64.4; 24 / 136.8; 24 / 101.5; 35 / 87.8 (mean = 24 / 97.63) session 6 av. mean = 28.92/ 112.59	1 / 1.4; 113 / 331.5; 22 / 88.2; 30 / 161.4 (mean = 41.5 / 145.63) session 6 av. mean = 39.33/ 149.11
sum of means - 1st 30 minutes	100.75 / 302.06	122.25 / 367.38
(sessions 4 to 6) - mid 30 minutes	60.25 / 247.35 (sum of av. means)	94.75 / 397.48 (sum of av. means)
- last 30 minutes	65.5 / 273.91 (= 75.5 / 274.44)	98.5 / 359.03 (= 105.17/ 374.63)

Table C.16

Frequency and duration of ***propping*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	3 / 1.47; 11 / 25.17; 15 / 54.69; 7 / 8.69 (mean = 9 / 22.51)	8 / 12.64; 9 / 23.28; 6 / 11.26; 9 / 28.51 (mean = 8 / 18.92)
mid 30 mins	17 / 52.21; 26 / 85.51; 14 / 64.59; 8 / 37.06 (mean = 16.25 / 59.84)	1 / 4.33; 45 / 87.91; 16 / 45.13; 18 / 40.99 (mean = 20 / 44.59)
last 30 mins	4 / 28.53; 12 / 42.53; 19 / 81.92; 24 / 66.42 (mean = 14.75 / 54.85)	6 / 41.15; 7 / 23.26; 28 / 111.10; 14 / 33.97 (mean = 13.75 / 52.37)
	session 1 av. mean = 13.33 / 45.73	session 1 av. mean = 13.92 / 38.63
session 2; 1st 30 mins	28/ 49.96; 25/ 104.32; 18/ 55.49; 12 / 31.73 (mean = 20.75 / 60.38)	6 / 23.74; 13 / 29.82; 17 / 45.52; 20 / 76.29 (mean = 14 / 43.84)
mid 30 mins	13 / 52.02; 8 / 33.76; 14 / 64.05; 0 / 0 (mean = 8.75 / 37.46)	6 / 17.92; 37 / 87.27; 40 / 91.23; 14 / 59.38 (mean = 24.25 / 63.95)
last 30 mins	9 / 26.93; 26/ 153.55; 10/ 59.15; 9 / 34.18 (mean = 13.5 / 68.45)	2 / 2.76; 47 / 80.78; 5 / 23.59; 9 / 35.98 (mean = 15.75 / 35.78)
	session 2 av. mean = 14.33 / 55.43	session 2 av. mean = 18 / 47.86
session 3; 1st 30 mins	35 / 87.93; 16 / 46.17; 10/ 22.50; 7 / 15.18 (mean = 17 / 42.95)	2 / 5.28; 23 / 51.61; 9 / 15.05; 18 / 88.23 (mean = 13 / 40.04)
mid 30 mins	22 / 68.07; 9 / 21.51; 9 / 58.99; 5 / 22.90 (mean = 11.25 / 42.87)	8 / 17.70; 72 / 259.72; 12 / 34.40; 11 / 40.49 (mean = 25.75 / 88.08)
last 30 mins	7 / 11.12; 10 / 36,88; 13 / 66.31; 0 / 0 (mean = 7.5 / 28.58)	1 / 0.61; 90 / 269.77; 57 / 167.93; 8 / 16.38 (mean = 39 / 113.67)
	session 3 av. mean = 11.92 / 38.13	session 3 av. mean = 25.92 / 80.60
sum of means -1st 30 minutes	46.75 / 125.84	35 / 102.8
(sessions 1 to 3) - mid 30 minutes	36.25 / 140.17 (sum of av. means)	70 / 196.62 (sum of av. means)
- last 30 minutes	35.75 / 151.88 (= 39.58/ 139.29)	68.5 / 201.82 (= 57.84 / 167.09)

Table C.17

Mean frequency and duration of ***propping*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***propping*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	118.5	46.75	39.45
- dur.	288.88	125.84	43.56
mid 30 mins- freq.	61.25	36.25	59.18
- dur.	204.91	140.17	68.41
last 30 mins- freq.	54.75	35.75	65.30
- dur.	209.21	151.88	72.60
FIOS 1st 30 mins - freq.	87.75	35	39.89
- dur.	207.13	102.8	49.63
mid 30 mins- freq.	113.25	70	61.81
- dur.	318.93	196.62	61.65
last 30 mins- freq.	91.75	68.5	74.66
- dur.	261.5	201.82	77.18

Table C.18

Frequency and duration of ***displacement*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	40 / 35.3; 20 / 97.2; 51 / 265.3; 26 / 142.8 (mean = 34.25/ 135.15)	34 / 149.7; 7 / 7.5; 9 / 13.1; 60 / 204.5 (mean = 27.5 / 93.7)
mid 30 mins	24 / 40.8; 11 / 50.5; 28 / 367.33; 35 / 340.6 (mean = 24.5 / 199.8)	27 / 208.0; 27 / 94.6; 24 / 92.9; 42 / 455.7* (mean = 30 / 212.8)
last 30 mins	17 / 224.9; 17 / 98.6; 28 / 488.4*; 38 / 234.1 (mean = 25 / 261.5)	11 / 77.7; 16 / 42.1; 54 / 286.7; 25 / 204.1 (mean = 26.5 / 152.65)
	session 1 av. mean = 27.92/ 198.82	session 1 av. mean = 28 / 153.05
session 2; 1st 30 mins	24 / 98.2; 22 / 101.3; 42 / 236.3; 38 / 373.8 (mean = 31.5 / 202.4)	27 / 109.4; 20 / 39.1; 24 / 48.7; 54 / 359.0 (mean = 31.25/ 139.05)
mid 30 mins	35 / 283.8; 16 / 198.9; 21 / 295.2; 23 / 277.7 (mean = 23.75 / 263.9)	30 / 256.0; 22 / 47.5; 57 / 398.1; 47 / 373.4 (mean = 39 / 268.75)
last 30 mins	21 / 194.0; 10 / 41.6; 22 / 341.6; 24 / 206.6 (mean = 19.25/ 195.95)	13 / 147.1; 32 / 55.1; 47 / 279.3; 88 / 394.8 (mean = 45 / 219.08)
	session 2 av. mean = 24.83/ 220.75	session 2 av. mean = 38.42/ 208.96
session 3; 1st 30 mins	36 / 139.5; 26 / 280.2; 36 / 276.3; 28 / 179.5 (mean = 31.5 / 218.88)	12 / 40.2; 7 / 14.3; 20 / 54.4; 62 / 294.9 (mean = 25.25/ 100.95)
mid 30 mins	18 / 93.8; 10 / 282.3; 28 / 237.9; 19 / 224.9 (mean = 18.75/ 209.73)	13 / 139.1; 13 / 27.5; 26 / 155.6; 37 / 272.8 (mean = 22.25/ 148.75)
last 30 mins	20 / 107.7; 32 / 452.1*; 25 / 269.8; 10 / 278.3 (mean = 21.75/ 276.98)	23 / 198.1; 10 / 81.7; 34 / 170.6; 51 / 351.3 (mean = 29.5 / 200.43)
	session 3 av. mean = 24 / 235.20	session 3 av. mean = 25.67/ 150.04
sum of means -1st 30 minutes	97.25 / 556.43	84 / 333.7
(sessions 1 to 3) - mid 30 minutes	67 / 673.43 (sum of av. means)	91.25 / 630.3 (sum of av. means)
- last 30 minutes	66 / 734.43 (= 76.75 / 654.77)	101 / 572.16 (= 92.09 / 512.05)
session 4; 1st 30 mins	28 / 63.6; 17 / 42.4; 40 / 346.2; 21 / 116.1 (mean = 26.5 / 142.08)	29 / 426.7; 7 / 24.1; 3 / 33.4; 39 / 410.3 (mean = 19.5 / 223.63)
mid 30 mins	14 / 297.3; 6 / 33.0; 11 / 76.0; 22 / 262.5 (mean = 13.25 / 167.2)	23 / 1163.7*; 5 / 122.3; 14 / 324.5; 16 / 108.0 (mean = 14.5 / 429.63)
last 30 mins	10 / 222.3; 13 / 124.0; 16 / 215.1; 20 / 561.5* (mean= 14.75/280.73)	11 / 150.9; 7 / 54.9; 6 / 82.7; 20 / 109.8 (mean = 11 / 99.58)
	session 4 av. mean = 18.17/ 196.67	session 4 av. mean = 15 / 250.95
session 5; 1st 30 mins	32 / 279.4; 21 / 353.9; 39 / 788.6*; 36 / 589.9* (mean = 32 / 502.95)	23 / 208.8; 16 / 37.7; 7 / 23.3; 56 / 814.0 (mean = 25.5 / 270.95)
mid 30 mins	12 / 624.1; 8 / 87.6; 32 / 259.1; 2 / 19.4 (mean = 13.5 / 247.55)	13 / 799.9*; 36 / 442.0; 10 / 244.0; 23 / 216.1 (mean = 20.5 / 425.5)
last 30 mins	15 / 299.8; 14 / 268.6; 48 / 831.0*; 18 / 626.9* (mean = 23.75/506.58)	35 / 807.1*; 2 / 12.3; 18 / 135.5; 21 / 110.4 (mean = 19 / 266.33)
	session 5 av. mean = 23.08/ 419.03	session 5 av. mean = 21.67/ 320.93
session 6; 1st 30 mins	15 / 54.8; 17 / 154.4; 20 / 214.9; 28 / 546.9* (mean = 20 / 242.75)	18 / 731.0*; 36 / 594.5*; 9 / 85.0; 34 / 532.3* (mean = 24.25/ 485.7)
mid 30 mins	17 / 310.8; 3 / 26.1; 15 / 285.0; 13 / 465.8* (mean = 12 / 271.93)	24 / 635.1*; 26 / 603.4*; 15 / 69.6; 31 / 148.1 (mean = 24 / 364.05)
last 30 mins	2 / 105.1; 7 / 34.9; 7 / 107.7; 27 / 491.6* (mean = 10.75/184.83)	2 / 43.4; 14 / 83.8; 10 / 118.4; 11 / 43.9 (mean = 9.25 / 72.38)
	session 6 av. mean = 14.25/ 233.17	session 6 av. mean = 19.17/ 307.38
sum of means - 1st 30 minutes	78.5 / 887.78	69.25 / 980.28
(sessions 4 to 6) - mid 30 minutes	38.75 / 686.68 (sum of av. means)	59 / 1219.18 (sum of av. means)
- last 30 minutes	49.25 / 972.14 (= 55.5 / 848.87)	39.25 / 438.29 (= 55.84 / 879.26)

Table C.19

Frequency and duration of ***displacement*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	12 / 5.36; 11 / 72.22; 23 / 152.89; 13 / 106.87 (mean = 14.75/ 84.34)	19/ 125.62; 2 / 1.18; 4 / 6.70; 23 / 124.66 (mean = 12 / 64.54)
mid 30 mins	7 / 9.45; 11 / 50.48; 22 / 355.08; 32 / 310.59 (mean = 18 / 181.4)	21/ 176.61; 19 / 30.87; 7 / 41.50; 38 / 439.51 (mean =21.25/172.12)
last 30 mins	3 / 19.19; 11 / 77.70; 25 / 446.54; 25 / 112.32 (mean = 16 / 163.94)	7 / 51.98; 5 / 16.24; 42 / 259.08; 24 / 201.72 (mean = 19.5/ 132.26)
	session 1 av. mean = 16.25/ 143.23	session 1 av. mean = 17.58/ 122.97
session 2; 1st 30 mins	13 / 60.42; 9 / 58.74; 21 / 89.15; 23 / 342.61 (mean = 16.5/ 137.73)	18 / 81.54; 8 / 26.26; 15 / 27.77; 29 / 238.90 (mean = 17.5 / 93.62)
mid 30 mins	23/ 246.38; 14/198.17; 19/293.59; 20 / 234.93 (mean = 19 / 243.27)	23/232.23; 15/23.68; 47/381.31; 41 / 360.52 (mean = 31.5 / 249.44)
last 30 mins	21/ 193.98; 5/ 38.79; 12/ 267.85; 16 / 190.82 (mean = 13.5/ 172.86)	11/141.32; 20/29.68; 41/270.24; 35 / 240.53 (mean= 26.75/ 170.44)
	session 2 av. mean = 16.33/ 184.62	session 2 av. mean = 25.25/ 171.17
session 3; 1st 30 mins	24/128.53; 19/243.43; 25/249.66; 17 / 113.01 (mean =21.25/183.66)	8 / 32.42; 5 / 8.90; 15 / 39.83; 40 / 256.65 (mean = 17 / 84.45)
mid 30 mins	15/ 92.08; 10/ 282.28; 16/ 220.54; 17 / 224.24 (mean= 14.5/ 204.79)	12/ 138.20; 6/ 16.98; 22/ 146.24; 33 / 266.69 (mean = 18.25/142.03)
last 30 mins	15/102.71; 32/452.10;* 16/223.52; 9 / 277.72 (mean = 18 / 264.01)	18/ 186.34; 7/ 69.99; 30/ 162.23; 32 / 300.74 (mean= 21.75/ 179.83)
	session 3 av. mean = 17.92/ 217.49	session 3 av. mean = 19 / 135.44
sum of means -1st 30 minutes	52.5 / 405.73	46.5 / 242.61
(sessions 1 to 3) - mid 30 minutes	51.5 / 629.46 (sum of av. means)	71 / 563.59 (sum of av. means)
- last 30 minutes	47.5 / 600.81 (= 50.5 / 545.34)	68 / 482.53 (= 61.83 / 429.58)

Table C.20

Mean frequency and duration of ***displacement*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***displacement*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	97.25	52.5	53.98
- dur.	556.43	405.73	72.92
mid 30 mins- freq.	67	51.5	76.87
- dur.	673.43	629.46	93.47
last 30 mins- freq.	66	47.5	71.97
- dur.	734.43	600.81	81.81
FIOS 1st 30 mins - freq.	84	46.5	55.36
- dur.	333.7	242.61	72.70
mid 30 mins- freq.	91.25	71	77.81
- dur.	630.3	563.59	89.42
last 30 mins- freq.	101	68	67.33
- dur.	572.16	482.53	84.33

