The Role of the Reintroduction of Greater Bilbies (*Macrotis lagotis*) and Burrowing Bettongs (*Bettongia lesueur*) in the Ecological Restoration of an Arid Ecosystem: Foraging Diggings, Diet, and Soil Seed Banks

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Abstract

Arid Recovery, a fenced reserve free of feral predators in arid South Australia, has successfully reintroduced two critical weight range (CWR) mammals, greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) to facilitate the restoration of arid Australian ecosystems. This thesis evaluates the ecological roles of these reintroduced species and their relationship to ecosystem functioning and the restoration of these ecosystems.

Surveys of foraging diggings and soil seed banks, and dietary analysis were used to measure impacts of these species on three main habitats within the Reserve. The results showed that bilbies and bettongs have three major roles in ecosystem functioning: consumers, ecosystem engineers, and dispersers of seeds and fungi.

Both bilbies and bettongs were omnivorous, though their diets were distinctly different, with the bilbies focused more on invertebrates and seeds, while the bettongs consumed a greater proportion of coarser plant materials. The seed portion of the diets of both species during 2003-04 differed from a similar study three years previously, shortly after the animals had been reintroduced to Arid Recovery in 2000-01. During 2003-04, the bilbies consumed a lower proportion of seeds of species of grasses and more of forbs, while seed consumption by bettongs narrowed to be almost exclusively the seeds of shrubs.

The number of bilby and bettong diggings varied significantly both spatially and temporally, with averages of 7,530 ± 820 diggings ha^{-1} in Dunes, 10,560 ± 980 diggings ha^{-1} in Mulga, and 7,120 ± 610 diggings ha^{-1} in Swale. This resulted in an average of 2 to 3% disturbance of soil surface area, which is similar to or higher than reported for other Australian or overseas semi-fossorial species. The temporal variation in rates of digging was correlated with minimum daily temperatures and rainfall but not moonlight. This variation was also correlated with counts of bilby but not bettong tracks, suggesting that the temporal variability of diggings was related to levels of bilby activity.

The persistence of bilby and bettong diggings differed between the three habitat types, with the majority of the diggings in the Mulga (94%) and Swale (87%) persisting for over 12 months, while Dune diggings filled much faster, with only 15% persisting over 12 months. These diggings were shown to accumulate and bury seeds and litter, and, under some conditions, enhance germination.

The seeds of two plant species, the annual grass, *Dactyloctenium radulans,* and the shrub, *Enchylaena tomentosa,* germinated from bilby faecal pellets, and over a third of bilby faecal pellets contained fungal spores. Therefore bilbies have the potential to be dispersers of both seeds and fungi.

All three major roles of the bilbies and bettongs in ecosystem functioning (consumers, ecosystem engineers, and dispersers of seeds and fungi) have the potential to affect the flows of organic, soil and water resources, and therefore vegetation structure and overall productivity. Soil seed bank densities differed between areas with and without bilbies and bettongs. However, the heterogeneity of the system made it difficult to confidently relate these differences to any particular effects of the bilbies and bettongs.

Both bilbies and bettongs were able to locate and dig seeds buried 20 cm deep, and the caches of seed-harvester ants. Experiments showed that in areas of high digging density, 71 to 94% of seed rain accumulated and became buried in diggings. Since bilbies and bettongs have the potential to use buried seed resources, they have the potential to significantly affect soil seed banks through their consumption of seeds, redistribution of seeds through their digging activities and their interactions with other granivorous species.

This study is a first step towards understanding the roles of reintroducing CWR mammals to arid ecosystems. Possible longer term effects of these reintroductions will depend on suitable regulation of animal numbers, and climatic patterns, as restorative effects of diggings would be greatest during periods of good rainfall, whereas droughts would slow restorative processes.

Although the results of this research are unique for Arid Recovery, the principles of evaluating all major ecological roles of reintroduced species and their interactions with their environment could provide guidance for other reintroductions. These interactions are complex and would require longer-term studies over a range of conditions and locations to further understand the role of reintroducing CWR mammals to ecological restoration.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for in all forms of media, now or hereafter known.

Signature

Date

“When we try to pick out anything by itself,

we find it hitched to everything else in the universe”

John Muir

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CHAPTER 1 Introduction

1.1 MAMMALIAN EXTINCTIONS IN ARID AUSTRALIA

Since European settlement, the arid and semi-arid regions of Australia have had the highest rate of extinctions of terrestrial mammals in the world (SoE 1996). Eleven of the 72 mammal species known to have originally inhabited the arid zone, have become extinct, five are now confined to islands, and fifteen more have declined dramatically in range (Morton 1990).

Most of the mammal species that have declined or disappeared, including greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*), have body weights that are within the 'critical weight range' (CWR) of 35g to 5500g (Burbidge and McKenzie 1989). Although there has been a large amount of research into the possible causes of the local disappearances of CWR mammals, there is still no general agreement on the relative importance of the suggested causes (Morton 1990). Possibilities include introduced predators (feral cats (*Felis catus*) and foxes (*Vulpes vulpes*)), competition from introduced herbivores (rabbits (*Oryctolagus cuniculus*) and stock), changes in fire regimes, diseases, and droughts (Burbidge *et al.* 1988, Burbidge and McKenzie 1989, Morton 1990). Burbidge and McKenzie (1989) and Morton (1990) suggested that a combination of these factors resulted in a reduction in resource availability, which then resulted in the loss of those species with relatively high daily nutrient requirements and that were less able to move large distances in search of food (Figure 1.1).

There is limited available information on the specific factors that led to local disappearances of bilbies and bettongs. Major factors in the extinction of bilbies from southwest Western Australia include foxes, drought and disease (Abbott 2001, 2008). Lunney (2001) considered overgrazing by sheep in the western division of New South Wales a major factor in the disappearance of 24 species of mammals, including bilbies and bettongs, between 1840 to 1900. Disease was probably important in the disappearance of bettongs from southwest Western Australia, though foxes, and poisoning by farmers who considered these abundant animals pests, were likely also major factors (Abbott 2008).

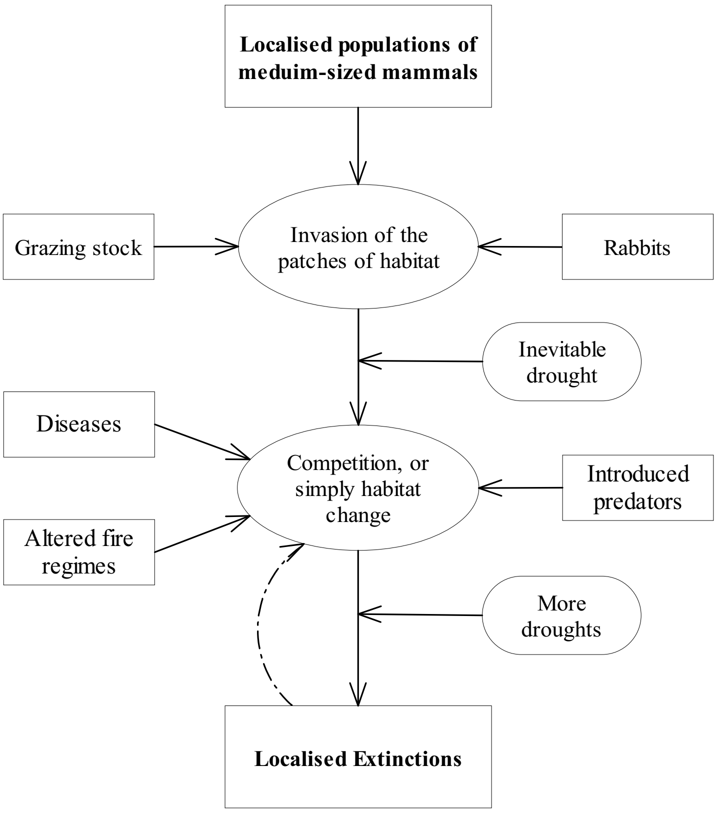


Figure 1.1: The factors that are thought to have contributed to the loss of 'critical weight range' mammals in arid and semi-arid Australia (adapted from Morton (1990)). A feedback loop (dashed line) was included because if any of the mammal species that were lost had been keystone species (Mills et al. 1993) or ecosystem engineers (Jones et al. 1994), their loss could have influenced the loss of other species.

1.2 ROLE OF REINTRODUCTIONS

Reintroduction of endangered species into their former habitat is increasingly becoming an important part of species recovery programmes and habitat restoration initiatives worldwide (Serena 1994). Reintroductions can enhance the long-term survival of a species by establishing additional viable populations or by bolstering existing populations (Southgate 1994b, Southgate and Possingham 1995).

There have been many attempts at reintroducing some of Australia's endangered CWR mammals back into their former habitats in arid regions, but very few attempts have succeeded (Richards and Short 2003). Failure of these programs has generally been because the factors that caused the decline of these species have not been identified and resolved (Fischer and Lindenmayer 2000). Predation by feral cats and foxes is an all too common factor to most of these unsuccessful programs (Short *et al.* 1992, Christensen and Burrows 1994, Short and Smith 1994, Southgate and Possingham 1995).

Most of the reintroductions of CWR mammals that appear to have been successful were onto islands that are free from introduced predators, or have involved erecting and maintaining feral-proof fences around protected areas from which introduced predators have been eradicated. Examples of such fenced sanctuaries include Yookamurra Sanctuary (SA), Scotia Sanctuary (NSW) (Australian Wildlife Conservancy 2002), Heirisson Prong (WA) (Short and Turner 2000) and Arid Recovery (SA), where the field work for this project was conducted.

The success of the reintroduction of a species is usually measured by assessing the condition and reproductive output of the reintroduced animals. The reintroduction is considered successful when the reintroduced population is self-sustaining (Fischer and Lindenmayer 2000). The ultimate goal of most reintroduction projects should, however, not be just to conserve the reintroduced species, but to restore the diversity and functioning of the ecosystems. Therefore it is important to monitor the consequences of projects such as Arid Recovery on the whole ecosystem (Armstrong *et al.* 1994).

1.3 ECOSYSTEM FUNCTIONS

The term 'ecosystem function' has been given several meanings by different authors (Ehrenfeld 2000) but on the simplest level, ecosystem functions are the processes of capturing, storing, and transferring energy, carbon dioxide, nutrients and water (Woodward 1993 in Hobbs 1992, Hobbs and Morton 1999). Main (1992) considered the most important ecosystem functions to be the fixation of carbon and nitrogen; to provide an architectural structure or habitat; to interact with other species so that one or several do not dominate the use of resources; and to recycle resources so that the net loss from the ecosystem is minimised.