Table C.21

Frequency and duration of ***digging/burying*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	group FIOE	group FIOS
session 1; 1st 30 mins	64 / 93.2; 18 / 29.8; 46 / 48.8; 31 / 24.1 (mean = 39.75 / 48.98)	10 / 6.8; 7 / 22.3; 6 / 8.5; 17 / 16.9 (mean = 10 / 13.63)
mid 30 mins	50 / 49.1; 0 / 0; 42 / 45.3; 11 / 7.5 (mean = 25.75 / 25.48)	12 / 42.4; 18 / 17.1; 7 / 11.5; 14 / 9.2 (mean = 12.75 / 20.05)
last 30 mins	34 / 33.6; 11 / 27.4; 71 / 78.0; 8 / 11.1 (mean = 31 / 37.53)	0 / 0; 0 / 0; 7 / 16.3; 43 / 34.4 (mean = 12.5 / 12.68)
	session 1 av. mean = 32.17 / 37.33	session 1 av. mean = 11.75 / 15.45
session 2; 1st 30 mins	26 / 29.3; 15 / 25.8; 44 / 42.2; 22 / 14.2 (mean = 26.75 / 27.88)	12 / 10.1; 4 / 6.4; 6 / 3.1; 17 / 17.3 (mean = 9.75 / 9.23)
mid 30 mins	10 / 5.2; 0 / 0; 51 / 72.4; 1 / 0.3 (mean = 15.5 / 19.48)	14 / 28.9; 9 / 11.7; 2 / 11.9; 11 / 10.8 (mean = 9 / 15.83)
last 30 mins	13 / 16.1; 9 / 16.7; 4 / 3.4; 3 / 0.9 (mean = 7.25 / 9.28)	1 / 0.5; 3 / 3.0; 1 / 1.1; 42 / 87.3 (mean = 11.75 / 22.98)
	session 2 av. mean = 16.5 / 18.88	session 2 av. mean = 10.17 / 16.01)
session 3; 1st 30 mins	28 / 39.8; 16 / 27.1; 37 / 34.6; 24 / 26.4 (mean = 26.25 / 31.98)	2 / 1.6; 20 / 67.8; 5 / 10.9; 59 / 43.5 (mean = 21.5 / 30.95)
mid 30 mins	15 / 13.7; 3 / 1.0; 18 / 12.9; 17 / 18.3 (mean = 13.25 / 11.48)	4 / 5.5; 4 / 5.5; 5 / 9.3; 10 / 13.4 (mean = 5.75 / 8.43)
last 30 mins	27 / 20.3; 2 / 2.0; 14 / 7.9; 1 / 0.8 (mean = 11 / 7.75),	5 / 5.5; 6 / 6.1; 4 / 1.8; 14 / 17.6 (mean = 7.25 / 7.75)
	session 3 av. mean = 16.83 / 17.07	session 3 av. mean = 11.5 / 15.71
sum of means -1st 30 minutes	92.75 / 108.84	41.25 / 53.81
(sessions 1 to 3) - mid 30 minutes	54.5 / 56.44 (sum of av. means)	27.5 / 44.31 (sum of av. means)
- last 30 minutes	49.25 / 54.56 (= 65.5 / 73.28)	31.5 / 43.41 (= 33.42 / 47.17)
session 4; 1st 30 mins	52 / 60.5; 25 / 60.1; 34 / 25.1; 15 / 11.4 (mean = 31.5 / 39.28)	28 / 37.3; 17 / 32.8; 5 / 4.3; 42 / 46.6 (mean = 23 / 30.25)
mid 30 mins	13 / 8.8; 9 / 18.9; 26 / 13.5; 7 / 4.2 (mean = 13.75 / 11.35)	6 / 11.9; 5 / 17.1; 1 / 1.2; 42 / 59.8 (mean = 13.5 / 22.5)
last 30 mins	17 / 9.8; 6 / 12.4; 19 / 15.5; 11 / 11.3 (mean = 13.25 / 12.25)	16 / 25.2; 0 / 0; 5 / 5.2; 29 / 17.4 (mean = 12.5 / 11.95)
	session 4 av. mean = 19.5 / 20.96	session 4 av. mean = 16.33 / 21.57
session 5; 1st 30 mins	80 / 69.3; 8 / 6.0; 41 / 34.0; 29 / 11.0 (mean = 39.5 / 30.08)	42 / 77.9; 52 / 110.7; 8 / 6.0; 28 / 19.2 (mean = 32.5 / 53.45)
mid 30 mins	7 / 17.1; 0 / 0; 17 / 13.4; 0 / 0 (mean = 6 / 7.63)	9 / 17.3; 12 / 10.0; 0 / 0; 36 / 38.6 (mean = 14.25 / 16.48)
last 30 mins	6 / 3.0; 4 / 6.0; 1 / 0.4; 0 / 0 (mean = 2.75 / 2.35)	29 / 33.3; 7 / 6.7; 8 / 6.7; 36 / 27.5 (mean = 20 / 18.55)
	session 5 av. mean = 16.08 / 13.35	session 5 av. mean = 22.25 / 29.49
session 6; 1st 30 mins	31 / 24.0; 30 / 41.5; 96 / 79.6; 16 / 15.8 (mean = 43.25 / 40.23)	39 / 53.6; 29 / 43.5; 6 / 6.6; 38 / 23.8 (mean = 28 / 31.88)
mid 30 mins	4 / 7.8; 3 / 5.5; 16 / 14.8; 2 / 1.4 (mean = 6.25 / 7.38)	40 / 50.0; 8 / 16.2; 1 / 0.8; 45 / 51.2 (mean = 23.5 / 29.55)
last 30 mins	7 / 10.5; 2 / 3.8; 36 / 26.1; 3 / 8.9 (mean = 12 / 12.33)	0 / 0; 17 / 19.3; 1 / 1.4; 21 / 23.7 (mean = 9.75 / 11.1)
	session 6 av. mean = 20.5 / 19.98	session 6 av. mean = 20.42 / 24.18
sum of means - 1st 30 minutes	114.25 / 109.59	83.5 / 115.58
(sessions 4 to 6) - mid 30 minutes	26 / 26.36 (sum of av. means)	51.25 / 68.53 (sum of av. means)
- last 30 minutes	28 / 26.93 (= 56.08 / 54.29)	42.25 / 41.6 (= 59 / 75.24)

Table C.22

Frequency and duration of ***digging/burying*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	36 / 55.08; 14 / 26.45; 30 / 37.01; 13 / 5.90 (mean = 23.25 / 31.11)	6 / 5.10; 3 / 6.60; 2 / 1.07; 12 / 14.01 (mean = 5.75 / 6.70)
mid 30 mins	27 / 30.04; 0 / 0; 41 / 45.04; 11 / 7.53 (mean = 19.75 / 20.65)	10 / 40.82; 9 / 10.18; 1 / 3.21; 13 / 8.58 (mean = 8.25 / 15.70)
last 30 mins	20 / 20.21; 8 / 20.56; 60 / 67.50; 8 / 11.13 (mean = 24 / 29.85)	0 / 0; 0 / 0; 7 / 16.31; 43 / 34.45 (mean = 12.5 / 12.69)
	session 1 av. mean = 22.33 / 27.20	session 1 av. mean = 8.83 / 11.70
session 2; 1st 30 mins	16 / 18.16; 12 / 19.78; 30 / 33.96; 10 / 7.48 (mean = 17 / 19.85)	10 / 7.26; 1 / 2.54; 4 / 1.49; 12 / 13.16 (mean = 6.75 / 6.11)
mid 30 mins	8 / 4.53; 0 / 0; 43 / 67.56; 1 / 0.33 (mean = 13 / 18.11)	14 / 28.86; 9 / 11.71; 2 / 11.92; 11 / 10.82 (mean = 9 / 15.83)
last 30 mins	9 / 14.03; 5 / 13.32; 4 / 3.45; 3 / 0.89 (mean = 5.25 / 7.92)	1 / 0.48; 2 / 1.73; 1 / 1.13; 35 / 82.28 (mean = 9.75 / 21.41)
	session 2 av. mean = 11.75 / 15.29	session 2 av. mean = 8.5 / 14.45
session 3; 1st 30 mins	18 / 27.52; 8 / 10.85; 19 / 16.00; 17 / 22.41 (mean = 15.5 / 19.20)	0 / 0; 16 / 64.31; 1 / 7.24; 27 / 25.44 (mean = 11 / 24.25)
mid 30 mins	12 / 12.69; 3 / 1.05; 17 / 12.20; 15 / 17.28 (mean = 11.75 / 10.81)	4 / 5.50; 3 / 3.80; 4 / 4.47; 10 / 13.40 (mean = 5.25 / 6.79)
last 30 mins	20 / 17.34; 2 / 1.96; 10 / 6.59; 1 / 0.80 (mean = 8.25 / 6.67)	5 / 5.49; 4 / 5.70; 4 / 1.83; 14 / 17.57 (mean = 6.75 / 7.65)
	session 3 av. mean = 11.83 / 12.23	session 3 av. mean = 7.67 / 12.90
sum of means -1st 30 minutes	55.75 / 70.16	23.5 / 37.06
(sessions 1 to 3) - mid 30 minutes	44.5 / 49.57 (sum of av. means)	22.5 / 38.32 (sum of av. means)
- last 30 minutes	37.5 / 44.44 (= 45.91 / 54.72)	29 / 41.75 (= 25 / 39.05)

Table C.23

Mean frequency and duration of ***digging/burying*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***digging/burying*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	92.75	55.75	60.11
- dur.	108.84	70.16	64.46
mid 30 mins- freq.	54.5	44.5	81.65
- dur.	56.44	49.57	87.83
last 30 mins- freq.	49.25	37.5	76.14
- dur.	54.56	44.44	81.45
FIOS 1st 30 mins - freq.	41.25	23.5	56.97
- dur.	53.81	37.06	68.87
mid 30 mins- freq.	27.5	22.5	81.82
- dur.	44.31	38.32	86.48
last 30 mins- freq.	31.5	29	92.06
- dur.	43.41	41.75	96.18

Table C.24

Frequency and duration of ***sniff bottle*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	31 / 24.3; 21 / 9.2; 27 / 15.1; 34 / 13.2 (mean = 28.25 / 15.45)	31 / 12.7; 42 / 116.4; 37 / 28.4; 38 / 16.0 (mean = 37 / 43.38)
mid 30 mins	28 / 19.9; 4 / 2.5; 27 / 11.3; 18 / 9.8 (mean = 19.25 / 10.88)	14 / 30.0; 28 / 27.4; 36 / 15.6; 23 / 11.5 (mean = 25.25 / 21.13)
last 30 mins	27 / 14.5; 3 / 5.4; 22 / 10.3; 41 / 23.7 (mean = 23.25 / 13.48) session 1 av. mean = 23.58 / 13.27	13 / 12.3; 24 / 17.0; 24 / 15.7; 24 / 9.8 (mean = 21.25 / 13.7) session 1 av. mean = 27.83 / 26.07
session 2; 1st 30 mins	42 / 19.2; 26 / 13.7; 27 / 11.5; 31 / 13.2 (mean = 21 / 14.4)	37 / 22.7; 18 / 10.8; 30 / 13.6; 27 / 9.8 (mean = 28 / 14.23)
mid 30 mins	21 / 9.9; 12 / 6.0; 28 / 10.1; 26 / 19.6 (mean = 21.75 / 11.4)	17 / 14.7; 22 / 18.4; 26 / 14.3; 21 / 14.3 (mean = 21.5 / 15.43)
last 30 mins	18 / 9.1; 24 / 11.2; 39 / 24.3; 22 / 16.3 (mean = 25.75 / 15.23) session 2 av. mean = 22.83 / 13.68	8 / 5.9; 17 / 7.5; 20 / 12.1; 18 / 10.2 (mean = 15.75 / 8.93) session 2 av. mean = 21.75 / 12.86
session 3; 1st 30 mins	37 / 23.4; 45 / 27.1; 31 / 12.1; 29 / 10.0 (mean = 35.5 / 18.15)	27 / 16.1; 18 / 11.8; 34 / 12.2; 27 / 8.0 (mean = 26.5 / 12.03)
mid 30 mins	37 / 30.6; 31 / 17.8; 30 / 13.5; 26 / 10.1 (mean = 31 / 18.0)	16 / 6.4; 18 / 7.2; 33 / 16.9; 24 / 14.3 (mean = 22.75 / 11.2)
last 30 mins	30 / 30.5; 19 / 7.7; 32 / 13.0; 25 / 10.5 (mean = 26.5 / 15.43) session 3 av. mean = 31 / 17.19	6 / 10.0; 26 / 32.2; 23 / 10.9; 26 / 11.1 (mean = 20.25 / 16.05) session 3 av. mean = 23.17 / 13.09
sum of means -1st 30 minutes	84.75 / 48.0	91.5 / 69.64
(sessions 1 to 3) - mid 30 minutes	72 / 40.28 (sum of av. means)	69.5 / 47.76 (sum of av. means)
- last 30 minutes	75.5 / 44.14 (= 77.41 / 44.14)	57.25 / 38.68 (= 72.75 / 52.02)
session 4; 1st 30 mins	23 / 17.0; 33 / 19.1; 18 / 7.5; 33 / 14.2 (mean = 26.75 / 14.45)	19 / 10.5; 39 / 13.8; 25 / 11.6; 28 / 10.7 (mean = 27.75 / 11.65)
mid 30 mins	7 / 2.9; 23 / 10.9; 6 / 2.8; 16 / 15.1 (mean = 13 / 7.93)	4 / 3.8; 14 / 11.8; 14 / 6.3; 12 / 3.1 (mean = 11 / 6.25)
last 30 mins	6 / 5.7; 23 / 15.2; 9 / 2.5; 24 / 19.4 (mean = 15.5 / 10.7) session 4 av. mean = 18.42 / 11.03	5 / 4.8; 20 / 19.5; 13 / 9.5; 11 / 4.2 (mean = 12.25 / 9.5) session 4 av. mean = 17 / 9.13
session 5; 1st 30 mins	29 / 29.9; 29 / 20.3; 14 / 4.4; 17 / 9.3 (mean = 22.25 / 15.98)	11 / 5.8; 33 / 18.5; 18 / 12.4; 20 / 5.0 (mean = 20.5 / 10.43)
mid 30 mins	11 / 5.3; 15 / 47.1; 15 / 6.2; 0 / 0 (mean = 10.25 / 14.65)	3 / 2.0; 10 / 7.1; 8 / 3.0; 16 / 11.2 (mean = 9.25 / 5.83)
last 30 mins	12 / 29.5; 23 / 16.2; 9 / 6.3; 9 / 13.2 (mean = 13.25 / 16.3) session 5 av. mean = 15.25 / 15.64	8 / 7.4; 12 / 10.7; 13 / 9.5; 4 / 1.4 (mean = 9.25 / 7.25) session 5 av. mean = 13 / 7.84
session 6; 1st 30 mins	10 / 9.7; 34 / 30.4; 7 / 2.1; 8 / 3.0 (mean = 14.75 / 11.3)	10 / 8.6; 21 / 15.2; 14 / 6.2; 17 / 8.6 (mean = 15.5 / 9.65)
mid 30 mins	4 / 2.2; 26 / 45.6; 13 / 4.4; 6 / 11.8 (mean = 12.25 / 16.0)	5 / 15.3; 5 / 3.1; 13 / 6.4; 7 / 1.8 (mean = 7.5 / 6.65)
last 30 mins	6 / 4.4; 23 / 25.9; 10 / 3.0; 11 / 14.7 (mean = 12.5 / 12.0) session 6 av. mean = 13.17 / 13.1	2 / 2.1; 14 / 9.0; 9 / 16.7; 4 / 1.0 (mean = 7.25 / 7.2) session 6 av. mean = 10.08 / 7.83
sum of means - 1st 30 minutes	63.75 / 41.73	63.75 / 31.73
(sessions 4 to 6) - mid 30 minutes	35.5 / 38.58 (sum of av. means)	27.75 / 18.73 (sum of av. means)
- last 30 minutes	41.25 / 39.0 (= 46.84 / 39.77)	28.75 / 23.95 (= 40.08 / 24.8)

Table C.25

Frequency and duration of ***sniff bottle*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	group FIOE	group FIOS
session 1; 1st 30 mins	7 / 13.31; 10 / 3.28; 11 / 7.52; 17 / 7.0 (mean = 11.25 / 7.78)	14 / 4.80; 13 / 57.19; 11 / 6.16; 23 / 8.0 (mean = 15.25 / 19.04)
mid 30 mins	7 / 6.30; 4 / 2.51; 22 / 10.02; 16 / 9.01 (mean = 12.25 / 6.96)	10 / 24.51; 18 / 22.29; 5 / 2.72; 19 / 9.47 (mean = 13 / 14.75)
last 30 mins	14 / 8.90; 3 / 5.38; 19 / 8.74; 29 / 15.10 (mean = 16.25 / 9.53)	11 / 8.98; 15 / 9.93; 20 / 12.69; 20 / 8.67 (mean = 16.5 / 10.07)
	session 1 av. mean = 13.25 / 8.09	session 1 av. mean = 14.92 / 14.62
session 2; 1st 30 mins	15 / 7.29; 11 / 6.65; 14 / 5.99; 21 / 7.99 (mean = 15.25 / 6.98)	22 / 13.67; 9 / 4.91; 17 / 8.42; 15 / 5.80 (mean = 15.75 / 8.2)
mid 30 mins	14 / 7.23; 10 / 5.58; 23 / 7.84; 25 / 19.09 (mean = 18 / 9.94)	17 / 14.67; 18 / 14.87; 20 / 9.02; 17 / 12.64 (mean = 18 / 12.8)
last 30 mins	9 / 5.26; 16 / 7.52; 24 / 15.97; 15 / 11.68 (mean = 16 / 10.11)	8 / 5.92; 15 / 6.49; 13 / 6.86; 13 / 8.71 (mean = 12.25 / 7.0)
	session 2 av. mean = 16.42 / 9.01	session 2 av. mean = 15.33 / 9.33
session 3; 1st 30 mins	31 / 20.85; 28 / 13.20; 17 / 6.51; 16 / 6.63 (mean = 23 / 11.80)	19 / 12.55; 13 / 10.51; 20 / 6.64; 22 / 6.59 (mean = 18.5 / 9.07)
mid 30 mins	26 / 24.06; 29 / 16.83; 21 / 6.94; 23 / 9.33 (mean = 24.75 / 14.29)	14 / 5.56; 13 / 6.04; 24 / 11.35; 23 / 13.67 (mean = 18.5 / 9.16)
last 30 mins	21 / 18.26; 19 / 7.75; 31 / 12.53; 23 / 8.73 (mean = 23.5 / 11.82)	6 / 10.04; 23 / 31.48; 14 / 5.23; 22 / 10.23 (mean = 16.25 / 14.25)
	session 3 av. mean = 23.75 / 12.64	session 3 av. mean = 17.75 / 10.83
sum of means -1st 30 minutes	49.5 / 26.56	49.5 / 36.31
(sessions 1 to 3) - mid 30 minutes	55 / 31.19 (sum of av. means)	49.5 / 36.71 (sum of av. means)
- last 30 minutes	55.75 / 31.46 (= 53.42 / 29.74)	45 / 31.32 (= 48 / 34.78)

Table C.26

Mean frequency and duration of ***sniff bottle*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***sniff bottle*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	84.75	49.5	58.41
- dur.	48.0	26.56	55.33
mid 30 mins- freq.	72	55	76.39
- dur.	40.28	31.19	77.43
last 30 mins- freq.	75.5	55.75	73.84
- dur.	44.14	31.46	71.27
FIOS 1st 30 mins - freq.	91.5	49.5	54.10
- dur.	69.64	36.31	52.14
mid 30 mins- freq.	69.5	49.5	71.22
- dur.	47.76	36.71	76.86
last 30 mins- freq.	57.25	45	78.60
- dur.	38.68	31.32	80.97

Table C.27

Frequency and duration of ***sniff and touch bottle*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	27 / 70.3; 35 / 62.9; 24 / 31.6; 42 / 213.7 (mean = 32 / 94.63)	30 / 51.8; 10 / 31.7; 61 / 72.9; 26 / 31.4 (mean = 31.75 / 46.95)
mid 30 mins	29 / 39.4; 37 / 50.6; 54 / 278.7; 27 / 158.6 (mean = 36.75/ 131.83)	2 / 3.5; 0 / 0; 37 / 68.8; 21 / 90.8 (mean = 15 / 40.78)
last 30 mins	18 / 21.5; 34 / 34.2; 37 / 162.9; 39 / 128.7 (mean = 32 / 86.83)	8 / 24.6; 18 / 25.8; 23 / 34.7; 7 / 15.4 (mean = 14 / 25.13)
	session 1 av. mean = 33.58/ 104.43	session 1 av. mean = 20.25 / 37.62
session 2; 1st 30 mins	38 / 50.3; 30 / 40.2; 51 / 76.6; 45 / 156.9 (mean = 41 / 81.0)	9 / 11.6; 35 / 29.4; 34 / 27.1; 19 / 39.9 (mean = 24.25 / 27.0)
mid 30 mins	13 / 14.9; 47 / 138.2; 43 / 175.2; 33 / 208.8 (mean = 34 / 134.28)	3 / 5.7; 11 / 11.5; 15 / 14.6; 12 / 47.4 (mean = 10.25 / 19.8)
last 30 mins	10 / 14.6; 56 / 115.1; 46 / 190.8; 29 / 197.8 (mean = 35.25/ 129.58)	4 / 2.9; 19 / 13.9; 31 / 50.0; 20 / 61.2 (mean = 18.5 / 32.0)
	session 2 av. mean = 36.75/ 114.95	session 2 av. mean = 17.67 / 26.27
session 3; 1st 30 mins	29 / 52.0; 62 / 102.9; 52 / 80.7; 42 / 136.9 (mean = 46.25 / 93.13)	4 / 6.0; 26 / 31.6; 35 / 57.7; 38 / 55.7 (mean = 25.75 / 37.75)
mid 30 mins	21 / 39.4; 56 / 92.9; 62 / 293.7; 43 / 145.1 (mean = 45.5 / 142.78)	3 / 7.8; 19 / 9.6; 37 / 37.9; 15 / 32.0 (mean = 18.5 / 21.83)
last 30 mins	14 / 28.8; 41 / 57.2; 62 / 202.4; 28 / 137.8 (mean = 36.25/ 106.55)	0 / 0; 18 / 18.3; 38 / 55.0; 21 / 65.2 (mean = 19.25 / 34.63)
	session 3 av. mean = 42.67/ 114.15	session 3 av. mean = 21.17 / 31.40
sum of means -1st 30 minutes	119.25 / 268.76	81.75 / 111.7
(sessions 1 to 3) - mid 30 minutes	116.25 / 408.89 (sum of av. means)	43.75 / 82.41 (sum of av. means)
- last 30 minutes	103.5 / 322.96 (= 113 / 333.53)	51.75 / 91.76 (= 59.09 / 95.29)
session 4; 1st 30 mins	33 / 46.0; 34 / 53.5; 30 / 44.3; 26 / 57.9 (mean = 30.75 / 50.43)	10 / 18.7; 59 / 45.9; 44 / 50.4; 23 / 54.7 (mean = 34 / 42.43)
mid 30 mins	4 / 3.4; 46 / 82.2; 13 / 34.3; 10 / 51.6 (mean = 18.25 / 42.88)	3 / 4.8; 29 / 50.8; 34 / 160.6; 17 / 105.0 (mean = 20.75 / 80.3)
last 30 mins	7 / 8.8; 24 / 39.7; 11 / 26.8; 26 / 130.8 (mean = 17 / 51.53)	2 / 7.6; 23 / 58.3; 17 / 29.3; 25 / 110.1 (mean = 16.75 / 51.33)
	session 4 av. mean = 22 / 48.28	session 4 av. mean = 23.83 / 58.02
session 5; 1st 30 mins	27 / 49.9; 32 / 49.8; 19 / 68.9; 17 / 72.9 (mean = 23.75 / 60.38)	11 / 42.2; 32 / 36.9; 54 / 87.9; 31 / 75.1 (mean = 32 / 60.53)
mid 30 mins	7 / 16.4; 12 / 243.6; 18 / 53.0; 0 / 0 (mean = 9.25 / 78.25)	1 / 2.3; 25 / 29.8; 11 / 11.6; 15 / 70.3 (mean = 13 / 28.5)
last 30 mins	20 / 82.8; 26 / 32.9; 11 / 34.8; 14 / 149.4 (mean = 17.75 / 74.98)	9 / 24.2; 8 / 7.1; 43 / 95.3; 5 / 13.1 (mean = 16.25 / 34.93)
	session 5 av. mean = 16.92 / 71.20	session 5 av. mean = 20.42 / 41.32
session 6; 1st 30 mins	33 / 78.7; 25 / 29.2; 10 / 27.2; 21 / 109.2 (mean = 22.25 / 61.08)	17 / 37.6; 24 / 29.2; 43 / 54.1; 19 / 59.0 (mean = 25.75 / 44.98)
mid 30 mins	16 / 34.4; 13 / 21.4; 14 / 48.5; 7 / 36.2 (mean = 12.5 / 35.13)	2 / 0.7; 13 / 16.7; 43 / 164.0; 18 / 60.4 (mean = 19 / 60.45)
last 30 mins	2 / 3.1; 14 / 17.8; 14 / 42.3; 17 / 90.7 (mean = 11.75 / 38.48)	1 / 1.2; 26 / 34.9; 31 / 154.2; 37 / 213.0 (mean = 23.75/ 100.83)
	session 6 av. mean = 15.5 / 44.90	session 6 av. mean = 22.83 / 68.75
sum of means - 1st 30 minutes	76.75 / 171.89	91.75 / 147.94
(sessions 4 to 6) - mid 30 minutes	40 / 156.26 (sum of av. means)	52.75 / 169.25 (sum of av. means)
- last 30 minutes	46.5 / 164.99 (= 54.42 / 164.38)	56.75 / 187.09 (= 67.08 / 168.09)

Table C.28

Frequency and duration of ***sniff and touch bottle*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins mid 30 mins last 30 mins	8 / 22.63; 25 / 44.27; 13 / 18.51; 28 / 119.87 (mean = 18.5 / 51.32) 9 / 12.23; 32/ 45.01; 49/ 187.10; 24 / 137.42 (mean = 28.5 / 95.44) 8 / 7.98; 24/ 22.99; 36/ 161.63; 30 / 105.66 (mean = 24.5 / 74.57) session 1 av. mean = 23.83 / 73.78	18 / 32.33; 4 / 16.82; 21 / 32.67; 18 / 22.34 (mean = 15.25 / 26.04) 0 / 0; 0 / 0; 7 / 15.42; 19 / 74.69 (mean = 6.5 / 22.53) 7 / 21.76; 11 / 16.63; 20 / 31.54; 6 / 14.61 (mean = 11 / 21.14) session 1 av. mean = 10.92 / 23.24
session 2; 1st 30 mins mid 30 mins last 30 mins	13 / 26.63; 16 / 21.41; 32 / 31.17; 38 / 114.85 (mean = 24.75/ 48.52) 10/ 13.97; 44/ 129.06; 37/ 154.59; 31 / 188.25 (mean = 30.5/ 121.47) 5 / 2.64; 42/ 102.37; 37/ 154.76; 23 / 160.31 (mean =26.75/105.02) session 2 av. mean = 27.33 / 91.67	5 / 5.44; 18 / 15.49; 19 / 9.73; 13 / 26.34 (mean = 13.75 / 14.25) 3 / 5.66; 9 / 10.65; 14 / 14.38; 12 / 47.45 (mean = 9.5 / 19.54) 4 / 2.91; 18 / 13.69; 22 / 27.07; 14 / 45.56 (mean = 14.5 / 22.31) session 2 av. mean = 12.58 / 18.7
session 3; 1st 30 mins mid 30 mins last 30 mins	25 / 45.38; 47/ 77.74; 28/ 47.91; 27 / 72.92 (mean = 31.75 / 60.99) 21/ 39.43; 52/ 87.41; 59/ 287.95; 40 / 139.39 (mean = 43 / 138.55) 11/ 17.04; 41/ 57.15; 59/ 191.67; 26 / 125.57 (mean = 34.25/ 97.86) session 3 av. mean = 36.33 / 99.13	3 / 4.91; 18 / 24.16; 23 / 34.84; 34 / 52.32 (mean = 19.5 / 29.06) 3 / 7.80; 15 / 7.90; 27 / 30.99; 10 / 24.22 (mean = 13.75 / 17.73) 0 / 0; 18 / 18.29; 31 / 42.25; 17 / 58.80 (mean = 16.5 / 29.84) session 3 av. mean = 16.58 / 25.54
sum of means -1st 30 minutes (sessions 1 to 3) - mid 30 minutes - last 30 minutes	75 / 160.83 102 / 355.46 (sum of av. means) 85.5 / 277.45 (= 87.49 / 264.58)	48.5 / 69.35 29.75 / 59.8 (sum of av. means) 42 / 73.29 (= 40.08 / 67.48)

Table C.29

Mean frequency and duration of ***sniff and touch bottle*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***sniff and touch bottle*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	119.25	75	62.89
- dur.	268.76	160.83	59.84
mid 30 mins- freq.	116.25	102	87.74
- dur.	408.89	355.46	86.93
last 30 mins- freq.	103.5	85.5	82.61
- dur.	322.96	277.45	85.91
FIOS 1st 30 mins - freq.	81.75	48.5	59.33
- dur.	111.7	69.35	62.09
mid 30 mins- freq.	43.75	29.75	68.0
- dur.	82.41	59.8	72.56
last 30 mins- freq.	51.75	42	81.16
- dur.	91.76	73.29	79.87

Table C.30

Frequency and duration of ***chew/bite bottle*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	0 / 0; 19 / 120.3; 0 / 0; 0 / 0 (mean = 4.75 / 30.08)	0 / 0; 1 / 2.2; 25 / 868.8*; 0 / 0 (mean = 6.5 / 217.75)
mid 30 mins	0 / 0; 1 / 0.2; 0 / 0; 0 / 0 (mean = 0.25 / 0.05)	0 / 0; 0 / 0; 4 / 10.1; 0 / 0 (mean = 1 / 2.53)
last 30 mins	0 / 0; 4 / 18.5; 0 / 0; 0 / 0 (mean = 1 / 4.63) session 1 av. mean = 2 / 11.59	0 / 0; 51 / 415.2; 1 / 4.2; 0 / 0 (mean = 13 / 104.85) session 1 av. mean = 6.83 / 108.38
session 2; 1st 30 mins	3 / 6.8; 0 / 0; 0 / 0; 4 / 9.5 (mean = 1.75 / 4.08)	0 / 0; 16 / 113.0; 22 / 635.3*; 0 / 0 (mean = 9.5 / 187.08)
mid 30 mins	0 / 0; 2 / 5.7; 0 / 0; 0 / 0 (mean = 0.5 / 1.43)	0 / 0; 4 / 7.4; 6 / 14.5; 0 / 0 (mean = 2.5 / 5.48)
last 30 mins	0 / 0; 18 / 419.1; 0 / 0; 0 / 0 (mean = 4.5 / 104.78) session 2 av. mean = 2.25 / 36.76	0 / 0; 2 / 3.2; 11 / 163.9; 0 / 0 (mean = 3.25 / 41.78) session 2 av. mean = 5.08 / 78.11
session 3; 1st 30 mins	3 / 4.7; 22 / 130.8; 0 / 0; 0 / 0 (mean = 6.25 / 33.88)	0 / 0; 13 / 71.2; 28 / 465.9*; 0 / 0 (mean = 10.25 / 134.28)
mid 30 mins	11 / 216.3; 13 / 457.0; 0 / 0; 0 / 0 (mean = 6 / 168.33)	1 / 1.3; 1 / 1.7; 9 / 221.0; 0 / 0 (mean = 2.75 / 56.0)
last 30 mins	1 / 5.1; 11 / 137.9; 0 / 0; 0 / 0 (mean = 3 / 35.75) session 3 av. mean = 5.08 / 79.32	0 / 0; 1 / 2.4; 11 / 141.6; 0 / 0 (mean = 3 / 36.0) session 3 av. mean = 5.33 / 75.43
sum of means -1st 30 minutes **(sessions 1 to 3) - mid 30 minutes** **- last 30 minutes**	12.75 / 68.04 6.75 / 169.81 (sum of av. means) 8.5 / 145.16 (= 9.33 / 127.67)	26.25 / 539.11 6.25 / 64.01 (sum of av. means) 19.25 / 182.63 (= 17.24 / 261.92)
session 4; 1st 30 mins	14 / 140.1; 22 / 722.5*; 0 / 0; 0 / 0 (mean = 9 / 215.65)	0 / 0; 52 / 347.1; 18 / 368.0; 0 / 0 (mean = 17.5 / 178.78)
mid 30 mins	0 / 0; 5 / 59.0; 0 / 0; 0 / 0 (mean = 1.25 / 14.75)	0 / 0; 23 / 761.3*; 3 / 36.3; 0 / 0 (mean = 6.5 / 199.4)
last 30 mins	2 / 10.8; 13 / 181.7; 0 / 0; 0 / 0 (mean = 3.75 / 48.13) session 4 av. mean = 4.67 / 92.84	0 / 0; 0 / 0; 0 / 0; 0 / 0 (mean = 0 / 0) session 4 av. mean = 8 / 126.06
session 5; 1st 30 mins	8 / 66.5; 9 / 160.8; 0 / 0; 1 / 1.0 (mean = 4.5 / 57.08)	0 / 0; 11 / 37.2; 20 / 982.6*; 0 / 0 (mean = 7.75 / 254.95)
mid 30 mins	0 / 0; 2 / 4.1; 1 / 1.1; 0 / 0 (mean = 0.75 / 1.3)	0 / 0; 17 / 144.1; 1 / 0.5; 0 / 0 (mean = 4.5 / 36.15)
last 30 mins	0 / 0; 2 / 16.0; 0 / 0; 0 / 0 (mean = 0.5 / 4.0) session 5 av. mean = 1.92 / 20.79	0 / 0; 38 / 1094.9*; 3 / 4.3; 0 / 0 (mean = 10.25 / 274.8) session 5 av. mean = 7.5 / 188.63
session 6; 1st 30 mins	16 / 767.3*; 21 / 595.7*; 0 / 0; 2 / 3.4 (mean = 9.75 / 341.6)	0 / 0; 10 / 54.1; 12 / 512.6*; 0 / 0 (mean = 5.5 / 141.68)
mid 30 mins	3 / 10.0; 2 / 72.8; 0 / 0; 0 / 0 (mean = 1.25 / 20.7)	0 / 0; 10 / 68.8; 4 / 10.6; 0 / 0 (mean = 3.5 / 19.85)
last 30 mins	0 / 0; 1 / 9.6; 0 / 0; 1 / 1.9 (mean = 0.5 / 2.88) session 6 av. mean = 3.83 / 121.73	0 / 0; 22 / 130.4; 0 / 0; 8 / 293.8 (mean = 7.5 / 106.05) session 6 av. mean = 5.5 / 89.19
sum of means - 1st 30 minutes **(sessions 4 to 6) - mid 30 minutes** **- last 30 minutes**	23.25 / 614.33 3.25 / 36.75 (sum of av. means) 4.75 / 55.01 (= 10.42 / 235.36)	30.75 / 575.41 14.5 / 255.4 (sum of av. means) 17.75 / 380.85 (= 21 / 403.88)