The role of an organism in an ecosystem can be defined by its ecosystem function, which includes a combination of its trophic and non-trophic functions and interactions. Organisms can be grouped into functional groups that contain functionally similar taxa (functional analogues). Two important indicators of healthy ecosystem function, resistance and resilience, require functional groups to have a high degree of redundancy of species as different species within the group respond differently to environmental disturbances (Chapin *et al.* 1997, Hobbs and Morton 1999).

Some species may have an effect on their environment that is out of proportion to their commonness or biomass (Stiling 1999). These are referred to as keystone species, i.e. species, which if lost from an ecosystem, would cause the loss of many other species from that ecosystem (Mills *et al.* 1993). Although this term is poorly defined and broadly used, Mills *et al.* (1993) suggested that there are two hallmarks of keystone species. First, their presence is crucial in maintaining the organisation and diversity of their ecological communities, and second, it is implicit that these species are exceptional in their importance relative to the rest of the community.

Keystone species may be divided into several types including keystone predators, keystone prey, and keystone habitat modifiers (Stiling 1999). The latter group, the keystone habitat modifiers, are often also called ecosystem engineers. These are of most interest to the present study which focuses on the environmental effects of greater bilbies and burrowing bettongs, both of which are ecosystem engineers, as they create numerous foraging diggings (James and Eldridge 2007). Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic and abiotic materials (Jones *et al.* 1994). In doing so they modify, maintain and/or create habitat that other species use. Boogert *et al.* (2006) extended the concept of keystone species, to a new classification of key ecosystem engineer to emphasise that the primary effects of some species are through non-trophic effects of their ecosystem engineering (Crain and Bertness 2006).

1.4 ECOSYSTEM FUNCTIONS OF BILBIES AND BETTONGS

The loss of critical-weight range (CWR) mammals may have had a profound impact on arid ecosystems as their disappearance meant the loss of both the ecosystem engineering function of their foraging diggings (Martin 2003), and interactions with other species as consumers. It is however, very difficult to predict the actual effects of these losses, or of reintroducing CWR species on ecosystem functioning because of the complexity of interactions between species in an ecosystem (Chapin *et al.* 2002).

1.4.1 Consumers

Both bilbies and bettongs would have been important parts of the trophic networks of arid Australian ecosystems before European settlement (Flannery *et al.* 1990) as they were two of the most numerous and widespread of the CWR mammals (Southgate 1990b, Noble *et al.* 2007a). Both species are omnivorous, and consume varying amounts of seed, vegetation, invertebrates, and fungi according to season and availability (Gibson 2001, Robley *et al.* 2001, Southgate and Carthew 2006, Bice and Moseby 2008). As granivores, bilbies would have influenced both the overall level of granivory, and the balance between the various granivorous taxa, including ants (Morton 1985). As no Australian rodents have been found to show a preference for grass seed, a major food seed for bilbies (Southgate and Carthew 2006), and no Australian mammalian species forage for deeply buried seeds (Murray and Dickman 1994, C. Dickman, pers. comm. in Moles *et al.* 2003), it is possible that some of the functional roles of bilbies and bettongs as granivores have not been replaced over time by other species with similar functions.

1.4.2 Non-trophic functions (ecosystem engineering)

The reintroduction of CWR mammals would also affect ecosystem functioning through the non-trophic functions related to their foraging diggings. Bilbies and burrowing bettongs are considered ecosystem engineers (Wright and Jones 2004) because of their digging for both foraging and creating burrows for shelter (James and Eldridge 2007). These activities may previously have had an even greater impact on the total ecosystem than the species' trophic functions (Boogert *et al.* 2006, Crain and Bertness 2006), with historical records mentioning "several acres of ground covered with (bettong) holes" (Krefft 1866 quoted in Martin 2003). This digging activity created both small and large patch disturbances that are thought to be important in maintaining diversity in the vegetation (Dean and Milton 1991), while their burrows may have provided habitat and shelter for many other species including invertebrates and lizards (Hawkins 1996).

Until recently, little research has been conducted in Australia into the effects of animal diggings. However, with the growing awareness of the potential importance of ecosystem engineering on the functioning of Australia's ecosystems (Martin 2003, Eldridge and Mensinga 2007, James and Eldridge 2007), more emphasis is being put into research in this area. At Arid Recovery, the diggings of bilbies and bettongs have been found to accumulate seeds and organic matter, facilitate seed germination (Sparkes 2001), and increase soil carbon (James and Eldridge 2007). Eldridge and Mensinga (2007) showed that echidna diggings capture litter and increased soil micro-arthropod abundance. The diggings of brush-tailed bettongs (*Bettongia penicillata*) in the Dryandra woodland in Western Australia were found to increase water infiltration in water repellent soils (Garkaklis *et al.* 1998), although old diggings were found to increase the sub-soil water repellence through the accumulation of water repellent organic matter and increased growth of fungal hyphae (Garkaklis *et al.* 2000). Diggings are also thought to assist in the redistribution of mycorrhizal fungi and other microorganisms beneficial to plant growth and productivity (Claridge and May 1994, Martin 2003, Noble *et al.* 2007a).

Although European rabbits (*Oryctolagus cuniculus*) also make foraging diggings, it is likely that damage resulting from their browsing of perennial shrubs, herbs and grasses would outweigh any beneficial effects of their diggings (Ryan *et al.* 2003, Noble *et al.* 2007a). Other differences between rabbits and bilbies and bettongs suggest that bilbies and bettongs might be potentially more effective than rabbits as ecosystem engineers. Rabbit diggings may be biologically less effective as they are a different shape and shallower than diggings by bilbies and bettongs (Sparkes 2001, James and Eldridge 2007). Since rabbits are not known to consume fungi (Robley *et al.* 2001, Ryan *et al.* 2003), they would also probably be less effective at redistributing fungal spores, which might be important for plant productivity.

The most detailed research into the ecological effects of foraging diggings that are comparable in size to those of bilbies and bettongs is the long-term (>30 years) of research into the diggings of the Indian crested porcupine (*Hystrix indica*) in the arid Negev Desert highlands of Israel (reviewed in Alkon 1999). These diggings have been found to alter the physical environment by affecting soil texture and structure, fertility, infiltration, soil mixing, inorganic distribution, mineralisation rates, and surface runoff (Alkon 1999, Whitford and Kay 1999). In this way they act as small soil pockets in which soil, moisture, organic matter and seeds accumulate, producing a favourable microhabitat for seed germination and plant growth (Gutterman *et al.* 1990, Gutterman 1993, Alkon 1999). This results in pockets of increased species richness, plant density, and productivity that increase landscape heterogeneity (Boeken *et al.* 1995, Whitford and Kay 1999).

The importance of ecosystem engineering effects of diggings might vary across environments, increasing in harsher, arid environments where the increased resources within diggings might be comparatively more important than in more benign environments (Crain and Bertness 2006). However, as the effectiveness of diggings is possibly dependent on the entrapment of water flows by these diggings (Alkon 1999), diggings in dune sand might be much less effective than ones where soil type or a soil crust means that run-off occurs with small amounts of rain. Most studies demonstrating the ecological effectiveness of diggings have been in either less arid areas than Arid Recovery (Whitford 1998, Eldridge and Mensinga 2007), or in similarly arid areas with large areas of rock to focus runoff into the diggings (Yair and Shachak 1982).

1.5 LANDSCAPE FUNCTIONALITY

One way of evaluating the capacity of bilbies and bettongs to restore and maintain ecosystem functions is to consider the effects of these functional roles on the structural components of the ecosystem (King and Hobbs 2006, Shachak *et al.* 2008). Overall landscape function and productivity in arid regions is limited by the inputs, especially water (Noy-Meir 1973, Stafford Smith and McAllister 2008). The overall productivity of these ecosystems is therefore determined by the way flows of organic, soil, and water resources are maintained within the ecosystems (Holm *et al.* 2003), which in turn depends on patches of vegetation and other surface structures such as logs, and rocks to control these flows (Tongway *et al.* 2003). Functional ecosystems have sufficient patches to minimize flows of resources out of the system, thus conserving scarce resources (Ludwig and Tongway 1995, Ludwig *et al.* 2000). By contrast, 'dysfunctional' ecosystems lose nutrients and water, and have reduced capacity to convert rainfall into biomass (Holm *et al.* 2002, Tongway *et al.* 2003).

Patchy distribution of scarce resources can increase productivity per unit area in systems where water and nutrient flows are coupled and retained within the system (Tongway *et al.* 2003). The concentration of soil nutrients and runoff water to form enriched or fertile patches has been well documented for many semiarid landscapes in Australia (Ludwig *et al.* 2005) and elsewhere (Schlesinger *et al.* 1990). The primary process behind this regulation of ecosystem function is redistribution (Ludwig *et al.* 2000). Excess water from rainfall usually is redistributed as runoff, which is captured as run-on by landscape patches that act as "traps" for runoff soil water, nutrients, and organic matter. For example, when runoff encounters a grass clump (a small patch), the flowing water is slowed by this obstruction, and has more time to infiltrate into the soils of the clump. Any rich topsoil sediments, litter, and seeds being carried in the runoff also may be trapped in this clump, leaving poor subsoils exposed on the surface of interpatches. The clump will grow and maintain itself as nutrients are assimilated into biomass by the plants and animals living in the clump. The positive feedback between patches and resource concentration processes creates self-organizing patterns in landscapes (Ludwig *et al.* 2000).

Foraging diggings of goannas have been shown to function like small landscape patches in banded mulga landscapes in eastern Australia (Whitford 1998), confirming the similarity in functions of diggings in controlling of resource flows (Alkon 1999) to those of small grass clumps (Ludwig *et al.* 2000). In addition, diggings might initiate the formation of new landscape patches (Boeken *et al.* 1995, Whitford and Kay 1999) through growth of seeds germinating within the diggings.

1.6 ECOLOGICAL RESTORATION

The aims of Arid Recovery are 'to facilitate the ecological restoration of arid ecosystems' through the 'establishment of a cat, fox and rabbit free reserve' and the 're-establishment of endemic species, particularly threatened or locally extinct species' (Arid Recovery 2006). It is important that these goals are not interpreted as a return to the past since some of the ecological damage caused by overgrazing and rabbits might be irreversible (Sparrow *et al.* 2003), and environmental conditions are rapidly changing with time (Choi 2004).