Table C.31

Frequency and duration of ***chew/bite bottle*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	0 / 0; 12 / 94.82; 0 / 0; 0 / 0 (mean = 3 / 23.71)	0 / 0; 0 / 0; 8 / 297.70; 0 / 0 (mean = 2 / 74.43)
mid 30 mins	0 / 0; 1 / 0.25; 0 / 0; 0 / 0 (mean = 0.25 / 0.06)	0 / 0; 0 / 0; 2 / 3.03; 0 / 0 (mean = 0.5 / 0.76)
last 30 mins	0 / 0; 2 / 3.87; 0 / 0; 0 / 0 (mean = 0.5 / 0.97)	0 / 0; 34 / 295.31; 1 / 4.24; 0 / 0 (mean = 8.75 / 74.89)
	session 1 av. mean = 1.25 / 8.25	session 1 av. mean = 3.75 / 50.03
session 2; 1st 30 mins	1 / 4.35; 0 / 0; 0 / 0; 1 / 3.07 (mean = 0.5 / 1.86)	0 / 0; 11 / 77.19; 17 / 581.23;* 0 / 0 (mean = 7 / 164.61)
mid 30 mins	0 / 0; 2 / 5.73; 0 / 0; 0 / 0 (mean = 0.5 / 1.43)	0 / 0; 4 / 7.38; 5 / 9.97; 0 / 0 (mean = 2.25 / 4.34)
last 30 mins	0 / 0; 10 / 220.04; 0 / 0; 0 / 0 (mean = 2.5 / 55.01)	0 / 0; 2 / 3.17; 6 / 137.34; 0 / 0 (mean = 2 / 35.13)
	session 2 av. mean = 1.17 / 19.43	session 2 av. mean = 3.75 / 68.03
session 3; 1st 30 mins	3 / 4.68; 14 / 90.42; 0 / 0; 0 / 0 (mean = 4.25 / 23.78)	0 / 0; 10 / 67.87; 22 / 402.27; 0 / 0 (mean = 8 / 117.54)
mid 30 mins	11 / 216.32; 12 / 446.35; 0 / 0; 0 / 0 (mean = 5.75 / 165.67)	1 / 1.34; 1 / 1.70; 7 / 180.75; 0 / 0 (mean = 2.25 / 45.95)
last 30 mins	0 / 0; 11 / 137.93; 0 / 0; 0 / 0 (mean = 2.75 / 34.48)	0 / 0; 1 / 2.40; 10 / 108.79; 0 / 0 (mean = 2.75 / 27.80)
	session 3 av. mean = 4.25 / 74.64	session 2 av. mean = 4.33 / 63.76
sum of means -1st 30 minutes **(sessions 1 to 3) - mid 30 minutes** **- last 30 minutes**	7.75 / 49.35 6.5 / 167.16 (sum of av. means) 5.75 / 90.46 (= 6.67 / 102.32)	17 / 356.58 5 / 51.05 (sum of av. means) 13.5 / 137.82 (= 11.83 / 181.82)

Table C.32

Mean frequency and duration of ***chew/bite bottle*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***chew/bite bottle*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	12.75	7.75	60.78
- dur.	68.04	49.35	72.53
mid 30 mins- freq.	6.75	6.5	96.30
- dur.	169.81	167.16	98.44
last 30 mins- freq.	8.5	5.75	67.65
- dur.	145.16	90.46	62.32
FIOS 1st 30 mins - freq.	26.25	17	64.76
- dur.	539.11	356.58	66.14
mid 30 mins- freq.	6.25	5	80.0
- dur.	64.01	51.05	79.75
last 30 mins- freq.	19.25	13.5	70.13
- dur.	182.63	137.82	75.46

Table C.33

Frequency and duration of ***drinking*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	17 / 70.5; 32 / 279.3; 8 / 74.0; 2 / 29.8 (mean = 14.75 / 113.4)	11 / 89.4; 24 / 97.2; 5 / 37.9; 4 / 47.5 (mean = 11 / 68.0)
mid 30 mins	9 / 55.2; 1 / 0.3; 14 / 131.9; 1 / 25.7 (mean = 6.25 / 53.28)	4 / 37.3; 32 / 258.5; 1 / 1.4; 1 / 96.7 (mean = 9.5 / 98.48)
last 30 mins	6 / 34.2; 8 / 59.3; 1 / 1.5 1 / 43.5 (mean = 4 / 34.63)	3 / 17.6; 23 / 176.5; 15 / 83.2; 2 / 11.8 (mean = 10.75 / 72.28)
	session 1 av. mean = 8.33 / 67.10	session 1 av. mean = 10.42 / 79.59
session 2; 1st 30 mins	12 / 157.1; 15 / 192.3; 14 / 183.0; 5 / 76.7 (mean = 11.5 / 152.28)	16 / 137.7; 30 / 255.0; 13 / 117.4; 2 / 33.3 (mean = 15.25 / 135.85)
mid 30 mins	7 / 30.1; 4 / 53.7; 7 / 67.1; 4 / 85.1 (mean = 5.5 / 59.0)	3 / 34.3; 26 / 284.1; 11 / 63.2; 1 / 51.7 (mean = 10.25 / 108.33)
last 30 mins	8 / 121.2; 7 / 33.3; 6 / 43.5; 0 / 0 (mean = 5.25 / 49.5)	1 / 13.9; 27 / 284.3; 23 / 174.3; 1 / 33.4 (mean = 13 / 126.48)
	session 2 av. mean = 7.42 / 86.93	session 2 av. mean = 12.83/ 123.55
session 3; 1st 30 mins	12 / 111.4; 14 / 151.5; 19 / 180.0; 5 / 88.6 (mean = 12.5 / 132.88)	9 / 114.8; 24 / 291.3; 27 / 239.9; 7 / 98.8 (mean = 16.75 / 186.2)
mid 30 mins	7 / 166.4; 7 / 195.0; 14 / 131.1; 3 / 43.9 (mean = 7.75 / 134.1)	5 / 60.9; 23 / 285.2; 23 / 217.8; 1 / 50.8 (mean = 13 / 153.68)
last 30 mins	2 / 19.6; 7 / 123.0; 17 / 188.5; 0 / 0 (mean = 6.5 / 82.78)	1 / 1.0; 28 / 282.2; 9 / 80.4; 2 / 23.1 (mean = 10 / 96.68)
	session 3 av. mean = 8.92 / 116.59	session 3 av. mean = 13.25/ 145.52
sum of means -1st 30 minutes	38.75 / 398.56	43 / 390.05
(sessions 1 to 3) - mid 30 minutes	19.5 / 246.38 (sum of av. means)	32.75 / 360.49 (sum of av. means)
- last 30 minutes	15.75 / 166.91 (= 24.67 / 270.62)	33.75 / 295.44 (= 36.5 / 348.66)
session 4; 1st 30 mins	1 / 1.0; 8 / 54.0; 6 / 61.2; 3 / 22.4 (mean = 4.5 / 34.65)	5 / 57.5; 8 / 35.0; 8 / 23.5; 2 / 33.3 (mean = 5.75 / 37.33)
mid 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0 (mean = 0 / 0)	0 / 0; 3 / 7.8; 2 / 11.6; 0 / 0 (mean = 1.25 / 4.85)
last 30 mins	0 / 0; 2 / 1.8; 2 / 7.4 0 / 0 (mean = 1 / 2.3)	0 / 0; 0 / 0; 2 / 12.3; 2 / 8.4 (mean = 1 / 5.18)
	session 4 av. mean = 1.83 / 12.32	session 4 av. mean = 2.67 / 15.79
session 5; 1st 30 mins	0 / 0; 5 / 100.1; 9 / 79.5; 1 / 0.8 (mean = 3.75 / 45.1)	2 / 23.3; 3 / 10.1; 6 / 22.0; 3 / 9.5 (mean = 3.5 / 16.23)
mid 30 mins	0 / 0; 0 / 0; 2 / 19.6; 0 / 0 (mean = 0.5 / 4.9)	1 / 1.4; 0 / 0; 1 / 8.8; 1 / 19.8 (mean = 0.75 / 7.5)
last 30 mins	1 / 0.5; 1 / 0.2; 2 / 13.3; 0 / 0 (mean = 1 / 3.5)	0 / 0; 0 / 0; 1 / 0.4; 0 / 0 (mean = 0.25 / 0.1)
	session 5 av. mean = 1.75 / 17.83	session 5 av. mean = 1.5 / 7.94
session 6; 1st 30 mins	0 / 0; 5 / 39.1; 4 / 10.8; 0 / 0 (mean = 2.25 / 12.48)	8 / 41.6; 3 / 20.2; 10 / 25.8; 2 / 35.2 (mean = 5.75 / 30.7)
mid 30 mins	2 / 99.5; 0 / 0; 0 / 0; 0 / 0 (mean = 0.5 / 24.88)	0 / 0; 6 / 34.9; 2 / 12.1; 2 / 2.1 (mean = 2.5 / 12.28)
last 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0 (mean = 0 / 0)	0 / 0; 1 / 7.4; 4 / 17.4; 0 / 0 (mean = 1.25 / 6.2)
	session 6 av. mean = 0.92 / 12.45	session 6 av. mean = 3.17 / 16.39
sum of means - 1st 30 minutes	10.5 / 92.23	15 / 84.26
(sessions 4 to 6) - mid 30 minutes	1.0 / 29.78 (sum of av. means)	4.5 / 24.63 (sum of av. means)
- last 30 minutes	2 / 5.8 (= 4.5 / 42.6)	2.5 / 11.48 (= 7.34 / 40.12)

Table C.34

Frequency and duration of ***drinking*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	6 / 34.63; 25 / 234.94; 7 / 71.20; 2 / 29.84 (mean = 10 / 92.65)	10 / 84.09; 20 / 89.71; 5 / 37.89; 4 / 47.54 (mean = 9.75 / 64.81)
mid 30 mins	8 / 54.52; 1 / 0.29; 14 / 131.87; 1 / 25.66 (mean = 6 / 53.09)	2 / 18.74; 31 / 250.02; 0 / 0; 1 / 96.70 (mean = 8.5 / 91.37)
last 30 mins	4 / 30.67; 6 / 34.87; 1 / 1.50; 0 / 0 (mean = 2.75 / 16.76)	3 / 17.58; 18 / 151.34; 15 / 83.18; 2 / 11.80 (mean = 9.5 / 65.98)
	session 1 av. mean = 6.25 / 54.17	session 1 av. mean = 9.25 / 74.05
session 2; 1st 30 mins	6 / 97.59; 6 / 73.18; 11 / 145.93; 5 / 76.66 (mean = 7 / 98.34)	10 / 97.92; 25 / 236.43; 9 / 52.04; 2 / 33.25 (mean = 11.5 / 104.91)
mid 30 mins	7 / 30.11; 4 / 53.73; 6 / 66.79; 4 / 85.07 (mean = 5.25 / 58.93)	3 / 34.33; 22 / 246.91; 10 / 62.75; 1 / 51.72 (mean = 9 / 98.93)
last 30 mins	8 / 121.23; 4 / 2.03; 6 / 43.51; 0 / 0 (mean = 4.5 / 41.69)	1 / 13.86; 25/ 261.08; 20/ 161.87; 0 / 0 (mean = 11.5 / 109.20)
	session 2 av. mean = 5.58 / 66.32	session 2 av. mean = 10.67/ 104.35
session 3; 1st 30 mins	12/111.40; 13/150.19; 14/159.56; 5 / 88.56 (mean = 11 / 127.43)	8/ 113.74; 22/ 279.02; 24/ 231.17; 7 / 98.83 (mean = 15.25 / 180.69)
mid 30 mins	7/ 166.42; 7/ 194.96; 14/ 131.06; 3 / 43.87 (mean = 7.75 / 134.08)	5 / 60.88; 22/ 276.24; 21/ 216.28; 1 / 50.84 (mean = 12.25 / 151.06)
last 30 mins	2 / 19.63; 7/ 123.0; 16/ 177.68; 0 / 0 (mean = 6.25 / 80.08)	1 / 0.99; 27/ 271.06; 9/ 80.44; 1 / 3.63 (mean = 9.5 / 89.03)
	session 3 av. mean = 8.33 / 113.86	session 3 av. mean = 12.33/ 140.26
sum of means -1st 30 minutes	28 / 318.42	36.5 / 350.41
(sessions 1 to 3) - mid 30 minutes	19 / 246.1 (sum of av. means)	29.75 / 341.36 (sum of av. means)
- last 30 minutes	13.5 / 138.53 (= 20.16 / 234.35)	30.5 / 264.21 (= 32.25 / 318.66)

Table C.35

Mean frequency and duration of ***drinking*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***drinking*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	38.75	28	72.26
- dur.	398.56	318.42	79.89
mid 30 mins- freq.	19.5	19	97.44
- dur.	246.38	246.1	99.89
last 30 mins- freq.	15.75	13.5	85.71
- dur.	166.91	138.53	83.00
FIOS 1st 30 mins - freq.	43	36.5	84.88
- dur.	390.05	350.41	89.84
mid 30 mins- freq.	32.75	29.75	90.84
- dur.	360.49	341.36	94.69
last 30 mins- freq.	33.75	30.5	90.37
- dur.	295.44	264.21	89.43