Arid ecosystems in Australia have changed dramatically since European settlement, although the nature and extent of these changes are largely unknown because little is known about the original appearance of the land or about the species composition of the vegetation (Morton 1990). Much of the impact on the vegetation has been due to overgrazing by introduced herbivores (cattle, sheep, goats, rabbits, and camels) (Lunney 2001, Edwards *et al.* 2004), and by larger native herbivores such as red and grey kangaroos (*Macropus rufus, M. giganteus* and *M. fuliginosus*) whose numbers have increased with the increased availability of water in artificial dams (Low 1984, Morton 1990). The scarcity, variability, and unpredictability of rainfall in these regions means that impact of grazing may not be readily separable from that of other factors (Tongway *et al.* 2003).

Vegetation changes in Australia following overgrazing by introduced herbivores have varied depending on location and seasonal conditions as well as grazing management (Westoby *et al.* 1989), but have most frequently involved a loss of perennial plants, ranging from grasses to trees (Tongway and Ludwig 1994). The low rainfall (160 mm annual average), and lack of permanent surface water at Arid Recovery might mean the area was rarely, if ever, heavily grazed. The timing and intensity of such grazing would have been important in determining the extent of any damage to landscape functionality (Friedel *et al.* 2003, Lunt *et al.* 2007). Although grazing had little effect on survival of chenopod shrubs during periods of average rainfall in a semi-arid region (Eldridge *et al.* 1990), very few heavily browsed shrubs survived a drought near Arid Recovery (Read 2004).

The ecological consequences of overgrazing, and similar destructive land use in other parts of the world, have been severe, often resulting in desertification (Le Houerou 2002). Decreases in vegetation from overgrazing can lead to decreased litter production, which in turn leads to decreased organic matter in the soil and breakdown of soil structure, which in turn leads to further loss of vegetation in a relentless feed-forward cycle (Le Houerou 2002, King and Hobbs 2006). This cycle has led to large areas of semi-arid grassland in the United States being replaced with shrublands (Reynolds *et al.* 1999), while many other areas of the world, most notably the Sahara in Africa, have become man-made deserts, with little or no remaining vegetation (Le Houerou 2002). By contrast, grazing by livestock and feral animals has prevented recruitment of native trees and shrubs in some areas of semi-arid Australia, thus converting shrublands to grasslands (Lunt *et al.* 2007).

Most levels of ecosystem degradation, especially those involving only changes to vegetation or fauna, are readily reversible by just removing the cause, or reintroducing the lost species or species with similar functions (Havstad and Herrick 2003). However, when the structure and integrity of vegetation patches are damaged in dysfunctional landscapes, the system becomes increasingly ‘leaky’ and less productive (Anderson and Hodgkinson 1997, Ludwig *et al.* 2000). Since the differences in fertility between shrub patches and bare interpatch areas increase with increasing size of the interpatch areas (Ludwig *et al.* 2000), the concentration of resources in shrub patches favours continuity of these patches (Schlesinger *et al.* 1990). Plant communities therefore cross a threshold between grassland and woodland that may be very difficult to reverse (Schlesinger *et al.* 1990, Friedel 1991). Other threshold changes in arid areas may occur when soil erosion outstrips replenishment (Friedel 1991), and vegetation will not revert to previous state after grazing pressure ceases (Tongway *et al.* 2003). Such changes may require outside inputs to rehabilitate the soil before restoration of vegetation and fauna can proceed, and natural heterogeneity restored (Didham and Watts 2005, Blanke *et al.* 2007). Recent studies have suggested that ecosystem engineers might be able to play important roles in achieving the reversal of such soil degradation (Boogert *et al.* 2006, Byers *et al.* 2006, Eldridge and Mensinga 2007, James and Eldridge 2007).

Applying the concept of restoration to ecosystems at Arid Recovery is difficult because of the limited information on the changes to the ecosystems at Arid Recovery following the extinction of CWR mammals, grazing by cattle and sheep, and the introduction of rabbits (Moseby and O'Donnell 2003). Known vegetation changes in the region since European settlement include a reduction in the abundance and distribution of sandalwood (*Santalum lanceolatum*) due to harvesting for incense early this last century (K. Moseby, personal communication, 2008). Additionally, some sand dunes have bare and mobile areas, and many long-lived trees and shrubs have shown limited recruitment and have been replaced by short-lived colonising species (Arid Recovery, unpublished data). These additional changes are possibly related to the effects of rabbits, which are known to damage perennial plant species (Noble *et al.* 2007a), and cause erosion (Coman 1999). While the presence of bare mobile areas suggests that these habitats might be 'leaking' resources such as soil and water (Ludwig *et al.* 2002), it is difficult to assess what assistance might be needed to stabilise such areas (Hobbs 2007). A major question in determining restoration goals are whether the ecosystems have crossed any biotic or abiotic thresholds that require outside inputs to restore original structure and function (King and Hobbs 2006).

Fenced reserves such as Arid Recovery, where the populations of reintroduced species are confined in relatively small areas, face the problem that the animals cannot move out of the area during periods of environmental stress like drought. The remaining wild populations of bilbies are thought to be very mobile (Southgate and Carthew 2006, Southgate *et al.* 2007). Bilby populations also fluctuate greatly with changing seasonal conditions (Southgate 1990a, Short and Turner 1999, Arid Recovery 2006), and thus would normally minimise their impact on any given area. Bettong populations are more stable as animals consume roots and bark of perennial vegetation during dry periods, and thus are more likely to cause damage to perennial vegetation (Bice and Moseby 2008).

1.7 THIS RESEARCH THESIS

1.7.1 Objectives

Arid Recovery, a fenced feral free reserve in arid South Australia, has successfully reintroduced two endangered critical weight range (CWR) marsupials, greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*), as a step towards achieving its goal of facilitating the restoration of arid zone ecosystems in Australia (Arid Recovery 2006).

This thesis evaluates some of the changes these faunal reintroductions have made to the ecosystem functioning of the Reserve in order to determine the role these once common and wide-spread species might have in regulating and restoring these arid ecosystems. The goal of this research is to provide information to assist in both the current management of Arid Recovery and in planning future reintroductions outside the Reserve.

The specific objectives of this research include:

- to document the characteristics and extent of the trophic and non-trophic functions of greater bilbies and burrowing bettongs at Arid Recovery;
- to determine whether the reintroductions of bilbies and bettongs have affected the soil seed banks within Arid Recovery, and to explore the possibly reasons for such changes; and
- to provide recommendations for the management of Arid Recovery and future reintroductions of CWR mammals outside of reserves based on the results of this research.

1.7.2 Study period

The research described in this thesis was conducted over a two year period between September 2003 and September 2005.

1.7.3 Structure of the thesis

Chapter one provides a background for the research described in this thesis through an overview of reintroduction, the ecological functions of bilbies and bettongs as related to ecological restoration, and the possible consequences of their reintroductions.

Chapter two provides background on the study site Arid Recovery, their routine monitoring program, and a brief summary of the biology of greater bilbies and burrowing bettongs.

The research described in this thesis is presented in chapters three through to seven. These chapters are each presented as separate papers in preparation for publication, which has resulted in some repetition in the introduction and methods between chapters.

Chapter three is an investigation of the characteristics, extent, and temporal persistence of bilby and bettong foraging diggings in each of the three habitat types in Arid Recovery. Changes in rates of digging over time are compared with changes in animal numbers/activity, dietary intakes, and abiotic factors.

Chapter four describes the diet of the bilbies and bettongs at Arid Recovery during the study period as determined by faecal analysis, focusing on the identification of the species of seeds consumed in order to relate their diet to potential effects on soil seed banks. The results of this study are also compared to those of a similar study three years previously (Bice and Moseby 2008) to assess temporal changes in dietary consumption, particularly of seeds.

Chapter five compares the soil seed banks of the different management areas of Arid Recovery to determine the effects of the reintroduction of bilbies and bettongs. The results are discussed in relation to the possible effects of trophic (granivory, herbivory) and non-trophic (digging) functions, and to the limitations on ascribing causality to inter-area differences in seed banks.

Chapter six describes two experiments that explore the potential of the trophic activities of the bilbies and bettongs to affect soil seed banks. The first experiment was conducted to test whether bilbies and bettongs are able to locate and dig for buried seeds, and if so, the effect of size and depth seed cache on the probability of digging. For the second experiment the nests of seed harvester ants (*Pheidole sp.*) were excavated to determine depth and size of ant seed caches. The relationship of seed consumption by harvester ants to digging by bilbies and/or bettongs at the nests was examined by feeding seed to nests of *Pheidole* sp. ants.

Chapter seven describes an experiment using plastic and glass beads as seed mimics to determine whether the collection and burial of seeds in foraging diggings would affect the density of seeds in shallow soil seed banks.

Chapter eight summarises the findings from this research in relation to the balance between the trophic and ecosystem engineering functions of bilbies and bettongs, and to the potential for the reintroduction of these species to assist in the restoration of ecosystems at Arid Recovery. The chapter also includes recommendations for further research, for management of Arid Recovery and for further reintroductions of CWR mammals outside of reserves.

The two appendices of this thesis present the results of two small trials that were conducted as part of this thesis but were not followed up because of insufficient time. However these trials are included in this thesis as appendices as they may be of interest for future researchers.

Appendix one describes a seed preference trial that was conducted in the three management areas of Arid Recovery in order to compare the effects of the Reserve on the overall level of seed predation.

Appendix two describes a trial of different termite baits aimed at determining the best method for surveying for subterranean termites at Arid Recovery, and comparing termite abundances between habitats.

CHAPTER 2 Study site and species

2.1 ARID RECOVERY

This research was conducted at Arid Recovery (30°29'S, 136°53'E), located approximately 20 km north of the township of Roxby Downs in central South Australia. Arid Recovery is an ecosystem restoration initiative working to restore Australia's arid lands. It is a joint program between BHP Billiton (formally WMC Resources), South Australian Department for Environment and Heritage, The University of Adelaide and the community (Friends of Arid Recovery).

Arid Recovery is a 60 km^2 reserve surrounded by a 1.8 m high predator and rabbit proof fence (Figure 2.1). All feral cats (*Felis catus*), foxes (*Vulpes vulpes*) and rabbits (*Oryctolagus cuniculus*) have been removed from the Reserve, and four locally extinct species of critical weight range (CWR) mammals reintroduced. These are the Greater Stick-nest Rats (*Leporillus conditor*), Greater Bilbies (*Macrotis lagotis*), Burrowing Bettongs (*Bettongia lesueur*), and Western Barred Bandicoots (*Perameles bougainville*).