Table C.36

Frequency and duration of ***resting/sleeping*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	0 / 0; 0 / 0; 0 / 0; 3 / 19.7 (mean = 0.75 / 4.93)	2 / 8.3; 0 / 0; 0 / 0; 1 / 6.1 (mean = 0.75 / 3.6)
mid 30 mins	0 / 0; 43 / 616.3*; 3 / 8.2; 18 / 194.7 (mean = 16 / 204.8)	9 / 278.4; 0 / 0; 5 / 23.3; 9 / 38.0 (mean = 5.75 / 84.93)
last 30 mins	0 / 0; 33 / 389.0; 9 / 124.1; 30 / 117.2 (mean = 18 / 157.58)	12 / 887.8*; 0 / 0; 4 / 11.0; 19 / 307.8 (mean = 8.75 / 301.65)
	session 1 av. mean = 11.58/ 122.44	session 1 av. mean = 5.08 / 130.06
session 2; 1st 30 mins	0 / 0; 3 / 29.3; 1 / 4.1; 3 / 31.1 (mean = 1.75 / 16.13)	1 / 14.9; 0 / 0; 1 / 8.2; 0 / 0 (mean = 0.5 / 5.78)
mid 30 mins	0 / 0; 52 / 479.8*; 7 / 31.6; 19 / 663.5* (mean = 19.5/ 293.73)	2 / 5.7; 0 / 0; 2 / 7.2; 29 / 102.6 (mean = 8.25 / 28.88)
last 30 mins	0 / 0; 6 / 44.5; 31 / 312.9; 20 / 839.9* (mean =14.25/299.33)	1 / 14.4; 0 / 0; 4 / 13.0; 11 / 143.5 (mean = 4 / 42.73)
	session 2 av. mean = 11.83/ 203.06	session 2 av. mean = 4.25 / 25.80
session 3; 1st 30 mins	0 / 0; 2 / 6.9; 1 / 5.5; 6 / 71.5 (mean = 2.25 / 20.98)	0 / 0; 0 / 0; 1 / 1.9; 0 / 0 (mean = 0.25 / 0.48)
mid 30 mins	0 / 0; 8 / 57.7; 4 / 53.9; 26 / 241.0 (mean = 9.5 / 88.15)	1 / 2.7; 0 / 0; 4 / 10.6; 32 / 351.5 (mean = 9.25 / 91.2)
last 30 mins	2 / 10.8; 17 / 171.3; 24 / 242.7; 24 / 1038.1* (mean=16.75/365.73)	2 / 57.5; 0 / 0; 12 / 90.0; 27 / 324.2 (mean = 10.25/ 117.93)
	session 3 av. mean = 9.5 / 158.29	session 3 av. mean = 6.58 / 69.87
sum of means -1st 30 minutes	4.75 / 42.04	1.5 / 9.86
(sessions 1 to 3) - mid 30 minutes	45 / 586.68 (sum of av. means)	23.25 / 205.01 (sum of av. means)
- last 30 minutes	49 / 822.64 (= 32.91 / 483.79)	23 / 462.31 (= 15.91 / 225.73)
session 4; 1st 30 mins	0 / 0; 0 / 0; 0 / 0; 3 / 13.6 (mean = 0.75 / 3.4)	2 / 3.3; 0 / 0; 0 / 0; 3 / 34.3 (mean = 1.25 / 9.4)
mid 30 mins	17 / 342.4; 12 / 494.0*; 3 / 970.1*; 25 / 734.5* (mean=14.25/635.25*)	11 / 233.0; 0 / 0; 29 / 293.9; 22 / 633.4* (mean = 15.5/ 290.08)
last 30 mins	20 / 507.1*; 16/ 420.6; 19/ 758.4*; 35 / 198.6 (mean = 22.5/ 471.18*)	7/ 1175.9*; 9 / 387.2; 36/ 1005.5*; 32 / 769.4* (mean = 21 / 834.5*)
	session 4 av. mean = 12.5 / 369.94	session 4 av. mean =12.58 / 377.99
session 5; 1st 30 mins	0 / 0; 2 / 122.9; 1 / 12.0; 0 / 0 (mean = 0.75 / 33.73)	3 / 19.1; 4 / 324.0; 0 / 0; 0 / 0 (mean = 1.75 / 85.78)
mid 30 mins	11 / 281.9; 27 / 185.9; 16 / 602.6*; 11/1603.3* (mean=16.25/668.43*)	8 / 435.6; 2 / 34.7; 30 / 1050.0*; 25 / 365.7 (mean = 16.25/ 471.5*)
last 30 mins	20 / 755.6*; 21 / 482.4; 12 / 407.7; 41 / 310.2 (mean = 23.5/ 488.98*)	9 / 92.7; 0 / 0; 20 / 786.4*; 36 / 883.9* (mean =16.25/440.75)
	session 5 av. mean = 13.5 / 397.05	session 5 av. mean = 11.42/ 332.68
session 6; 1st 30 mins	0 / 0; 0 / 0; 1 / 2.3; 4 / 189.0 (mean = 1.25 / 47.83)	2 / 32.9; 0 / 0; 3 / 12.7; 0 / 0 (mean = 1.25 / 11.4)
mid 30 mins	13/ 452.1*; 20/ 969.6*; 14/ 113.1; 7 / 694.3* (mean = 13.5/ 557.28*)	17/ 306.5; 1/ 257.8; 20/ 599.4*; 30 / 341.9 (mean = 17 / 376.4)
last 30 mins	15/ 562.2*; 19/ 705.9*; 12/ 939.9*; 37 / 324.0 (mean = 20.75 / 633.0)	9/ 1587.8*; 8/ 149.4; 43/ 926.2*; 44 / 493.5* (mean = 26 / 789.23*)
	session 6 av. mean = 11.83/ 412.70	session 6 av. mean =14.75 / 392.34
sum of means - 1st 30 minutes	2.75 / 84.96	4.25 / 106.58
(sessions 4 to 6) - mid 30 minutes	44 / 1860.96 (sum of av. means)	48.75 / 1137.98 (sum of av. means)
- last 30 minutes	66.75 / 1593.16 (=37.83/ 1179.69)	63.25 / 2064.48 (=38.75 / 1103.01)

Table C.37

Frequency and duration of ***resting/sleeping*** during the PRPs for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each ***fixed-interval*** session (sessions 1-3).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	0 / 0; 0 / 0; 0 / 0; 1 / 7.79 (mean = 0.25 / 1.95)	1 / 5.04; 0 / 0; 0 / 0; 1 / 6.06 (mean = 0.5 / 2.78)
mid 30 mins	0 / 0; 34 / 526.89*; 2 / 4.35; 12 / 89.45 (mean = 12 / 155.17)	8 / 268.75; 0 / 0; 0 / 0; 7 / 32.82 (mean = 3.75 / 75.39)
last 30 mins	0 / 0; 29 / 361.96; 9 / 124.05; 22 / 78.16 (mean = 15 / 141.04)	12 / 887.82*; 0 / 0; 3 / 10.22; 18 / 298.98 (mean = 8.25/ 299.26)
	session 1 av. mean = 9.08 / 99.39	session 1 av. mean = 4.17 / 125.81
session 2; 1st 30 mins	0 / 0; 3 / 29.32; 1 / 4.12; 0 / 0 (mean = 1 / 8.36)	1 / 14.89; 0 / 0; 0 / 0; 0 / 0 (mean = 0.25 / 3.72)
mid 30 mins	0 / 0; 49 / 471.20*; 5 / 25.97; 18 / 660.98* (mean = 18 / 289.54)	1 / 0.87; 0 / 0; 2 / 7.18; 22 / 70.43 (mean = 6.25/ 19.62)
last 30 mins	0 / 0; 6 / 44.51; 24 / 232.78; 16 / 834.65* (mean = 11.5/277.99)	1 / 14.40; 0 / 0; 3 / 7.43; 8 / 105.20 (mean = 3 / 31.76)
	session 2 av. mean = 10.17/ 191.96	session 2 av. mean = 3.17 / 18.37
session 3; 1st 30 mins	0 / 0; 1 / 3.96; 0 /0; 4 / 15.38 (mean = 1.25 / 4.84)	0 / 0; 0 / 0; 1 / 1.85; 0 / 0 (mean = 0.25 / 0.46)
mid 30 mins	0 / 0; 7 / 46.34; 3 / 49.20; 24 / 230.12 (mean = 8.5 / 81.42)	1 / 2.67; 0 / 0; 4 / 10.59; 31 / 350.14 (mean = 9 / 90.85)
last 30 mins	2 / 10.8; 17 / 171.31; 23 / 240.14; 23 / 952.85*(mean =16.25/343.78)	2 / 57.47; 0 / 0; 12 / 89.98; 25 / 311.87 (mean = 9.75/ 114.83)
	session 3 av. mean = 8.67 / 143.35	session 3 av. mean = 6.33 / 68.71
sum of means -1st 30 minutes	2.5 / 15.15	1 / 6.96
(sessions 1 to 3) - mid 30 minutes	38.5 / 526.13 (sum of av. means)	19 / 185.86 (sum of av. means)
- last 30 minutes	42.75 / 762.81 (= 27.92 / 434.7)	21 / 445.85 (= 13.67/ 212.89)

Table C.38

Mean frequency and duration of ***resting/sleeping*** during the PRPs (for both groups in Experiment 3), for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes, summed over the first three sessions (***fixed-interval***), as a percentage of the total mean frequency and duration of ***resting/sleeping*** summed over the first three sessions (for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes).

	total sum of means	sum of means in PRPs	% of total
FIOE 1st 30 mins- freq.	4.75	2.5	52.63
- dur.	42.04	15.15	36.04
mid 30 mins- freq.	45	38.5	85.56
- dur.	586.68	526.13	89.68
last 30 mins- freq.	49	42.75	87.25
- dur.	822.64	762.81	92.73
FIOS 1st 30 mins - freq.	1.5	1	66.67
- dur.	9.86	6.96	70.59
mid 30 mins- freq.	23.25	19	81.72
- dur.	205.01	185.86	90.66
last 30 mins- freq.	23	21	91.30
- dur.	462.31	445.85	96.44

Table C.39

Frequency and duration of ***push lid with snout*** for each rat in Experiment 3, for the ***first*** 30 minutes, ***middle*** 30 minutes and ***last*** 30 minutes of each session (sessions 1-3 are ***fixed-interval*** sessions, and sessions 4-6 are extinction sessions).

SESSION	**group FIOE**	**group FIOS**
session 1; 1st 30 mins	0 / 0; 1 / 1.6; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
mid 30 mins	1 / 1.3; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
last 30 mins	0 / 0; 2 / 2.0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
session 2; 1st 30 mins	0 / 0; 2 / 2.7; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
mid 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
last 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
session 3; 1st 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
mid 30 mins	0 / 0; 0 / 0; 2 / 0.1; 0 / 0	0 / 0; 8 / 15.0; 0 / 0; 0 / 0
last 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	1 / 0.1; 8 / 19.9; 0 / 0; 0 / 0
session 4; 1st 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
mid 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 4 / 6.1; 0 / 0; 0 / 0
last 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 8 / 19.0; 0 / 0; 0 / 0
session 5; 1st 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 33 / 62.7; 0 / 0; 0 / 0
mid 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
last 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
session 6; 1st 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
mid 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 0 / 0; 0 / 0; 0 / 0
last 30 mins	0 / 0; 0 / 0; 0 / 0; 0 / 0	0 / 0; 13 / 20.1; 0 / 0; 0 / 0

Table C.40

The mean frequency and duration of behaviours for the "object" grouping variable for all parts of every session in Experiment 3 (FIOE and FIOS groups).

BEHAVIOURAL MEASURE	SESSION 1 FIOE/ FIOS	SESSION 2 FIOE/ FIOS	SESSION 3 FIOE/ FIOS	SESSION 4 FIOE/ FIOS	SESSION 5 FIOE/ FIOS	SESSION 6 FIOE/ FIOS
FREQUENCIES						
Digging/Burying	32.17 / 11.75	16.5 / 10.17	16.83 / 11.5	19.5 / 16.33	16.08 / 22.25	20.5 / 20.42
Propping	30.5 / 34.92	26.5 / 26.92	21.17 / 35.75	18.58 / 26.42	28 / 39.42	28.92 / 39.33
Displacement	27.92 / 28	24.83 / 38.42	24 / 25.67	18.17 / 15	23.08 / 21.67	14.25 / 19.17
Bar-related behaviour	258.5 / 188	191.67 / 150.5	205.5 / 132.58	91.58 / 82.17	69.75 / 47.5	47.25 / 41.75
Sniff object	n/a / 83.42	n/a / 64.92	n/a / 70.25	84.08 / 64.33	62.5 / 60.67	49.83 / 54.5
Sniff & Touch object	n/a / 37.42	n/a / 32.67	n/a / 38.08	52.5 / 42.58	39.33 / 43.08	34.75 / 44.08
Chew/Bite object	n/a / 3.08	n/a / 6.92	n/a / 6.92	4.92 / 9.25	1.33 / 6.67	1.17 / 6
Bar-pressing	263.17 / 339.5	327 / 447.83	317.17/367.08	40.33 / 63.33	18.17 / 14	13 / 9.33
Sniff bottle	23.58 / 27.83	22.83 / 21.75	31 / 23.17	18.42 / 17	15.25 / 13	13.17 / 10.08
Sniff & Touch bottle	33.58 / 20.25	36.75 / 17.67	42.67 / 21.17	22 / 23.83	16.92 / 20.42	15.5 / 22.83
Chew/Bite bottle	2 / 6.83	2.25 / 5.08	5.08 / 5.33	4.67 / 8	1.92 / 7.5	3.83 / 5.5
Drinking	8.33 / 10.42	7.42 / 12.83	8.92 / 13.25	1.83 / 2.67	1.75 / 1.5	0.92 / 3.17
Resting/Sleeping	11.58 / 5.08	11.83 / 4.25	9.5 / 6.58	12.5 / 12.58	13.5 / 11.42	11.83 / 14.75
DURATIONS (in seconds)						
Digging/Burying	37.33 / 15.45	18.88 / 16.01	17.07 / 15.71	20.96 / 21.57	13.35 / 29.49	19.98 / 24.18
Propping	84.61 / 91.43	87.22 / 64.43	62.5 / 106.65	61.15 / 89.92	100.7 / 135.6	112.59/149.11
Displacement	198.82/153.05	220.75/208.96	235.2 / 150.04	196.67/250.95	419.03/320.93	233.17/307.38
Bar-related behaviour	224.68/138.49	143.68 / 96.05	154.6 / 68.78	162.03/110.34	102.41 / 45.51	120.54 / 46.53
Sniff object	n/a / 98.15	n/a / 47.09	n/a / 45.65	100.06 / 61.17	106.97 / 57.07	57.23 / 45.45
Sniff & Touch object	n/a / 79.23	n/a / 64.78	n/a / 70.08	218.69 / 114.7	227.45/143.35	241.24 / 177.1
Chew/Bite object	n/a / 23.19	n/a / 140.77	n/a / 199.81	51.42 / 87.31	5.33 / 43.73	32.33 / 80.03
Bar-pressing	72.24 / 128.02	90.83 / 96.34	86.43 / 81.4	11.52 / 15.49	6.39 / 4.2	4.03 / 2.76
Sniff bottle	13.27 / 26.07	13.68 / 12.86	17.19 / 13.09	11.03 / 9.13	15.64 / 7.84	13.1 / 7.83
Sniff & Touch bottle	104.43 / 37.62	114.95 / 26.27	114.15 / 31.4	48.28 / 58.02	71.2 / 41.32	44.9 / 68.75
Chew/Bite bottle	11.59 / 108.38	36.76 / 78.11	79.32 / 75.43	92.84 / 126.06	20.79 / 188.63	121.73 / 89.19
Drinking	67.1 / 79.59	86.93 / 123.55	116.59/145.52	12.32 / 15.79	17.83 / 7.94	12.45 / 16.39
Resting/Sleeping	122.44/130.06	203.06 / 25.8	158.29 / 69.87	369.94/377.99	397.05/332.68	412.7 / 392.34

Table C.41a

The mean frequency and duration of behaviours for the "part of session" grouping variable for both groups for the first three sessions in Experiment 3 (FIOE and FIOS groups).

BEHAVIOURAL MEASURE	SESSION 1 1^{st} / mid / last 30 minutes	SESSION 2 1^{st} / mid / last 30 minutes	SESSION 3 1^{st} / mid / last 30 minutes
FREQUENCIES			
Digging/Burying	24.88/ 19.25 / 21.75	18.25 / 12.25 / 9.5	23.88 / 9.5 / 9.13
Propping	33.88 / 42 / 22.25	36.13 / 20.13 / 23.88	33.13 / 25.13 / 27.13
Displacement	30.88 / 27.25 / 25.75	31.38 / 31.38 / 32.13	28.38 / 20.5 / 25.63
Bar-related behaviour	239.63 / 224.75 / 205.38	219.75 / 158.88 / 134.63	181.63 / 174.88 / 150.63
Sniff object	140 / 64 / 46.25	80.25 / 59.25 / 55.25	73.25 / 66.25 / 71.25
Sniff & Touch object	69 / 25.5 / 17.75	43.25 / 26 / 28.75	47 / 30.25 / 37
Chew/Bite object	5.5 / 1 / 2.75	7.25 / 5.5 / 8	9.25 / 5.5 / 6
Bar-pressing	311.88 / 289.5 / 302.63	369.63 / 409.25 / 383.38	374.63 / 340.88 / 310.88
Sniff bottle	32.63 / 22.25 / 22.25	24.5 / 21.63 / 20.75	31 / 26.88 / 23.38
Sniff & Touch bottle	31.88 / 25.88 / 23	32.63 / 22.13 / 26.88	36 / 32 / 27.75
Chew/Bite bottle	5.63 / 0.63 / 7	5.63 / 1.5 / 3.88	8.25 / 4.38 / 3
Drinking	12.88 / 7.88 / 7.38	13.38 / 7.88 / 9.13	14.63 / 10.38 / 8.25
Resting/Sleeping	0.75 / 10.88 / 13.38	1.13 / 13.88 / 9.13	1.25 / 9.38 / 13.5
DURATIONS (in seconds)			
Digging/Burying	31.31 / 22.77 / 25.11	18.56 / 17.66 / 16.13	31.47 / 9.96 / 7.75
Propping	70.03 / 115.82 / 78.23	92.12 / 58.88 / 76.49	85.87 / 87.23 / 80.64
Displacement	114.43 / 206.3 / 207.08	170.73 / 266.33 / 207.52	159.92 / 179.24 / 238.71
Bar-related behaviour	188.7 / 189.97 / 166.08	159.33 / 115.72 / 84.55	116.16 / 117.49 / 101.43
Sniff object	200.65 / 57.58 / 36.23	57.23 / 40.28 / 43.75	42.13 / 47.83 / 47
Sniff & Touch object	143.73 / 63.38 / 30.58	79.25 / 57.78 / 57.3	66.18 / 47.78 / 96.28
Chew/Bite object	13.1 / 2.23 / 54.25	78.05 / 113.7 / 230.55	250.28 / 220.45 / 128.7
Bar-pressing	153.14 / 75.49 / 71.77	89.84 / 98 / 92.93	90.82 / 84.75 / 76.19
Sniff bottle	29.42 / 16.01 / 13.59	14.32 / 13.42 / 12.08	15.09 / 14.6 / 15.74
Sniff & Touch bottle	70.79 / 86.31 / 55.98	54 / 77.04 / 80.79	65.44 / 82.31 / 70.59
Chew/Bite bottle	123.92 / 1.29 / 54.74	95.58 / 3.46 / 73.28	84.08 / 112.17 / 35.88
Drinking	90.71 / 75.88 / 53.46	144.07 / 83.67 / 87.99	159.54 / 143.89 / 89.73
Resting/Sleeping	4.27 / 144.87 / 229.62	10.96 / 161.31 / 171.03	10.73 / 89.68 / 241.83

Table C.41b

The mean frequency and duration of behaviours for the "part of session" grouping variable for both groups for the last three sessions in Experiment 3 (FIOE and FIOS groups).

BEHAVIOURAL MEASURE	**SESSION 4** **1st / mid / last** **30 minutes**	**SESSION 5** **1st / mid / last** **30 minutes**	**SESSION 6** **1st / mid / last** **30 minutes**
FREQUENCIES			
Digging/Burying	27.25 / 13.63 / 12.88	36 / 10.13 / 11.38	35.63 / 14.88 / 10.88
Propping	25.88 / 20 / 21.63	48.75 / 24.75 / 27.63	36.88 / 32.75 / 32.75
Displacement	23 / 13.88 / 12.88	28.75 / 17 / 21.38	22.13 / 18 / 10
Bar-related behaviour	109.63 / 65.38 / 85.63	61.5 / 56.13 / 58.25	40.88 / 42.13 / 50.5
Sniff object	121 / 47.38 / 54.25	91.88 / 48 / 44.88	71.88 / 47.75 / 36.88
Sniff & Touch object	85.25 / 29 / 28.38	65.38 / 29.88 / 28.38	53.13 / 35.5 / 29.63
Chew/Bite object	17.88 / 2.38 / 1	9.5 / 1.63 / 0.88	9.63 / 1.13 / 0
Bar-pressing	127.75 / 14.38 / 13.38	24 / 13.5 / 10.75	12.63 / 10.5 / 10.38
Sniff bottle	27.25 / 12 / 13.88	21.38 / 9.75 / 11.25	15.13 / 9.88 / 9.88
Sniff & Touch bottle	32.38 / 19.5 / 16.88	27.88 / 11.13 / 17	24 / 15.75 / 17.75
Chew/Bite bottle	13.25 / 3.88 / 1.88	6.13 / 2.63 / 5.38	7.63 / 2.38 / 4
Drinking	5.13 / 0.63 / 1	3.63 / 0.63 / 0.63	4 / 1.5 / 0.63
Resting/Sleeping	1 / 14.88 / 21.75	1.25 / 16.25 / 19.88	1.25 / 15.25 / 23.38
DURATIONS (in seconds)			
Digging/Burying	34.77 / 16.93 / 12.1	41.77 / 12.06 / 10.45	36.06 / 18.47 / 11.72
Propping	65.4 / 73.63 / 87.58	146.03 / 101.17 / 107.27	123.29 / 147.63 / 121.63
Displacement	182.86 / 298.42 / 190.16	386.95 / 336.53 / 386.46	364.23 / 317.99 / 128.61
Bar-related behaviour	80.7 / 147.44 / 180.43	56.97 / 74.42 / 90.5	49.47 / 41.63 / 159.52
Sniff object	112.61 / 56.54 / 72.7	82.17 / 117.94 / 45.95	67.03 / 50.24 / 36.76
Sniff & Touch object	202.02 / 145.36 / 152.72	177.92 / 154.11 / 224.19	178.58 / 262.47 / 186.48
Chew/Bite object	184.71 / 20.48 / 2.92	58.44 / 10.3 / 4.85	149.48 / 19.07 / 0
Bar-pressing	31.32 / 4.76 / 4.45	6.91 / 5.47 / 3.52	3.72 / 3.27 / 3.2
Sniff bottle	13.05 / 7.09 / 10.1	13.21 / 10.24 / 11.78	10.48 / 11.33 / 9.6
Sniff & Touch bottle	46.43 / 61.59 / 51.43	60.46 / 53.38 / 54.96	53.03 / 47.79 / 69.66
Chew/Bite bottle	197.22 / 107.08 / 24.07	156.02 / 18.73 / 139.4	241.64 / 20.28 / 54.47
Drinking	35.99 / 2.43 / 3.74	30.67 / 6.2 / 1.8	21.59 / 18.58 / 3.1
Resting/Sleeping	6.4 / 462.67 / 652.84	59.76 / 569.97 / 464.87	29.62 / 466.84 / 711.12

Table C.42

The mean frequency and duration of behaviours for the "session" grouping variable for both groups and all parts of every session in Experiment 3 (only the FIOS group had objects present during sessions 1-3).

BEHAVIOURAL MEASURE	**SESSION 1**	**SESSION 2**	**SESSION 3**	**SESSION 4**	**SESSION 5**	**SESSION 6**
FREQUENCIES						
Digging/Burying	21.96	13.33	14.17	17.92	19.17	20.46
Propping	32.71	26.71	28.46	22.5	33.71	34.13
Displacement	27.96	31.63	24.84	16.59	22.38	16.71
Bar-related behaviour	223.25	171.09	169.05	86.88	58.63	44.5
Sniff object	41.71	32.46	35.13	74.21	61.59	52.17
Sniff & Touch object	18.71	16.34	19.04	47.54	41.21	39.42
Chew/Bite object	1.54	3.46	3.46	7.09	4	3.59
Bar-pressing	301.34	387.42	342.13	51.84	16.08	11.17
Sniff bottle	25.71	22.29	27.09	17.71	14.13	11.63
Sniff & Touch bottle	26.92	27.21	31.92	22.92	18.67	19.17
Chew/Bite bottle	4.42	3.67	5.21	6.34	4.71	4.67
Drinking	9.38	10.13	11.09	2.25	1.63	2.04
Resting/Sleeping	8.34	8.05	8.04	12.54	12.46	13.29
DURATIONS (in seconds)						
Digging/Burying	26.4	17.45	16.39	21.27	21.43	22.08
Propping	88.03	75.83	84.58	75.54	118.16	130.85
Displacement	175.94	214.86	192.62	223.81	369.98	270.28
Bar-related behaviour	181.58	119.87	111.69	136.19	73.96	83.54
Sniff object	49.08	23.55	22.83	80.62	82.02	51.34
Sniff & Touch object	39.62	32.39	35.04	166.7	185.41	209.18
Chew/Bite object	11.6	70.39	99.91	69.37	24.53	56.18
Bar-pressing	100.13	93.59	83.92	13.51	5.3	3.4
Sniff bottle	19.67	13.27	15.14	10.08	11.74	10.47
Sniff & Touch bottle	71.03	70.61	72.78	53.15	56.27	56.83
Chew/Bite bottle	59.98	57.44	77.38	109.46	104.72	105.46
Drinking	73.35	105.24	131.05	14.05	12.89	14.42
Resting/Sleeping	126.25	114.43	114.08	373.97	364.87	402.53

Table C.43

The mean frequency and duration of behaviours during the PRPs for the "object" grouping variable for all parts of each ***fixed-interval*** session in Experiment 3 (FIOE and FIOS groups).

BEHAVIOURAL MEASURE	**SESSION 1 FIOE / FIOS**	**SESSION 2 FIOE / FIOS**	**SESSION 3 FIOE / FIOS**
FREQUENCIES			
Digging/Burying	22.33 / 8.83	11.75 / 8.5	11.83 / 7.67
Propping	13.33 / 13.92	14.33 / 18	11.92 / 25.92
Displacement	16.25 / 17.58	16.33 / 25.25	17.92 / 19
Bar-related behaviour	87.17 / 59.67	72.75 / 51.08	73.5 / 45.17
Sniff object	n/a / 43.83	n/a / 44.75	n/a / 51.25
Sniff & Touch object	n/a / 18.67	n/a / 21.92	n/a / 27.67
Chew/Bite object	n/a / 1.58	n/a / 5.58	n/a / 6.17
Sniff bottle	13.25 / 14.92	16.42 / 15.33	23.67 / 17.75
Sniff & Touch bottle	23.83 / 10.92	27.33 / 12.58	36.33 / 16.58
Chew/Bite bottle	1.25 / 3.75	1.17 / 3.75	4.25 / 4.33
Drinking	6.25 / 9.25	5.58 / 10.67	8.33 / 12.33
Resting/Sleeping	9.08 / 4.17	10.17 / 3.17	8.67 / 6.33
DURATIONS (in seconds)			
Digging/Burying	27.2 / 11.7	15.29 / 14.45	12.23 / 12.9
Propping	45.73 / 38.63	55.43 / 47.86	38.13 / 80.6
Displacement	143.23 / 122.97	184.62 / 171.17	217.49 / 135.44
Bar-related behaviour	99.4 / 58.78	62.35 / 41.25	75.49 / 28.09
Sniff object	n/a / 45.06	n/a / 34.31	n/a / 33.82
Sniff & Touch object	n/a / 37.39	n/a / 46.2	n/a / 51.02
Chew/Bite object	n/a / 17.38	n/a / 128.18	n/a / 181.79
Sniff bottle	8.09 / 14.62	9.01 / 9.33	12.64 / 10.83
Sniff & Touch bottle	73.78 / 23.24	91.67 / 18.7	99.13 / 25.54
Chew/Bite bottle	8.23 / 50.03	19.43 / 68.03	74.64 / 63.76
Drinking	54.17 / 74.05	66.32 / 104.35	113.86 / 140.26
Resting/Sleeping	99.39 / 125.81	191.96 / 18.37	143.35 / 68.71

Table C.44

The mean frequency and duration of behaviours during the PRPs for the "part of session" grouping variable for each ***fixed-interval*** session in Experiment 3 (FIOE and FIOS groups).

BEHAVIOURAL MEASURE	**SESSION 1 1st / mid / last 30 minutes**	**SESSION 2 1st / mid / last 30 minutes**	**SESSION 3 1st / mid / last 30 minutes**
FREQUENCIES			
Digging/Burying	14.5 / 14 / 18.25	11.88 / 11 / 7.5	13.25 / 8.5 / 7.5
Propping	8.5 / 18.13 / 14.25	17.38 / 16.5 / 14.63	15 / 18.5 / 23.25
Displacement	13.38 / 19.63 / 17.75	17 / 25.25 / 20.13	19.13 / 16.38 / 19.88
Bar-related behaviour	64.13 / 86.25 / 69.88	62.88 / 72.88 / 50	52.13 / 61.5 / 64.38
Sniff object	54.5 / 37.75 / 39.25	41.75 / 50.5 / 42	40 / 55.75 / 58
Sniff & Touch object	23 / 17.75 / 15.25	21.25 / 22.5 / 22	27.25 / 25.25 /30.5
Chew/Bite object	1.75 / 1 / 2	4.5 / 5 / 7.25	7.25 / 5.25 / 6
Sniff bottle	13.25 / 12.63 / 16.38	15.5 / 18 / 14.13	20.75 / 21.63 / 19.75
Sniff & Touch bottle	16.88 / 17.5 / 17.75	19.25 / 20 / 20.63	25.63 / 28.38 / 25.38
Chew/Bite bottle	2.5 / 0.38 / 4.63	3.75 / 1.38 / 2.25	6.13 / 4 / 2.75
Drinking	9.88 / 7.25 / 6.13	9.25 / 7.13 / 8	13.13 / 10 / 7.88
Resting/Sleeping	0.38 / 7.88 / 11.63	0.63 / 12.13 / 7.25	0.75 / 8.75 / 13
DURATIONS (in seconds)			
Digging/Burying	18.91 / 18.18 / 21.27	12.98 / 16.97 / 14.67	21.73 / 8.8 / 7.16
Propping	20.72 / 52.22 / 53.61	52.11 / 50.71 / 52.12	41.5 / 65.48 / 71.13
Displacement	74.44 / 176.76/ 148.1	115.68/246.36/ 171.65	134.06/173.41/ 221.92
Bar-related behaviour	71.23 / 91.33 / 74.73	56.69 / 62.65 / 36.06	36.84 / 56.66 / 61.89
Sniff object	68.29 / 35.11 / 31.78	33.55 / 33.66 / 35.72	21.34 / 40.31 / 39.81
Sniff & Touch object	43.12 / 42.19 / 26.85	37.67 / 53.21 / 47.73	35.12 / 39.92 / 78.01
Chew/Bite object	7.31 / 2.21 / 42.63	65.53 / 101.04/ 217.98	221.94/194.71/ 128.72
Sniff bottle	13.41 / 10.86 / 9.8	7.59 / 11.37 / 8.56	10.44 / 11.73 / 13.04
Sniff & Touch bottle	38.68 / 58.99 / 47.86	31.39 / 70.51 / 63.67	45.03 / 78.14 / 63.85
Chew/Bite bottle	49.07 / 0.41 / 37.93	83.24 / 2.89 / 45.07	70.66 / 105.81 / 31.14
Drinking	78.73 / 72.23 / 41.37	101.63 / 78.93 / 75.45	154.06/ 142.57/ 84.56
Resting/Sleeping	2.37 / 115.28 / 220.15	6.04 / 154.58/ 154.88	2.65 / 86.14 / 229.31

Table C.45

The mean frequency and duration of behaviours during the PRPs for the "session" grouping variable for both groups and all parts of the *fixed-interval* sessions in Experiment 3 (only the FIOS group had objects present during these sessions).

BEHAVIOURAL MEASURE	**SESSION 1**	**SESSION 2**	**SESSION 3**
FREQUENCIES			
Digging/Burying	15.58	10.13	9.75
Propping	13.63	16.17	18.92
Displacement	16.92	20.79	18.46
Bar-related behaviour	73.42	61.92	59.34
Sniff object	21.92	22.38	25.63
Sniff & Touch object	9.34	10.96	13.84
Chew/Bite object	0.79	2.79	3.09
Sniff bottle	14.09	15.88	20.71
Sniff & Touch bottle	17.38	19.96	26.46
Chew/Bite bottle	2.5	2.46	4.29
Drinking	7.75	8.13	10.34
Resting/Sleeping	6.63	6.67	7.5
DURATIONS (in seconds)			
Digging/Burying	19.45	14.87	12.56
Propping	42.18	51.65	59.37
Displacement	133.1	177.9	176.46
Bar-related behaviour	79.1	51.8	51.8
Sniff object	22.53	17.16	16.91
Sniff & Touch object	18.7	23.11	25.51
Chew/Bite object	8.7	64.09	90.9
Sniff bottle	11.36	9.17	11.74
Sniff & Touch bottle	48.51	55.19	62.34
Chew/Bite bottle	29.14	43.73	69.2
Drinking	64.11	85.34	127.06
Resting/Sleeping	112.6	105.17	106.03

APPENDIX D

Frequencies and durations of behaviours scored in Litchfield's 1987 study, and frequencies and durations of behavioural measures during PRPs in Litchfield's 1987 study.