Arid Recovery was initially only 14 km^2, with three further expansions added since. The Reserve is divided into four sections (Figure 2.2), the initial Main enclosure into which the reintroduced species were first reintroduced, the First and Northern expansions into which the endangered species were later released, and the Second expansion which has been kept free from the reintroduced species. The dates of completion of each of these sections of the Reserve, and the estimated populations of reintroduced species in each section are shown in Table 2.1.

Most of the research for this thesis was conducted in the Main exclosure (referred to in this thesis as **Inside**), where the reintroduced species have been present the longest and are at highest population levels (Figure 2.2, Table 2.1). In order to determine the effects of the Reserve, this was compared with the Second expansion (referred to in this thesis as **Control**) and Outside the Reserve (referred to in this thesis as **Outside**). All research Outside the Reserve was conducted south of the reserve on the Olympic Dam Mining Lease. Cattle have not been grazed in this area since 1986 (Read 2003), but feral cats, foxes and rabbits still occur in this area. On-going control measures for the feral cats and foxes may mean these populations are lower than normal in the region. Estimates from spotlighting counts suggests rabbit populations varied from approximately 30 to 90 individuals km^{-2} during this study from September 2003 to September 2005 (Arid Recovery 2006). Rabbit numbers Outside decreased considerably with the introduction of rabbit haemorrhagic disease in 1996 (Bowen and Read 1998), but have been slowly recovering since about 2000 (Arid Recovery 2006).

Figure 2.1: A view from outside showing the 1.8 m high predator-proof fence with floppy top, foot apron and two electric wires. The electric wires are only on the initial fence around the Main exclosure. Rubber matting and/or wider netting has been used on top of the 30 cm foot apron in areas of erosion-prone dunes and watercourses to prevent rabbit incursions (Moseby and Read 2006).

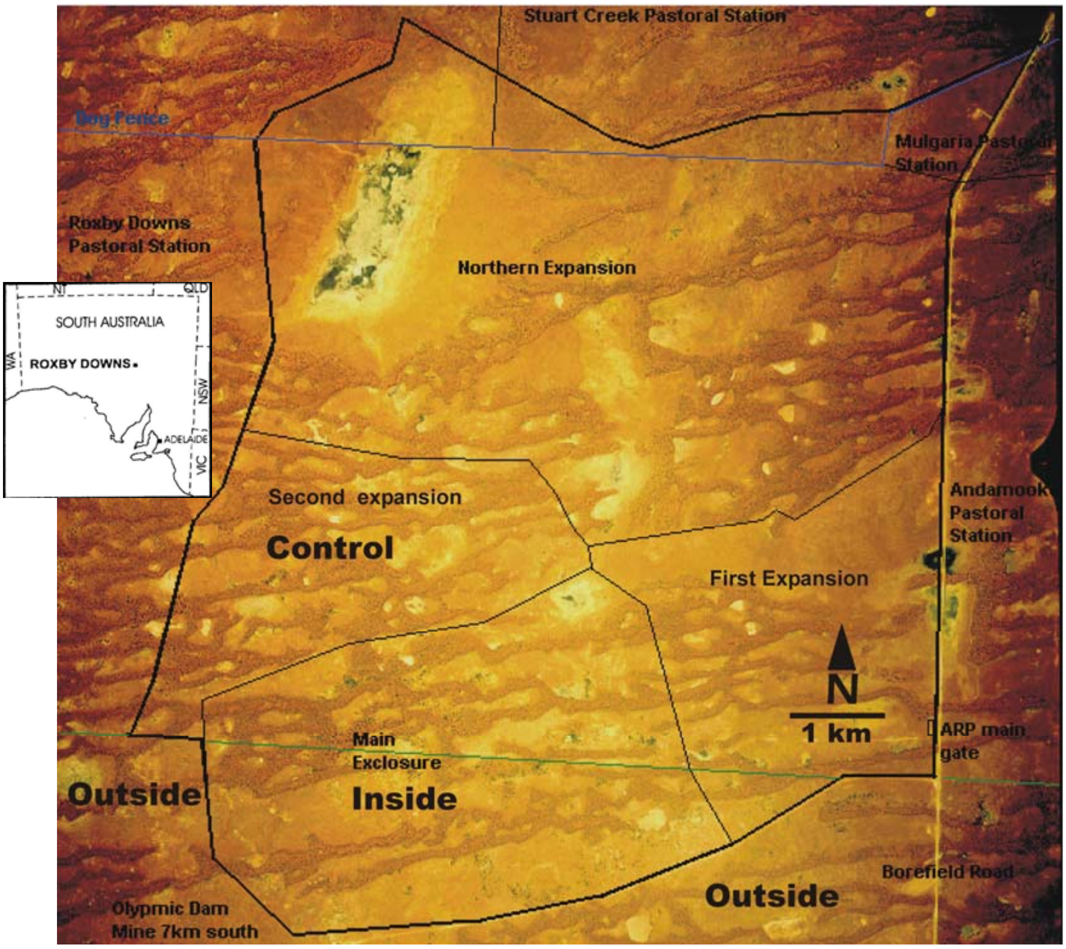


Figure 2.2: A map of Arid Recovery showing the four sections of the Reserve. Most of the research for this thesis was conducted in the Main exclosure (referred to in this thesis as Inside), where the reintroduced species have been present the longest and were at highest population levels. In order to determine the effects of the Reserve, this was compared with the Second expansion (referred to in this thesis as Control) and Outside the Reserve (referred to in this thesis as Outside).

Table 2.1: The dates of the construction of Arid Recovery and the removal of the feral species, and the reintroductions. For the reintroduced mammals, population estimates as of December 2004 (and the year first reintroduced) for each of the sections of the reserve are given (Arid Recovery 2004).

NOTE:
This table is included on page 15 of the print copy of the thesis held in the University of Adelaide Library.

2.1.1 Climate

Arid Recovery has an arid and variable climate with hot summers (mean daily maximum 37°C and minimum 21°C in January) and mild winters (mean daily maximum of 19°C and minimum of 4°C in July) (Bureau of Meteorology, Canberra).

The 10-year annual mean rainfall at Arid Recovery is 154 mm (CV 45%) (Arid Recovery, unpublished data), although it is very variable and unpredictable. The rainfall for the period of the research for this thesis was average to above average (2003: 152 mm, 2004: 193 mm), though variable as shown in Figure 2.3.

NOTE:
This figure is included on page 15 of the print copy of the thesis held in the University of Adelaide Library.

Figure 2.3: The monthly rainfall (mm) for Arid Recovery throughout the study period and for the three months proceeding (Arid Recovery, unpublished data). The monthly mean rainfall is approximately 14 mm.

2.1.2 Vegetation

Arid Recovery includes a diverse range of arid zone habitats including *Acacia* and *Dodonaea* dominated sand dunes, chenopod (saltbush/bluebush) inter-dunal swales, native pine and mulga sandplains, canegrass swamps, and claypans (Arid Recovery 2006).

The research for this thesis was conducted in the three main vegetation types within the Reserve: east/west orientated sand dunes dominated by sandhill wattle (*Acacia ligulata*) and sticky hopbush (*Dodonaea viscosa*) (referred to in this thesis as Dune, Figure 2.4), clay inter-dunal swales dominated by the chenopods bladder saltbush (*Atriplex vesicaria*) and low bluebush (*Maireana astrotricha*) (referred to in this thesis as Swale, Figure 2.5) and patches of mulga (*Acacia aneura*) woodlands (referred to in this thesis as Mulga, Figure 2.6) with sandy clay soils.

2.1.3 Routine monitoring

One of the aims of Arid Recovery is 'to research and monitor the processes of ecological restoration and provide transferable information and techniques for broad-scale environmental management of Australia's arid lands'. Arid Recovery has an on-going monitoring program which currently includes monitoring of the populations of reintroduced species populations (track transects, spotlighting counts and cage trapping), vegetation, landscape function analysis, and population levels of small mammals and reptiles, and birds (Arid Recovery 2006).

2.1.3.1 Reintroduced species

The population levels of the reintroduced species at Arid Recovery are monitored using three methods: track and spotlight transects and annual trapping using cage traps (Arid Recovery 2006). The track and spotlighting transects indicate fluctuating populations of both the bilbies and bettongs during the time of this study, September 2003 to September 2005 (Figure 2.7). The annual trapping, conducted in September, indicates slowly increasing populations of these species over the study period, with trap success for bettongs increasing from 43% in September 2003, through 40.5% in 2004, to 53% in 2005, and for bilbies (which are trap-shy) changing from 0% in 2003 to 3.6% in 2005.

Figure 2.4: Dune habitats in Arid Recovery. The sand dunes are generally east/west orientated and dominated by Sandhill Wattle (*Acacia ligulata*) and Sticky Hopbush (*Dodonaea viscosa*).

Figure 2.5: Clay inter-dunal swales in Arid Recovery, dominated by chenopods, Bladder Saltbush (*Atriplex vesicaria*) and Low Bluebush (*Maireana astrotricha*).

Figure 2.6: Patches of mulga (*Acacia aneura*) woodland in Arid Recovery, (a) under ‘average’ conditions, and (b) after rainfall (September 2004).

NOTE:
This figure is included on page 20 of the print copy of
the thesis held in the University of Adelaide Library.

Figure 2.7: Population monitoring for the reintroduced bilbies and burrowing bettongs in the Main enclosure (Inside) of Arid Recovery using (a) track transects (number of tracks km^{-1}) and (b) spotlighting (number of individuals seen km^{-1}). The spotlighting monitoring only commenced in April 2003. Data from Arid Recovery (2006).

2.1.3.2 Vegetation monitoring

The vegetation within Arid Recovery has been monitored annually in August since 1997 (Arid Recovery Project 2003). Overall vegetation cover, especially of annual species, appears to have been greater within the Reserve since 2002 (Arid Recovery Project 2003), although it is difficult to show significant changes from the vegetation surveys because of the large variability between sites and between years depending on rainfall patterns. Some plants, like the grass *Aristida holathera*, were more abundant Inside the Reserve than Outside during dry years, but showed little difference during periods of higher rainfall (Arid Recovery 2005).