The material included in Appendix D consists of a set of three tables per behavioural category scored. The four rats per group are included in the same cell of the table (*e.g.*, the four rats in the FROS group are lumped together). The set of three tables provides the following information:

1. the frequency and duration of the behaviour for each rat in each session (*i.e.*, raw data), the group mean for each session, and sum of means for sessions 1-3 and 4-6 (for each group of rats);
2. the frequency and duration of the behaviour during the PRPs for each rat in each ***fixed-ratio*** or ***CRF*** session (*i.e.*, raw data), the group mean for each session, the average mean and sum of means for sessions 1-3 (for each group of rats); and
3. the frequency and duration of the behaviour sum of means (over sessions 1-3), sum of means in PRPs (over sessions 1-3), and percentage of total for each group of rats.

It should be noted that for some of the behavioural categories, the tables are presented in a different sequence. For the ***bar-pressing*** category only the first table is relevant. A table presenting the frequency of reinforcement for each rat in each session is also provided. The behavioural categories are presented in the following order:

1. ***propping*** (Table D.1-D3);
2. ***displacement*** (Table D.4-D.6);
3. ***bar-related behaviour*** (Table D.7-D.9);
4. ***sniff object*** (Table D.10-D.12);
5. ***sniff and touch object*** (Table D.13-D.15);
6. ***jump at lid*** (Table D.16-D.18); and
7. ***bar-pressing*** (Table D.19).

Table D.1

Frequency and duration of ***propping*** for each rat in Litchfield's 1987 study, in each session (sessions 1-3 are ***fixed-ratio*** or ***CRF*** sessions, and sessions 4-6 are extinction sessions).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	91 / 240.5 75 / 233.4 103 / 308.6 81 / 187.1 mean= 87.5 / 242.4	1 / 0.7 2 / 6.4 1 / 1.1 12 / 34.6 mean= 4 / 10.7	88 / 163.4 164 / 213.9 43 / 70.9 89 / 174.1 mean= 96 / 155.58	2 / 2.1 0 / 0 11 / 13.1 4 / 3.4 mean= 4.25 / 4.65
SESSION 2	126 / 253.3 123 / 289.2 198 / 348.4 96 / 187.2 mea=135.75/269.53	2 / 2.6 11 / 10.0 4 / 6.3 22 / 29.1 mean= 9.75 / 12.0	69 / 94.8 346 / 353.3 47 / 76.3 97 / 153.4 mea=139.75/169.45	1 / 0.3 1 / 0.6 6 / 5.4 4 / 3.9 mean= 3 / 2.55
SESSION 3	97 / 132.1 114 / 198.5 174 / 264.8 61 / 91.2 mean=111.5/171.65	1 / 1.2 0 / 0 1 / 0.8 5 / 5.0 mean= 1.75 / 1.75	47 / 56.7 248 / 219.9 29 / 37.5 66 / 145.1 mean= 97.5 / 114.8	8 / 9.4 1 / 0.5 28 / 30.5 10 / 8.0 mean= 11.75 / 12.1
sum of means (for sessions 1 to 3)	334.75 / 683.58	15.5 / 24.45	333.25 / 439.83	19 / 19.3
SESSION 4	138 / 179.3 109 / 171.5 98 / 127.6 115 / 154.1 mean= 115 / 158.13	75 / 93.5 113 / 131.7 116 / 137.5 115 / 148.6 mea=104.75/127.83	73 / 69.6 180 / 155.4 68 / 92.6 84 / 117.3 mea=101.25/108.73	173 / 184.8 121 / 115.0 168 / 223.5 80 / 119.6 mean=135.5/160.73
SESSION 5	76 / 112.3 176 / 338.0 215 / 237.1 172 / 262.5 mea=159.75/237.48	63 / 86.6 135 / 170.9 188 / 201.9 162 / 218.9 mean= 137 / 169.58	105 / 90.6 159 / 145.0 108 / 140.8 81 / 86.9 mea=113.25/115.83	121 / 144.7 129 / 150.6 175 / 220.9 110 / 195.8 mean= 133.75 / 178
SESSION 6	101 / 103.3 177 / 397.8 144 / 206.8 145 / 258.2 mea=141.75/241.53	54 / 73.8 163 / 172.5 210 / 262.1 117 / 173.0 mean= 136 / 170.35	88 / 81.4 107 / 155.2 92 / 121.5 69 / 103.4 mean= 89 / 115.38	97 / 156.3 108 / 132.9 169 / 266.4 99 / 128.5 mea=118.25/171.03
sum of means (for sessions 4 to 6)	416.5 / 637.14	377.75 / 467.76	303.5 / 339.94	387.5 / 509.76

Table D.2

Mean frequency and duration of ***propping*** during the PRPs (for all four groups in Litchfield's 1987 study) summed over the first three sessions (***fixed-ratio*** or ***CRF***), as a percentage of the total mean frequency and duration of ***propping*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FROS	frequency	334.75	119.5	35.70
	duration (seconds)	683.58	246.73	36.09
FROE	frequency	333.25	120.25	36.08
	duration (seconds)	439.83	171.83	39.07

Table D.3

Frequency and duration of ***propping*** during the PRPs, for each rat in Litchfield's 1987 study in each ***fixed-ratio*** or ***CRF*** session (sessions 1-3).

	FROS (A1-A4)	CRFOS (B1-B4)	FROE (C1-C4)	CRFOE (D1-D4)
SESSION 1	18 / 42.7 40 / 127.0 38 / 102.4 58 / 124.1 mean= 38.5 / 99.05	1 / 0.7 0 / 0 1 / 1.1 12 / 34.6 mean= 3.5 / 9.1	80 / 142.7 35 / 40.7 27 / 47.8 8 / 16.4 mean= 37.5 / 61.9	2 / 2.1 0 / 0 10 / 12.2 4 / 3.4 mean= 4 / 4.43
SESSION 2	18 / 35.4 52 / 122.0 50 / 99.3 65 / 120.3 mean= 46.25/ 94.25	2 / 2.6 11 / 10.0 4 / 6.3 22 / 29.1 mean= 9.75 / 12	66 / 91.6 36 / 43.2 28 / 46.6 36 / 59.8 mean= 41.5 / 60.3	1 / 0.3 0 / 0 2 / 2.3 3 / 2.9 mean= 1.5 / 1.38
SESSION 3	28 / 45.8 46 / 69.7 51 / 77.1 14 / 21.1 mean= 34.75/ 53.43	1 / 1.2 0 / 0 1 / 0.8 5 / 5.0 mean= 1.75 / 1.75	41 / 48.0 77 / 69.4 19 / 23.8 28 / 57.3 mean=41.25 / 49.63	8 / 9.4 1 / 0.5 26 / 29.1 10 / 8.0 mean= 11.25/ 11.75
sum of means (for sessions 1 to 3)	119.5 / 246.73	15 / 22.85	120.25 / 171.83	16.75 / 17.56

Table D.4

Frequency and duration of ***displacement*** during the PRPs, for each rat in Litchfield's 1987 study in each ***fixed-ratio*** or ***CRF*** session (sessions 1-3).

	FROS (A1-A4)	CRFOS (B1-B4)	FROE (C1-C4)	CRFOE (D1-D4)
SESSION 1	10 / 37.6 44 / 58.3 16 / 17.0 26 / 34.2 mean= 24 / 36.78	0 / 0 1 / 1.0 0 / 0 2 / 4.0 mean= 0.75 / 1.25	54 / 80.8 6 / 25.8 24 / 46.2 23 / 36.3 mean= 26.75/ 47.28	3 / 5.2 0 / 0 0 / 0 1 / 1.2 mean= 1 / 1.6
SESSION 2	20 / 41.8 18 / 33.4 6 / 16.0 19 / 28.1 mean= 15.75/ 29.83	0 / 0 1 / 0.6 0 / 0 5 / 8.9 mean= 1.5 / 2.38	23 / 43.5 3 / 1.6 11 / 23.8 32 / 49.3 mean= 17.25/ 29.55	1 / 1.8 0 / 0 0 / 0 0 / 0 mean= 0.25 / 0.45
SESSION 3	15 / 17.4 40 / 49.9 9 / 10.6 12 / 17.6 mean= 19 / 23.88	2 / 2.1 0 / 0 2 / 0.5 0 / 0 mean= 1 / 0.65	45 / 85.5 14 / 9.5 17 / 30.1 17 / 19.1 mean= 23.25/ 36.05	2 / 2.2 0 / 0 2 / 3.1 1 / 0.4 mean= 1.25 / 1.43
sum of means (for sessions 1 to 3)	58.75 / 90.49	3.25 / 4.28	67.25 / 112.88	2.5 / 3.48

Table D.5

Mean frequency and duration of ***displacement*** during the PRPs (for all four groups in Litchfield's 1987 study) summed over the first three sessions (***fixed-ratio*** or ***CRF***), as a percentage of the total mean frequency and duration of ***displacement*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FROS	frequency	150.5	58.75	39.04
	duration (seconds)	251.08	90.49	36.04
FROE	frequency	136.25	67.25	49.36
	duration (seconds)	218.23	112.88	51.73

Table D.6

Frequency and duration of ***displacement*** for each rat in Litchfield's 1987 study, in each session (sessions 1-3 are ***fixed-ratio*** or ***CRF*** sessions, and sessions 4-6 are extinction sessions).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	61 / 131.0 58 / 76.1 41 / 65.5 39 / 49.8 mean= 49.75 / 80.6	0 / 0 1 / 1.0 0 / 0 2 / 4.0 mean= 0.75 / 1.25	58 / 83.1 40 / 83.3 29 / 59.7 74 / 123.5 mean= 50.25 / 87.4	3 / 5.2 0 / 0 0 / 0 1 / 1.2 mean= 1 / 1.6
SESSION 2	77 / 164.3 45 / 108.4 25 / 33.4 27 / 32.2 mean= 43.5 / 84.58	0 / 0 1 / 0.6 0 / 0 5 / 8.9 mean= 1.5 / 2.38	30 / 49.7 19 / 51.7 30 / 59.1 95 / 105.3 mean= 43.5 / 66.45	1 / 1.8 0 / 0 0 / 0 0 / 0 mean= 0.25 / 0.45
SESSION 3	117 / 174.4 62 / 88.0 31 / 54.1 19 / 27.1 mean= 57.25 / 85.9	2 / 2.1 0 / 0 2 / 0.5 0 / 0 mean= 1 / 0.65	52 / 93.8 33 / 48.9 21 / 34.8 64 / 80.0 mean= 42.5 / 64.38	2 / 2.2 0 / 0 2 / 3.1 1 / 0.4 mea= 1.25 / 1.43
sum of means (for sessions 1 to 3)	150.5 / 251.08	3.25 / 4.28	136.25 / 218.23	2.5 / 3.48
SESSION 4	123 / 182.6 48 / 92.6 44 / 57.9 28 / 40.1 mean= 60.75 / 93.3	61 / 129.0 11 / 23.0 27 / 44.6 35 / 43.8 mean= 33.5 / 60.1	51 / 48.4 24 / 38.0 25 / 46.4 106 / 130.5 mean= 51.5 / 65.83	25 / 56.5 7 / 36.8 10 / 48.1 22 / 33.8 mean= 16 / 43.8
SESSION 5	57 / 137.6 67 / 91.8 48 / 61.3 41 / 55.4 mean= 53.25/ 86.53	43 / 97.9 27 / 41.4 45 / 49.8 10 / 49.8 mean= 31.25/ 59.73	77 / 124.3 34 / 50.1 37 / 71.8 91 / 115.5 mean= 59.75/ 90.43	77 / 111.1 16 / 52.7 30 / 82.5 26 / 73.3 mean= 37.25 / 79.9
SESSION 6	74 / 176.1 70 / 112.0 54 / 82.0 33 / 55.6 mean=57.75/106.43	73 / 252.4 17 / 27.6 61 / 91.9 24 / 63.9 mean=43.75/108.95	91 / 152.9 61 / 230.4 65 / 125.5 99 / 134.0 mean= 79 / 160.7	58 / 141.6 23 / 55.4 23 / 46.4 51 / 149.5 mean= 38.75/ 98.23
sum of means (for sessions 4 to 6)	171.75 / 286.26	108.5 / 228.78	190.25 / 316.96	92 / 221.93

Table D.7

Frequency and duration of ***bar-related behaviour*** for each rat in Litchfield's 1987 study, in each session (sessions 1-3 are ***fixed-ratio*** or ***CRF*** sessions, and sessions 4-6 are extinction sessions).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	50 / 90.1 48 / 66.8 67 / 115.0 32 / 51.1 mean=49.25 / 80.75	0 / 0 2 / 1.5 0 / 0 6 / 6.7 mean= 2 / 2.05	51 / 47.1 64 / 132.1 52 / 67.7 66 / 124.3 mean= 58.25 / 92.8	0 / 0 0 / 0 0 / 0 1 / 0.4 mean= 0.25 / 0.1
SESSION 2	78 / 148.3 34 / 38.9 40 / 54.4 21 / 18.0 mean= 43.25 / 64.9	2 / 1.0 4 / 2.5 5 / 3.5 11 / 12.9 mean= 5.5 / 4.98	59 / 57.6 85 / 106.1 34 / 43.5 60 / 104.3 mean= 59.5 / 77.88	2 / 0.4 2 / 1.4 4 / 1.8 1 / 0.4 mean= 2.25 / 1.0
SESSION 3	71 / 71.4 40 / 31.8 39 / 36.3 20 / 24.1 mean= 42.5 / 40.9	2 / 1.1 1 / 0.3 1 / 0.5 8 / 6.6 mean= 3 / 2.13	44 / 37.3 54 / 51.8 30 / 33.2 47 / 125.3 mean= 43.75 / 61.9	1 / 0.5 2 / 0.8 5 / 2.9 4 / 2.3 mean= 3 / 1.63
sum of means (for sessions 1 to 3)	135 / 186.55	10.5 / 9.16	161.5 / 232.58	5.5 / 2.73
SESSION 4	97 / 131.5 114 / 187.1 60 / 78.4 73 / 112.7 mean= 86 / 127.43	41 / 29.3 71 / 70.3 63 / 212.3 129 / 260.6 mean= 76 / 143.13	149 / 148.0 121 / 170.5 108 / 147.8 96 / 145.1 mean=118.5/152.85	123 / 78.0 59 / 48.4 107 / 161.8 95 / 140.8 mean= 96 / 107.25
SESSION 5	114 / 350.6 52 / 91.6 82 / 168.8 70 / 156.9 mean= 79.5/ 191.98	25 / 23.9 48 / 58.5 110 / 340.7 114 / 195.6 mean=74.25/154.68	108 / 162.5 107 / 227.5 153 / 318.1 73 / 115.2 mea=110.25/205.83	80 / 53.4 74 / 211.0 85 / 243.0 67 / 158.8 mean= 76.5/ 166.55
SESSION 6	112 / 310.6 77 / 195.3 116 / 240.2 45 / 104.4 mean= 87.5/ 212.63	43 / 206.0 75 / 120.7 90 / 198.6 69 / 121.7 mean=69.25/161.75	126 / 218.9 56 / 140.1 94 / 259.6 87 / 145.1 mean=90.75/190.93	68 / 82.6 31 / 88.1 87 / 196.1 48 / 156.2 mean= 58.5/ 130.75
sum of means (for sessions 4 to 6)	253 / 532.04	219.5 / 459.56	319.5 / 549.61	231 / 549.61

Table D.8

Mean frequency and duration of ***bar-related behaviour*** during the PRPs (for all four groups in Litchfield's 1987 study) summed over the first three sessions (***fixed-ratio*** or ***CRF***), as a percentage of the total mean frequency and duration of ***bar-related behaviour*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FROS	frequency duration (seconds)	135 186.55	49 62.86	36.30 33.70
FROE	frequency duration (seconds)	161.5 232.58	81 121.45	50.16 52.22

Table D.9

Frequency and duration of ***bar-related behaviour*** during the PRPs, for each rat in Litchfield's 1987 study in each ***fixed-ratio*** or ***CRF*** session (sessions 1-3).

	FROS (A1-A4)	CRFOS (B1-B4)	FROE (C1-C4)	CRFOE (D1-D4)
SESSION 1	13 / 25.0 37 / 49.9 16 / 33.6 20 / 34.2 mean= 21.5 / 35.68	0 / 0 0 / 0 0 / 0 5 / 6.2 mean= 1.25 / 1.55	41 / 37.2 8 / 16.0 33 / 51.6 21 / 56.2 mean= 25.75/ 40.25	0 / 0 0 / 0 0 / 0 1 / 0.4 mean= 0.25 / 0.1
SESSION 2	11 / 13.6 15 / 16.6 13 / 16.9 17 / 13.6 mean= 14 / 15.18	1 / 0.8 3 / 2.1 4 / 3.0 10 / 12.7 mean= 4.5 / 4.65	52 / 52.5 8 / 7.7 20 / 26.3 31 / 50.3 mean= 27.75 / 34.2	1 / 0.2 0 / 0 1 / 0.4 0 / 0 mean= 0.5 / 0.15
SESSION 3	15 / 10.6 23 / 21.0 10 / 12.0 6 / 4.4 mean= 13.5 / 12.0	1 / 0.6 1 / 0.3 0 / 0 7 / 6.2 mean= 2.25 / 1.78	36 / 33.5 16 / 14.7 25 / 29.5 33 / 110.3 mean= 27.5 / 47.0	1 / 0.5 1 / 0.3 4 / 2.6 3 / 1.9 mean= 2.25 / 1.33
sum of means (for sessions 1 to 3)	49 / 62.86	8 / 7.98	81 / 121.45	3 / 1.58

Table D.10

Frequency and duration of ***sniff object*** during the PRPs, for each rat in Litchfield's 1987 study in each ***fixed-ratio*** or ***CRF*** session (sessions 1-3).

	FROS (A1-A4)	CRFOS (B1-B4)	FROE (C1-C4)	CRFOE (D1-D4)
SESSION 1	10 / 3.9 40 / 14.8 35 / 8.0 55 / 16.5 mean= 35 / 10.8	6 / 1.9 4 / 1.2 3 / 0.6 20 / 6.2 mean= 8.25 / 2.48	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	23 / 4.8 22 / 6.3 27 / 5.6 54 / 19.8 mean= 31.5 / 9.13	5 / 1.3 3 / 2.1 7 / 1.6 22 / 4.6 mean= 9.25 / 2.4	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	14 / 8.9 22 / 14.1 12 / 7.6 9 / 4.7 mean= 14.25 / 8.83	4 / 1.8 4 / 0.9 7 / 3.6 7 / 3.7 mean= 5.5 / 2.5	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	80.75 / 28.76	23 / 7.38		

Table D.11

Mean frequency and duration of ***sniff object*** during the PRPs (for all four groups in Litchfield's 1987 study) summed over the first three sessions (***fixed-ratio*** or ***CRF***), as a percentage of the total mean frequency and duration of ***sniff object*** summed over the first three sessions.

		Sum of means	Sum of means in PRPs	% of total
FROS	frequency duration (seconds)	239.5 91.26	80.75 28.76	33.72 31.51
FROE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table D.12

Frequency and duration of ***sniff object*** for each rat in Litchfield's 1987 study, in each session (sessions 1-3 are ***fixed-ratio*** or ***CRF*** sessions, and sessions 4-6 are extinction sessions).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	105 / 56.6 87 / 29.9 110 / 30.3 104 / 29.7 mean= 101.5/ 36.63	9 / 3.0 14 / 5.4 6 / 2.9 28 / 8.3 mean= 14.25 / 4.9	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	110 / 29.7 66 / 19.5 72 / 15.3 83 / 28.5 mean= 82.75/ 23.25	6 / 1.5 36 / 9.3 7 / 1.6 25 / 5.2 mean= 18.5 / 4.4	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	49 / 27.6 45 / 27.5 79 / 39.4 48 / 31.0 mean= 55.25/ 31.38	4 / 1.8 6 / 1.4 7 / 3.6 9 / 4.6 mean= 6.5 / 2.85	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	239.5 / 91.26	39.25 / 12.15		
SESSION 4	64 / 41.2 49 / 40.5 87 / 81.1 90 / 66.2 mean= 72.5 / 57.25	86 / 74.3 99 / 83.9 88 / 62.8 94 / 57.2 mean= 91.75/ 69.55	111 / 106.3 86 / 56.2 90 / 83.6 101 / 67.4 mean= 97 / 78.38	114 / 69.4 93 / 71.3 98 / 67.0 98 / 100.5 mean=100.75/77.05
SESSION 5	39 / 37.4 42 / 30.6 82 / 39.4 52 / 18.0 mean=53.75 / 31.35	75 / 50.3 60 / 42.6 71 / 29.4 47 / 28.5 mean= 63.25 / 37.7	97 / 61.8 64 / 36.8 61 / 33.2 61 / 33.2 mean= 70.75/ 41.25	95 / 38.5 87 / 38.8 103 / 48.6 112 / 53.5 mean= 99.25/ 44.85
SESSION 6	72 / 61.2 54 / 53.4 87 / 35.4 67 / 39.4 mean= 70 / 47.35	77 / 66.8 93 / 51.2 57 / 20.6 85 / 48.4 mean= 78 / 46.75	95 / 85.3 103 / 55.0 94 / 46.4 53 / 26.1 mean= 86.25 / 53.2	82 / 57.8 104 / 41.5 103 / 40.0 112 / 43.7 mean=100.25/45.75
sum of means (for sessions 4 to 6)	196.25 / 135.95	233 / 154.0	254 / 172.83	300.25 / 167.65

Table D.13

Frequency and duration of ***sniff and touch object*** for each rat in Litchfield's 1987 study, in each session (sessions 1-3 are ***fixed-ratio*** or ***CRF*** sessions, and sessions 4-6 are extinction sessions).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	67 / 267.4 39 / 132.7 71 / 308.0 74 / 291.6 mean=62.75/249.93	5 / 13.8 10 / 47.9 2 / 4.3 17 / 41.5 mean= 8.5 / 26.88	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	73 / 191.6 40 / 92.1 61 / 164.9 42 / 132.3 mean= 54 / 145.23	5 / 18.0 21 / 40.8 7 / 23.5 15 / 29.1 mean= 12 / 27.85	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	24 / 46.5 15 / 29.7 37 / 85.9 8 / 14.8 mean= 21 / 44.23	2 / 2.6 4 / 5.3 2 / 2.2 0 / 0 mean= 2 / 2.53	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	137.75 / 439.39	22.5 / 57.26		
SESSION 4	31 / 151.7 28 / 226.8 47 / 118.4 41 / 148.8 mean=36.75/161.43	54 / 162.7 46 / 111.0 48 / 148.1 39 / 100.3 mean=46.75/130.53	41 / 125.2 48 / 82.6 38 / 117.7 56 / 150.7 mean=45.75/119.05	54 / 155.3 52 / 155.6 52 / 96.3 39 / 92.0 mean= 49.25/ 124.8
SESSION 5	19 / 130.3 18 / 138.6 68 / 135.2 43 / 102.3 mean= 37 / 126.6	58 / 329.7 37 / 215.3 41 / 76.4 25 / 62.5 mean=40.25/170.98	46 / 132.6 32 / 72.1 25 / 82.7 40 / 122.6 mean= 35.75/ 102.5	59 / 228.6 51 / 115.0 59 / 78.8 70 / 216.9 mean=59.75/159.83
SESSION 6	37 / 121.8 20 / 77.4 64 / 178.5 48 / 135.9 mean= 42.25/ 128.4	42 / 234.0 64 / 268.8 41 / 129.1 45 / 123.0 mean= 48 / 188.73	46 / 196.7 60 / 129.8 43 / 94.9 31 / 58.9 mean= 45 / 120.08	38 / 134.0 77 / 175.7 65 / 144.5 76 / 177.1 mean= 64 / 157.83
sum of means (for sessions 4 to 6)	116 / 416.43	135 / 490.24	126.5 / 341.63	173 / 442.46

Table D.14

Mean frequency and duration of ***sniff and touch object*** during the PRPs (for all four groups in Litchfield's 1987 study) summed over the first three sessions (***fixed-ratio*** or ***CRF***), as a percentage of the total mean frequency and duration of ***sniff and touch object*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FROS	frequency duration (seconds)	137.75 439.39	46.25 142.28	33.58 32.38
FROE	frequency duration (seconds)	NO OBJECTS PRESENT		

Table D.15

Frequency and duration of ***sniff and touch object*** during the PRPs, for each rat in Litchfield's 1987 study in each ***fixed-ratio*** or ***CRF*** session (sessions 1-3).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	2 / 2.3 17 / 59.0 24 / 103.7 41 / 140.8 mean= 21 / 76.45	3 / 8.4 2 / 2.4 1 / 3.9 12 / 30.2 mean= 4.5 / 11.23	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 2	19 / 50.1 14 / 30.4 22 / 59.1 27 / 93.6 mean= 20.5 / 58.3	4 / 16.3 18 / 38.3 7 / 23.5 14 / 28.8 mean= 10.75/ 26.73	NO OBJECTS PRESENT	NO OBJECTS PRESENT
SESSION 3	6 / 9.0 6 / 14.8 6 / 5.4 1 / 0.9 mean= 4.75 / 7.53	2 / 2.6 2 / 4.3 2 / 2.2 0 / 0 mean= 1.5 / 2.28	NO OBJECTS PRESENT	NO OBJECTS PRESENT
sum of means (for sessions 1 to 3)	46.25 / 142.28	16.75 / 40.24		

Table D.16

Frequency and duration of ***jump at lid*** during the PRPs, for each rat in Litchfield's 1987 study in each ***fixed-ratio*** or ***CRF*** session (sessions 1-3).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	1 / 0.7 0 / 0 0 / 0 4 / 1.3 mean= 1.25 / 0.5	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	1 / 0.6 40 / 19.5 0 / 0 0 / 0 mean= 10.25 / 5.03	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
SESSION 2	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 16 / 5.7 0 / 0 2 / 0.8 mean= 4.5 / 1.63	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
SESSION 3	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 52 / 20.1 0 / 0 0 / 0 mean= 13 / 5.03	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
sum of means (for sessions 1 to 3)	1.25 / 0.5	0 / 0	27.75 / 11.69	0 / 0

Table D.17

Mean frequency and duration of ***jump at lid*** during the PRPs (for all four groups in Litchfield's 1987 study) summed over the first three sessions (***fixed-ratio*** or ***CRF***), as a percentage of the total mean frequency and duration of ***jump at lid*** summed over the first three sessions.

		Sum of means	**Sum of means in PRPs**	**% of total**
FROS	frequency	2	1.25	62.5
	duration (seconds)	0.98	0.5	51.02
FROE	frequency	150.25	27.75	18.47
	duration (seconds)	71.78	11.69	16.29

Table D.18
Frequency and duration of ***jump at lid*** for each rat in Litchfield's 1987 study, in each session (sessions 1-3 are ***fixed-ratio*** or ***CRF*** sessions, and sessions 4-6 are extinction sessions).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	3 / 2.1 0 / 0 0 / 0 4 / 1.3 mean= 1.75 / 0.85	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	2 / 1.0 256 / 143.6 1 / 0.1 3 / 1.9 mean= 65.5 / 36.65	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
SESSION 2	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 204 / 86.8 0 / 0 2 / 0.8 mean= 51.5 / 21.9	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
SESSION 3	0 / 0 1 / 0.5 0 / 0 0 / 0 mean= 0.25 / 0.13	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0	0 / 0 133 / 52.9 0 / 0 0 / 0 mean=33.25 / 13.23	0 / 0 0 / 0 0 / 0 0 / 0 mean= 0 / 0
sum of means (for sessions 1 to 3)	2 / 0.98	0 / 0	150.25 / 71.78	0 / 0
SESSION 4	4 / 1.9 0 / 0 0 / 0 3 / 1.0 mean= 1.75 / 0.73	0 / 0 0 / 0 1 / 0.2 0 / 0 mean= 0.25 / 0.05	0 / 0 92 / 33.2 0 / 0 2 / 1.0 mean= 23.5 / 8.55	0 / 0 9 / 2.5 3 / 1.2 0 / 0 mean= 3 / 0.93
SESSION 5	0 / 0 2 / 0.6 0 / 0 0 / 0 mean= 0.5 / 0.15	0 / 0 18 / 7.9 13 / 4.3 3 / 1.1 mean= 8.5 / 3.33	4 / 0.9 67 / 29.7 0 / 0 3 / 1.2 mean= 18.5 / 7.95	3 / 1.0 23 / 8.1 55 / 19.6 0 / 0 mean= 20.25 / 7.18
SESSION 6	0 / 0 10 / 3.6 0 / 0 1 / 0.4 mean= 2.75 / 1.0	0 / 0 63 / 17.0 7 / 1.6 0 / 0 mean= 17.5 / 4.65	0 / 0 22 / 7.0 0 / 0 2 / 0.5 mean= 6 / 1.88	3 / 1.1 14 / 4.0 7 / 2.7 0 / 0 mean= 6 / 1.95
sum of means (for sessions 4 to 6)	5 / 1.88	26.25 / 8.03	48 / 18.38	29.25 / 10.06

Table D.19

Frequency and duration of ***bar-pressing*** for each rat in Litchfield's 1987 study, in each session (sessions 1-3 are ***fixed-ratio*** or ***CRF*** sessions, and sessions 4-6 are extinction sessions).

	FROS (A1-A4)	**CRFOS (B1-B4)**	**FROE (C1-C4)**	**CRFOE (D1-D4)**
SESSION 1	238 / 92.5 915 / 253.3 389 / 99.5 614 / 177.5 mean= 539 / 155.7	8 30 13 20 mean= 17.75	1155 / 304.2 73 / 34.9 1410 / 458.3 567 / 340.4 mea=801.25/284.45	38 2 47 18 mean= 26.25
SESSION 2	240 / 92.2 603 / 221.2 301 / 114.6 631 / 229.2 mean=443.75/164.3	8 20 10 21 mean= 14:75	1408 / 436.9 153 / 59.1 1324 / 505.7 722 / 293.8 mea=901.75/323.88	47 5 45 24 mean= 30.25
SESSION 3	390 / 169.3 760 / 249.9 452 / 170.9 1111 / 378.9 mea=678.25/242.25	13 25 15 37 mean= 22.5	1294 / 397.0 591 / 237.2 1506 / 522.5 605 / 255.6 mean= 999 / 353.08	43 19 50 20 mean= 33
sum of means (for sessions 1 to 3)	1661 / 562.25	55	2702 / 961.41	89.5
SESSION 4	298 / 123.2 315 / 121.2 389 / 133.3 361 / 131.7 mea=340.75/127.35	203 / 90.0 308 / 131.1 276 / 99.8 75 / 29.8 mean= 215.5/ 87.68	787 / 236.0 289 / 104.0 591 / 190.3 425 / 183.4 mean= 523 / 178.43	327 / 155.0 126 / 50.9 270 / 132.4 183 / 80.2 mean=226.5/104.63
SESSION 5	84 / 32.2 142 / 51.1 147 / 57.4 64 / 24.4 mean=109.25/41.28	28 / 16.7 72 / 30.4 56 / 20.5 63 / 28.7 mean=54.75 / 24.08	464 / 163.0 160 / 67.5 409 / 150.5 201 / 100.5 mean=308.5/120.38	101 / 54.5 66 / 37.6 79 / 49.0 63 / 44.2 mean= 77.25/ 46.33
SESSION 6	48 / 19.6 111 / 43.9 118 / 38.0 40 / 20.8 mean= 79.25/ 30.58	58 / 33.6 71 / 26.0 65 / 23.6 37 / 17.1 mean= 57.75/ 25.08	226 / 83.2 30 / 15.6 108 / 57.7 200 / 91.1 mean= 141 / 61.9	79 / 57.5 30 / 15.2 79 / 51.5 30 / 16.2 mean= 54.5 / 35.1
sum of means (for sessions 4 to 6)	529.25 / 199.21	328 / 136.84	972.5 / 360.71	358.25 / 186.06

N.B., for the CRFOS and CRFOE groups, only the frequency scores are provided for the schedule sessions, and these values correspond to the number of reinforcements received by its yoked FR "partner"

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