Initial monitoring of seedling recruitment of selected plant species in 2000 and 2003 showed that the survival of some shrub seedlings (*Acacia aneura*, *Senna artemisioides*, and *Acacia ligulata*) has been greater Inside the Reserve than Outside, while the survival and growth of three other species (*Santalum* *lanceolatum*, *Pittosporum phylliraeoides*, and *Dodonaea viscosa*) is not different between the areas (Arid Recovery 2005). Damage to perennial plants by bettongs browsing became noticeable in 2007, and more detailed monitoring has been commenced to further evaluate this damage (Arid Recovery 2007).

2.1.3.3 Landscape function analysis

Landscape function analysis (LFA) (Tongway and Hindley 2004) was conducted in October 2004 and will be repeated every five years as part of Arid Recovery's biological monitoring program (Arid Recovery 2007).

LFA measures the percentage of transects that are covered by patches, areas with vegetation cover or the accumulation of litter (Tongway and Hindley 2004). The initial survey found no significant differences between sites Inside the Reserve and Outside due to the high natural variability of the arid landscapes, and limited number of sites surveyed. However there were trends of higher patch percentage Inside than Outside the Reserve for the Dune and Swale, but lower for the Mulga (Hill and Reece 2004). Interestingly, the number of types of patches followed the same pattern, higher Inside than Outside for the Dune and Swale, but lower for the Mulga.

2.1.3.4 Small mammals and reptiles

Small mammals, reptiles and amphibians Inside and Outside Arid Recovery have been monitored annually in February since 1998 (Arid Recovery 2004). There was little difference in the small native mammal populations, mainly spinifex hopping-mice (*Notomys alexis*) and Bolam's mice (*Pseudomys bolami*), between Inside and Outside the Reserve until 2002 when significantly higher numbers were recorded Inside the Reserve than Outside (Figure 2.8). From 2003 to 2005 numbers in both Inside and Control continued to increase, with numbers in Control distinctly higher than Inside in 2005. However, as bettongs interfered with increasing numbers of traps Inside in 2004 and 2005, the actual difference in small animals between Inside and Control in these years is uncertain (Arid Recovery 2007).

Reptile captures also showed little difference between Inside and Outside in the first 3 years of monitoring (Arid Recovery 2007). However, since 2001 reptile numbers have been lower Inside and in the Control area than Outside (Figure 2.9).

Figure 2.8: The average number (±s.e.) of native mammal captures per site Inside (n=12), Outside (n=11) and in the Control area (n=7) of the Arid Recovery (Arid Recovery 2007).

Figure 2.9: The average number (±s.e.) of reptile captures per site Inside (n=12), Outside (n=11) and in the Control area (n=7) of the Arid Recovery (Arid Recovery 2007).

2.1.3.5 Birds

The numbers and occurrence of birds Inside and Outside the Reserve are surveyed each year in April. From 2003 to 2005, most predominately insectivorous species occurred in similar densities Inside and Outside, although both cinnamon quail-thrushes (*Cinclosoma cinnamomeum*) and chirruping wedgebills (*Psophodes cristatus*) were more numerous Inside (Arid Recovery 2006). Numbers of honeyeaters were higher Inside the Reserve and numbers of four granivorous bird species were lower (Arid

Recovery 2006). Species that either nest close to the ground or spend a large amount of time on the ground often had higher numbers Inside suggesting that increased protection from cats and foxes might be a factor in these differences (Arid Recovery 2007).

2.2 GREATER BILBY

The greater bilby (*Macrotis lagotis*) is a semi-fossorial, and nocturnally active marsupial that is within the 'critical weight range'. A member of the family Thylacomyidae in the Superfamily Perameloidea, bilbies are unique among the bandicoots in constructing burrows (Strahan 2000).

Bilbies were once widely distributed over 70% of the Australian mainland but now occupies less than 20% of its former range (Southgate 1994b) (Figure 2.10). Unlike most of the CWR species that have declined in Australia, the bilby has only survived in relatively unproductive areas such as the Tanami, Gibson and Great Sandy Deserts (Southgate 1990a). It is now classified as vulnerable both nationally and under the IUCN red list (Maxwell *et al.* 1996, IUCN 2002). Gibson *et al.* (2002) noted that current bilby refugia are where there is a lack of free water, providing a level of natural protection from exotic predators and competitors which are more dependent on access to water. Bilbies are known to have inhabited the Arid Recovery area previously from sub-fossil material collected 30 km from the Reserve, and from local pastoralists' accounts of bilbies in the local sand dunes until the 1930's (Moseby and O'Donnell 2003).

Historically, bilbies were once one of the most plentiful Central Australian CWR mammals, though numbers varied greatly as a result of seasonal conditions or possibly disease (Southgate 1990a). Overall bilby numbers declined rapidly in most areas between the late 1800's and 1935, a process that appears to be continuing (Abbott 2001, Gibson *et al.* 2002, Pavey 2005, Abbott 2008).

Remaining wild bilby populations generally consist of scattered individuals or small groups of individuals (Smyth and Philpott 1968, Watts 1969, Southgate 1990a). Estimated population densities range from 0.001 individuals ha^{-1} in central Australia to 0.16 individuals ha^{-1} in south-west Queensland (Southgate 1990a, Southgate *et al.* 2007). These remnant populations may undergo large fluctuations (Southgate *et al.* 2007) with individuals moving over large distances (Lavery and Kirkpatrick 1997).

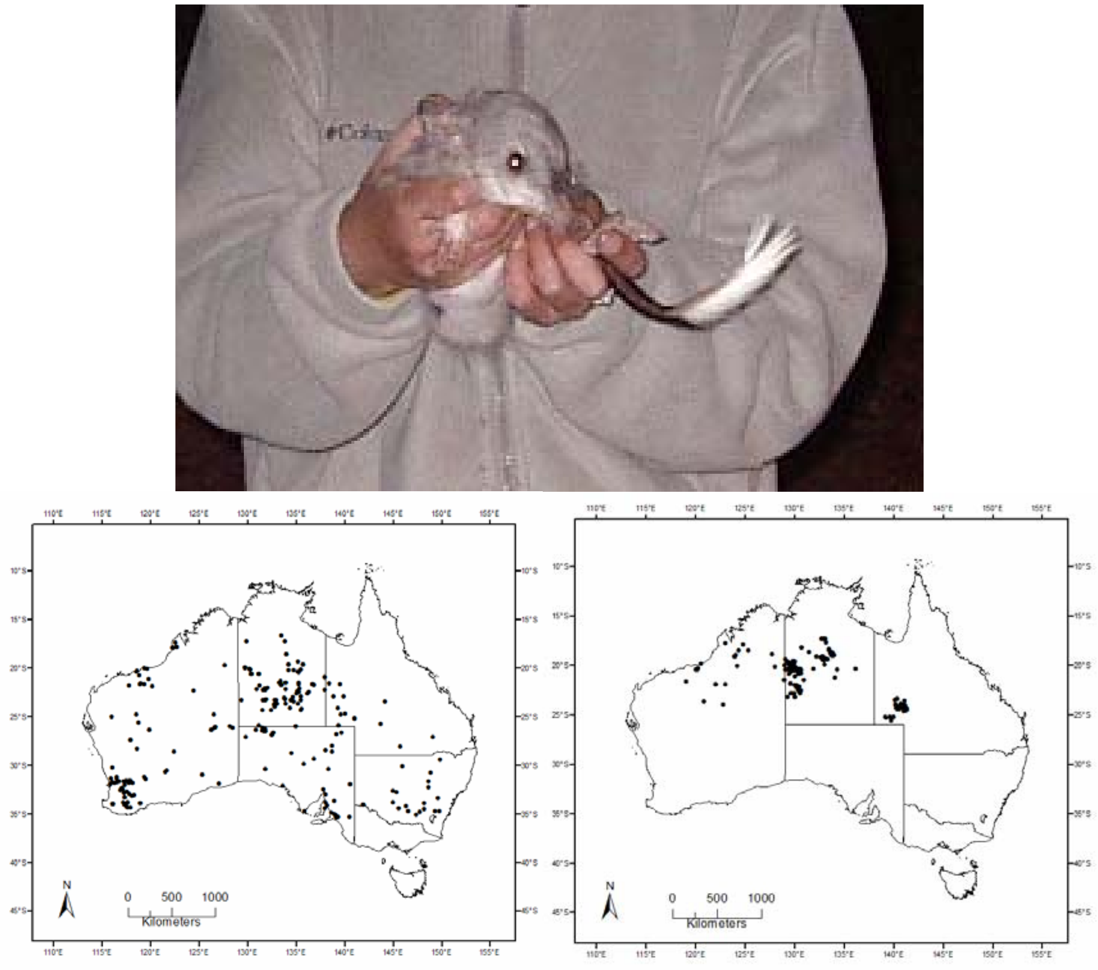


Figure 2.10: Photo of a greater bilby (*Macrotis lagotis*) from Arid Recovery. Map on left shows records of bilby distribution up to and including 1990, while map on right shows distribution from 1990 to 2004 (from Pavey 2005, data from National Greater Bilby Database).

2.2.1 Reintroduction

A programme was initiated in the mid 1980's to determine if reintroductions could be used to expand the bilbies current range (Southgate and Possingham 1995). Bilbies' are relatively easy to breed in captivity, with captive populations now maintained in many Australian zoos (Southgate 1994b). There have been many attempts of reintroduction into areas within their former range, but these appear to have only been successful in fenced reserves or off-shore islands. For example, attempted reintroductions into Simpson Gap and Watarrka National Park in the Northern Territory were unsuccessful (Southgate 1994b, Southgate and Possingham 1995). However, a reintroduction onto Thistle Island in South Australia (Hunwich 1999, van Weenen 2002), and reintroductions into fenced reserves such as Scotia Sanctuary in New South Wales, and Arid Recovery in South Australia have been particularly successful (Australian Wildlife Conservancy 2002). Unfortunately the reasons for the unsuccessful reintroductions remain unknown though predation was usually a major factor (Southgate 1994b, Southgate and Possingham 1995).

2.2.2 Habitat

The bilby appears to be highly flexible in its habitat requirements, occurring in a wide range of soil, vegetation and landform types (Southgate 1990a). There is a lack of knowledge about the environmental conditions that bilbies require (Southgate and Possingham 1995), although Southgate (1990b) found that a relatively low amount of ground cover was a factor common to all the habitats where bilbies currently occur. Southgate (1990a) classified the current habitats occupied by bilbies into three habitat associations according to landform, soils, vegetation characteristics, fire frequency and important food resources: sparse grass/forblands, mulga lands and hummock grasslands.

Where bilbies currently occur, their distribution is patchy and they appear to only utilise small parts of habitats which are thought to be able to support them (Smyth and Philpott 1968). Moseby and O'Donnell (2003) observed that the reintroduced bilbies at Arid Recovery had a significant preference for dune habitat. Within their home ranges, bilbies have several burrows and frequently change them (Lavery and Kirkpatrick 1997, Moseby and O'Donnell 2003).

2.2.3 Diet

Bilbies are considered omnivorous, although their diet ranges from insectivory to herbivory depending on habitat (Gibson 2001). For example, Smyth and Philpott (1968) found that bilbies near Warburton in Western Australia fed primarily on termites, ants and insect larvae, whereas Watts (1969) found that in central Australia their diet consisted of primarily bulbs, fungi and seeds. In a broad-scale comparison of bilby diet throughout their range, Southgate and Carthew (2006) recorded the following food items: seeds (most commonly *Dactyloctenium radulans* and *Yakirra australiense*), bulbs (*Cyperus bulbosus*), fungi, invertebrates (ants, termites, beetles, grasshoppers, spiders) and invertebrate larvae and eggs (Coleoptera, Lepidoptera and Orthoptera). The diet of reintroduced bilbies at Arid Recovery was monitored for the first year and half after their reintroduction and were found to feed on a wide variety of food, although they were primarily insectivorous in the hotter months and granivorous in the cooler months (Bice and Moseby 2008). A major component of the diet of most remaining wild bilby populations is the bulb of *Cyperus bulbosus* (Southgate 1990b, Southgate and Carthew 2006), which does not occur at Arid Recovery (Bice and Moseby 2008).

Gibson (2001) compared the diet of bilbies and food availability in south-western Queensland. Seasonal changes in food availability were reflected in the bilby diet, although the relative proportions of some dietary items differed from their availability. The bilbies consumed more invertebrates during summer than winter, while the proportion of plants consumed was relatively constant. This reflects the higher availability of invertebrates during the summer than winter, whereas the availability of plant food, mainly the seeds of the grass, *Dactyloctenium radulans*, did not differ seasonally.

Bilbies obtain their food from both the soil surface and below the ground (Johnson 1980, Gibson *et al.* 2002). They dig their food from the soil using their well equipped front feet (Southgate 1994a), and are thought to use their senses of smell and hearing to locate the food (Johnson 1989). Bilby diggings can be classified into three distinct types: (1) patches of shallow scratchings of irregular shapes, (2) shallow cylindrical or concave pits (5-20 cm deep and 4-15 cm wide) with the soil piled up in all directions from the mouths, and (3) deep conical pits (5-20 cm deep) that descended at an angle (Smyth and Philpott 1968, Sparkes 2001). It is hard to determine why bilbies dig, although the deep conical pits are usually observed under tussock grasses (Smyth and Philpott 1968), near an insect or spider hole, or at the roots of a *Dodonaea viscosa* bush (Sparkes 2001). The shallow pits are thought to be used to dig up insects (Smyth and Philpott 1968) or the seed stores in nests of harvester ants (Gibson *et al.* 2002). The shallow scratchings may be used to expose bulbs (Southgate 1994a).

2.2.4 Biology

Bilbies are sexually dimorphic in size, with males weighing up to 2500 g while a female weighs up to 1200 g. They have a gestation period of 12 to 14 days, leave the pouch at three months, and reach sexual maturity at about 6 months old (Southgate *et al.* 2000). Moseby and O'Donnell (2003) found that during the first 17 months after reintroduction, the female bilbies at Arid Recovery bred throughout the year, producing an average of 2.5 pouch young per year. This shows that bilby populations at Arid Recovery could quickly increase under favourable conditions.

2.3 BURROWING BETTONG

The burrowing bettong (*Bettongia lesueur*) is a semi-fossorial, and nocturnally active CWR marsupial. It is one of nine species of rat-kangaroos of the family Potoroidae. Bettongs once had one of the largest geographic ranges of any Australian mammal (Burbidge 1995), being widespread and abundant throughout much of the southern two-thirds of Australia and on five islands off the coast of Western Australia (Short and Turner 1993) (Figure 2.11). Their distribution however was patchy and discontinuous, and numbers fluctuated greatly (Finlayson 1958 in Morton 1990). Burrowing bettongs disappeared from the pastoral areas of South Australia by the 1930's and now only survive on three islands, Barrow, Bernier and Dorre Islands (Short and Turner 1993). They are classified as vulnerable nationally and as near threatened by the IUCN (DEWHA 2008, IUCN 2008).

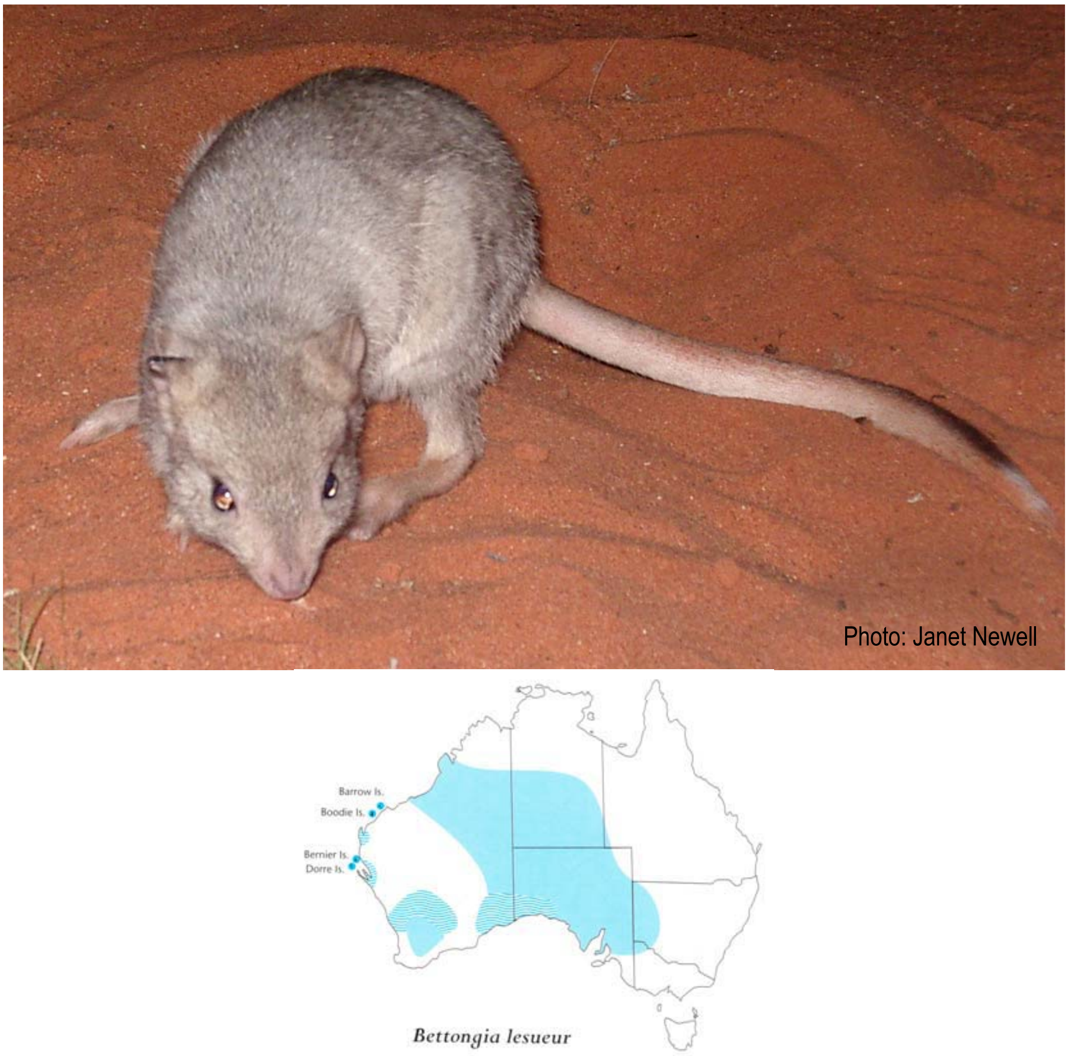


Photo: Janet Newell

Figure 2.11: Photo of a burrowing bettong (*Bettongia lesueur*) from Arid Recovery. The distribution map shows their former distribution (light blue) and current distribution (dark blue) (Strahan 2000). Reintroduced populations are not included on this distribution map.

2.3.1 Reintroduction

There have been a few attempts to reintroduce the burrowing bettong into its former habitat on mainland Australia. For example, 40 individuals were released in the Gibson Desert in Western Australia but no bettongs were seen alive after only two months (Christensen and Burrows 1994). Nearly all the deaths were thought to be due to predation by feral cats.

Only the projects where feral cats and foxes have been removed or tightly controlled have been successful. This includes Heirisson Prong in Western Australia (Short and Turner 2000), Faure Island in Western Australia (Australian Wildlife Conservancy n.d.), Scotia Sanctuary in New South Wales (Pizzuto *et al.* 2007), and Arid Recovery.

2.3.2 Habitat

The burrowing bettong once occurred in a broad range of habitats in semi-arid and arid Australia (Burbidge 1995). On Dorre, Bernier and Barrow Islands, they have been trapped in highest numbers on sandplains with *Triodia* habitat, and dunes with heath (Short and Turner 1999). These populations fluctuated greatly in size from year to year in response to variations in rainfall (Short *et al.* 1997). The reintroduced populations at Arid Recovery appear to prefer dune habitat rather than chenopod swales (Finlayson and Moseby 2004).

Burrowing bettongs are the only macropod species to live in their own permanent underground warrens (Burbidge 1995). Bettongs forage alone at night, but shelter during the day in groups of several females and one male (Sander *et al.* 1997). Individual bettongs use more than one warren (Finlayson and Moseby 2004), and groups of 20 to 40 have been recorded in one warren (Sander *et al.* 1997). However, warrens in coastal dunes are much smaller with only a few entrances (Sander *et al.* 1997), much like warrens at Arid Recovery (personal observation).

2.3.3 Diet

Although the burrowing bettong is omnivorous, it is largely herbivorous, feeding mainly on fungal sporocarps, tubers, roots, seeds, fruit, and other plant parts. Invertebrates such as Isoptera and Coleoptera also make up a small component of their diet (Burbidge 1995). The diet of reintroduced burrowing bettongs in Western Australia was seasonally variable and bettongs broadened their dietary niche during times of decreasing food resources (Robley *et al.* 2001). However Bice and Moseby (2008) found less seasonal variation in the diet of bettongs at Arid Recovery, and predicted that they would be likely to damage permanent vegetation due to their reliance on perennial plants.

Burrowing bettongs procure part of their food by digging (Short and Turner 1994). It appears that they locate this food by smell, as feeding animals have been observed moving along slowly with their nostrils very close to the ground (Burbidge 1995).

2.3.4 Biology

The size of burrowing bettongs varies considerably over their range, weighing an average 1500 kg (Burbidge 1995). Burrowing bettongs have a gestation period of 21 days, the single young remains in the pouch for about four months (Seebeck and Rose 1989) and reaches sexual maturity at five months old (Burbidge 1995). Breeding occurs throughout the year (Burbidge 1995) with a peak after the first post-summer rainfall (Short and Turner 1999).

2.4 GREATER STICK-NEST RAT AND WESTERN BARRED BANDICOOT

The greater stick-nest rat (*Leporillus conditor*) and western barred bandicoot (*Perameles bougainville*) are the two other species that have been successfully reintroduced into Arid Recovery. Although these species occur within the study areas, they have not been considered in this thesis due to their low population levels, and the fact that neither make as many foraging diggings as do the bilbies and bettongs. The western barred bandicoot is omnivorous consuming a wide variety of invertebrates, small vertebrates, seeds, roots and other plant material (Strahan 2000, Richards and Short 2003), while the greater stick-nest rat is exclusively herbivorous, feeding mainly on the succulent leaves and fruit of saltbush, bluebush and other succulents (Copley 1999, Murray *et al.* 1999, Richards *et al.* 2001, Ryan *et al.* 2003).

CHAPTER 3 Digging activities of greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) reintroduced into an arid ecosystem

3.1 INTRODUCTION

The greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*) are medium-sized, semi-fossorial marsupials that were both once numerous and widely distributed over much of Australia. The range and abundance of both species have declined dramatically since European settlement (Southgate 1990a, Short and Turner 1993). Bilbies presently occupy less than 20% of their former range, surviving only in relatively unproductive areas such as the Tamami, Gibson and Great Sandy Deserts (Southgate 1990a), while the burrowing bettong only survives naturally on three off-shore islands (Short and Turner 1993). Both species are classified nationally as vulnerable (Pavey 2005).

Bilbies and burrowing bettongs have been reintroduced to predator-free reserves within their former range as part of a national recovery effort for these species. One such reserve is Arid Recovery, the location of this study. Arid Recovery is a 60 km^2 reserve in arid South Australia surrounded by a predator and rabbit proof fence. All feral cats, foxes and rabbits have been removed from the Reserve, and four locally extinct species reintroduced, including bilbies and bettongs. One of the main objectives of Arid Recovery is to facilitate the ecological restoration of an arid ecosystem through the reintroduction of locally extinct species (Maxwell *et al.* 1996, Arid Recovery 2006). However, as bilbies and bettongs have been locally extinct for over 50 years, little is known about their ecological roles in these arid ecosystems, information which is important in evaluating their roles in ecological restoration.

Both bilbies and bettongs dig extensively while foraging (Burbidge 1995, Johnson 1995). These diggings enable both species to access buried foods that may be unavailable to non-fossorial taxa. In addition, diggings create fertile patches through the accumulation of soil, moisture, seeds and other organic matter (reviewed in Alkon 1999, Whitford and Kay 1999), and the redistribution of mycorrhizal fungi and other microorganisms beneficial to plant growth (Martin 2003, Mawson 2004, Noble *et al.* 2007a). As these diggings affect resource flows to other organisms by modifying the physical structure of the environment, both bilbies and bettongs are considered physical ecosystem engineers (Jones *et al.* 1994).

The overall impact of such physical engineering activities of a species depends on both the scale and the lifetime of the disturbance (Jones *et al.* 1997). In the Negev Desert in Israel where Indian crested porcupine (*Hystrix indica*) diggings form 0.2 to 2% disturbance of the area, diggings have been shown to have increased species richness and plant biomass at the landscape level as a result of species-rich patches growing inside the diggings (Boeken *et al.* 1995). Gutterman *et al.* (1990) found that the effects of diggings varied throughout the lifetime of the digging, with a maximum effect on the diversity and biomass productivity when the diggings were half full.

This study examines the digging activity of greater bilbies and burrowing bettongs as part of a wider study to determine how the ecological roles of these species affect arid ecosystems. Although bilby and bettong diggings at Arid Recovery have been shown to accumulate seeds and organic matter and to facilitate seed germination (Sparkes 2001, James 2004, James and Eldridge 2007), little is known about the temporal and spatial variation and persistence of these diggings, and their effects on seed burial and seedling growth, factors that would determine the nature and scope of their ecological effects.

In this study, the characteristics and the spatial and temporal variation of these diggings were investigated to determine their extent and persistence. The number of seeds buried in diggings and the number of seedlings growing in diggings were determined to obtain a measure of the ecological effects of diggings. The temporal variations in rate of digging were compared with temperature, moonlight and rainfall, and changes in population and/or activity levels and diet of the bilbies and bettongs over time. A better understanding of these aspects of foraging diggings of bilbies and bettongs at Arid Recovery is important in assessing the potential environmental impact of the reintroduction of these species, and the role of these species in arid ecosystems.

3.2 METHODS

3.2.1 Study area

This study was conducted at Arid Recovery (30°29’S, 136°53’E), located 20 km north of Roxby Downs in central South Australia. This 60 km^2 reserve is surrounded by a 1.8 m high predator and rabbit proof fence (Moseby and Read 2006). All feral cats, foxes and rabbits have been removed from the Reserve, and four locally extinct species reintroduced: greater bilbies (*Macrotis lagotis*), burrowing bettongs (*Bettongia lesueur*), greater stick-nest rats (*Leporillus conditor*) and western barred bandicoots (*Perameles bougainville*). This study was conducted in the 14 km^2 main enclosure of the Reserve, where bilbies and bettongs were first reintroduced in 2000 and 1999 respectively. Further information on Arid Recovery may be found in Chapter 2.

The climate of the area is characterised by hot summers (mean daily maximum 37°C and minimum 21°C in January) and mild winters (mean maximum of 19°C and minimum of 4°C in July) (Read 2002). The 10-year (1996 t0 2005) average annual rainfall at Arid Recovery was 154 mm (CV 45%), with greatest variability in summer (Arid Recovery unpublished data). For further details refer to Chapter 2. There was approximately average rainfall during the study period (2004: 193 mm, 2005: 161 mm).

The three main habitat types within the Reserve are longitudinal sand dunes dominated by sandhill wattle (*Acacia ligulata*) and sticky hopbush (*Dodonaea viscosa*); clay inter-dunal swales dominated by the chenopods, bladder saltbush (*Atriplex vesicaria*) and low bluebush (*Maireana astrotricha*) and patches of mulga (*Acacia aneura*) woodlands with sandy clay soils.

3.2.1.1 Population estimates

Bilby and bettong populations in the 14 km^2 main enclosure of Arid Recovery, where this study was conducted, were estimated to be 150 bilbies and 150 to 200 bettongs in 2004 (Arid Recovery 2005).

The populations of reintroduced mammals were monitored using two methods: track transects and spotlighting counts. Track transects were monitored quarterly or when conditions permitted by counting the number of animal tracks crossing a standard walked transect in Dune habitat (Arid Recovery 2007). This monitoring required a windy night to clear old tracks followed by a still night to collect the tracks, and a calm morning to count them. The spotlighting counts were also conducted approximately quarterly while driving a standard route throughout the Reserve. During spotlighting, the animals were more frequently seen in the more open Mulga and Swale, than the denser vegetation of Dune habitat.

Track transects and spotlight counts of the bilbies and bettongs at Arid Recovery resulted in different estimates of changes in relative animal numbers/activity between January 2004 and July 2005 (Figure 3.1). Both track transects and spotlighting give only a relative estimate of animal numbers that may be affected by changes in animal activity patterns (Edwards *et al.* 2000, Morris 2003, Robley *et al.* 2004).

NOTE:
This figure is included on page 33 of the print copy of
the thesis held in the University of Adelaide Library.

Figure 3.1: Track transect and spotlight counts of (a) bilbies and (b) bettongs in the study area from January 2004 to July 2004 (Data from Arid Recovery 2006). ■ Track counts, ◇ Spotlighting.

3.2.2 Digging density, disturbance and rate of digging

The extent and temporal variation of digging was measured by monitoring digging densities, the rate of digging and the percentage of area disturbed at 30 sites in the Inside area of Arid Recovery. The Inside area was stratified by habitat type and then 14 Dune, 11 Swale and 5 Mulga monitoring sites were randomly selected from a map. Each site was circular with a radius of 10 m around a central marker post (314 m^2).

The 30 sites were monitored at approximately three monthly intervals from January 2004 to July 2005, with digging density and disturbance monitoring starting in April 2004. During each sampling period, the sites were visited twice at an interval of two weeks. At the first visit, the digging density and area of disturbance was measured in 1 m wide x 10 m long transects along the four primary compass directions from the central marker post (total area of 40 m^2). The number of diggings, and percentage of the area that was disturbed by diggings and spoil from the diggings was scored for each of 40 1 m x 1 m quadrats along these transects. In addition, all diggings within the whole monitoring site were marked by placing small sticks in the diggings so that the number of diggings dug over a two week period could be identified during the second visit.

Two weeks later, these new diggings within the total monitoring area were counted to obtain a rate of digging over the two week period. These diggings were classified into five digging types based on their shape, size and direction of spoil heap: (1) shallow, irregular-shaped scratchings, (2) shallow, concave shape, (3) shallow (<20cm deep) conical shape, (4) deep conical shape (dig forms a 'tunnel'), (5) cylindrical (approximately round in shape and straight down). The number of diggings recorded at this second monitoring time was used to calculate the rate of digging.

Other animals in the study area that may make foraging diggings similar to those of bilbies and bettongs include indigenous spinifex hopping-mice (*Notomys alexis*), and goannas (*Varanus gouldii*), and the reintroduced western barred bandicoots. Diggings of all these species were often recognised by their distinctive shapes and tracks, and were not included in the overall count of diggings. However, the similarity of diggings of most species and the lack of clear tracks on some occasions means that some of these diggings by other species may have been inadvertently included in the counts of bilby and bettong diggings.

3.2.3 Digging size

To determine the average sizes of diggings in each habitat type, digging size was measured for a haphazard selection of recent diggings on the monitoring plots. Where the digging was angled so that its vertical depth could not be measured directly, its angled depth was measured using a ruler with one end inserted to the bottom of the digging. The vertical depth of the digging was then calculated by triangulation with the height of the top end of the ruler from the ground. The volumes of a selection of these diggings were determined by filling the digging with a known volume of sand. The size and volume of diggings for which the species (bilby or bettong) that dug them could be positively determined (using tracks or scats) were measured when found during field surveys throughout the Reserve in order to determine the differences between bilby and bettong diggings.

3.2.4 Environmental factors affecting diggings

The monthly rainfall over the study period was measured at Arid Recovery, whereas average monthly minimum and maximum temperatures were obtained from the Bureau of Meteorology (Canberra) for the Olympic Dam Meteorology Station, approximately 10 km south of Arid Recovery.

The overall intensity and duration of moonlight during the two week sampling periods was calculated as the sum of the nightly estimated moonlight intensity (Courter 2003) times an estimate of the relative time the moon was above the horizon (i.e. the number of days since the new moon) for each day of the sampling periods.

3.2.5 Digging persistence

The rate of filling of the diggings was measured by monitoring the fate of all the diggings that were new during the sampling periods in September 2003, April 2004, September 2004, and April 2005 at six sites (two in each of Dune, Mulga and Swale) that were used for soil seed bank sampling (Chapter 5). (These sites were different from the sites used in monitoring digging density and rate of digging.) Each digging was marked using a wire peg with a plastic flag. The size (length, width and depth) of each digging was measured during the first visit, and at approximately three-month intervals thereafter. Diggings were considered filled when there was no longer any visible sign of the digging.

3.2.6 Seeds accumulated in diggings

The number of seeds that accumulated and became buried in bilby and bettong diggings was determined in April 2005 by excavating 15 of the filled-in diggings that had been assessed for persistence in the Dune habitat. Diggings were categorised according to the amount of protection from wind by vegetation in order to assess the influence of wind on seed accumulation in diggings: (A) sheltered with accumulated litter, (B) partly sheltered with no accumulated surface litter, and (C) little to no shelter and no accumulated surface litter. No filled-in diggings were available in category A, as none of the limited number of diggings in these sheltered areas had filled completely at time of monitoring.

The selected diggings were excavated, and the soil was sieved on site using a sieve with 1 mm mesh as per the soil seed bank sampling methods used in Chapter 5. All the seeds retained in the sieve were identified and counted, and the leaf litter weighed. Eighteen control samples, six in each of the three shelter categories, were also excavated from nearby undisturbed locations. It is unlikely that any of these samples were at sites of filled-in diggings, as none contained the considerable amounts of litter that were characteristic of filled-in diggings.

3.2.7 Seedlings in diggings

The number of seedlings growing in the diggings that were being monitored for persistence were counted in summer (January 2005, average monthly max. temp. 36.3 ˚C), about a month after 25 mm rain, when the seedlings were approximately 3 to 5 cm tall, and compared with the number of seedlings growing in similar sized areas of undisturbed soil matrix near each digging.

This counting of seedlings was repeated in winter (July 2005, max. temp. 18 ˚C), about two weeks after 14 mm of rain, when new seedlings were very small with only cotyledons and possibly two true leaves visible.

3.2.8 Data analysis

The three separate factors measured in this study: digging densities at the first monitoring time, percentage of area disturbed measured at the same time, and rate of digging determined from counts of new diggings over a two week period, were each analysed for variation over time and between habitats using repeated measures ANOVA. Data for each site were transformed before analysis using natural log (x+1) to normalise the data (Osborne 2002). Tukey's HSD was used to determine significant differences between means. The differences in dimensions of diggings between habitat type and between bilbies and bettongs were examined using ANOVA. The differences between the distribution of diggings in the habitat types and the relative areas of each habitat available were tested by Chi-square analysis of 3 x 2 contingency tables.

Spearman's correlation was used to determine correlations between the temporal variations in rate of digging, digging density and in disturbance between habitats; with environmental factors; and with track and spotlighting counts. The number of seeds and seedlings in the diggings and comparable soil matrix areas were compared using non-parametric Kruskal-Wallis tests and Wilcoxon signed rank tests. The analysis was carried out using SPSS software (SPSS 2007).

The relationship between the rate of digging and the diets of the bilbies and bettongs (as determined by faecal analysis described in Chapter 4) was determined using Spearman's correlation to correlate the rate of digging with the sand content of their faecal pellets, as well as the main seeds consumed (chapter 4). In order to conduct these correlations, the data was normalised using (x – mean)/SD so that the mean values of all variables = 0. This normalisation also eliminated the bias of variables with larger numerical values on the regression. The overall rate of digging used for these correlations was a composite of the rates of diggings for the total study area calculated as the sum of the rate of digging for each of the three habitats multiplied by the relative area of that habitat within the study area.

3.3 RESULTS

3.3.1 Characteristics of diggings

The average measurements of the five digging types are shown in Table 3.1. However, digging types were not always exclusive, as there was a wide variety in the shapes and sizes of the diggings. The average size of all the diggings measured during this study was 11 x 7 x 10 cm deep, with a volume of 327 cm^3.

Table 3.1: The classification of bilby and bettong digging types at Arid Recovery, their average size and volume (± s.e) and the percentage occurrence of each of these digging types over all the diggings recorded during this survey. n is the number of diggings measured to determine digging size (or used to calculate volume).

Dig	Description	% occurrence (n = 2274)	Digging Size (cm)			Volume (cm^3)	n
			Length	Width	Depth		
1	Shallow, irregular shaped scratchings	24%	8.0 (±0.5)	4.8 (±0.4)	2.7 (±0.2)	34 (±6.5)	59 (20)
2	Shallow, concave shaped	4%	11.6 (±0.7)	6.8 (±0.4)	4.6 (±0.3)	194 (±69.5)	56 (7)
3	Shallow (<20cm deep) conical shaped	54%	10.7 (±0.3)	6.5 (±0.2)	6.9 (±0.2)	354 (±59.3)	281 (65)
4	Deep conical (dig forms a 'tunnel')	12%	14.2 (±0.7)	7.8 (±0.3)	13.7 (±1.0)	466 (±79.1)	91 (24)
5	Cylindrical (approx round and straight down)	6%	12.6 (±0.6)	10.0 (±0.5)	23.8 (±1.9)	503 (±106.0)	75 (10)
Total			11.3 (±0.2)	7.0 (±0.2)	9.6 (±0.4)	327 (±37.4)	562 (126)

The average size of diggings in the Dune (11 x 7 x 10 cm) and Mulga (12 x 8 x 9 cm) habitats were generally larger and deeper than those in Swale (10 x 7 x 8 cm), though this difference was only significant for digging length (length: $F_{2,564} = 5.2$, p = 0.01; width: $F_{2,564} = 1.9$, p = 0.1; depth: $F_{2,564} = 2.8$, p = 0.06).

In general, it was not possible to determine whether a digging had been dug by either a bilby or a bettong. However, for some diggings, fresh tracks and/or scats could be used to distinguish whether a bilby or bettong had made the digging. Bettong diggings (16 x 9 x 5 cm) were generally larger and shallower than bilby diggings (12 x 6 x 9 cm), though this difference was only significant for width (length: $F_{1,97} = 3.1$, p = 0.08; width: $F_{1,97} = 9.4$, p = 0.003; depth: $F_{1,97} = 3.1$, p = 0.08).

3.3.2 Digging density, disturbance and rate of digging

The average density of diggings in the Reserve over the period of the study was highest in Mulga, though not significantly different from that in Dune or Swale ($F_{2,27} = 1.2$, $p = 0.32$) (Table 3.2). The percentage area that was disturbed was also highest in Mulga, though again not significantly different from that in the other two habitats ($F_{2,27} = 0.9$, $p = 0.44$).

The rate of digging varied significantly between the three habitat types ($F_{2,27}=13.8$, $p<0.001$) (Table 3.2). The rate was higher, though not significantly so, in Dune than Mulga (Tukey HDS, $p = 0.28$). Both these habitat types had significantly higher rates of digging than Swale (Tukey HDS: Dune: $p<0.001$, Mulga: $p = 0.06$).

The estimated total volume of soil excavated by the bilbies and bettong diggings each year was greatest in Dune and lowest in Swale (Table 3.2).

The digging rate was 45,000 diggings individual^{-1} yr^{-1} or 120 diggings individual^{-1} night^{-1} using an estimate of 300 animals in the 14 ha enclosure, and averaging the rates of digging and volume excavated across all habitats by proportion of area of each habitat within the enclosure. Overall volume excavated was 18 m^3 individual^{-1} yr^{-1} or 0.05 m^3 individual^{-1} night^{-1} (30 tonnes individual^{-1} yr^{-1} or 0.08 tonnes individual^{-1} night^{-1} using a mass of 1.6 tonnes m^3).

Table 3.2: The average ± s.e. digging density (diggings ha^{-1}), percentage area of disturbance, rate of digging (diggings ha^{-1} yr^{-1}) and overall volume of soil excavated by the diggings in each of the habitat types in Arid Recovery.

	Digging Density (ha^{-1})	Disturbance (% area)	Rate of Digging (ha^{-1} yr^{-1})	Volume Excavated (m^3 ha^{-1} yr^{-1})
Dune	7,530 ± 820	2.8 ± 0.4	12,090 ± 1440	5.1 ± 1.1
Mulga	10,560 ± 980	3.0 ± 0.4	10,410 ± 2480	3.8 ± 1.3
Swale	7,120 ± 610	2.0 ± 0.3	4,680 ± 650	1.8 ± 0.6

3.3.3 Temporal variation

3.3.3.1 Digging density

Digging density varied between the sampling periods, though not significantly ($F_{10,46} = 1.9$, $p = 0.07$) (Figure 3.2). Variation in digging densities in the Dune habitat was 3-fold over time, twice the variation in Mulga or Swale. Digging density was significantly correlated over time between all three habitats (Dune: Mulga: $r = 0.93$, Dune: Swale: $r = 0.99$ and Swale: Mulga: $r = 0.88$, all $p <0.01$; all $n = 6$).

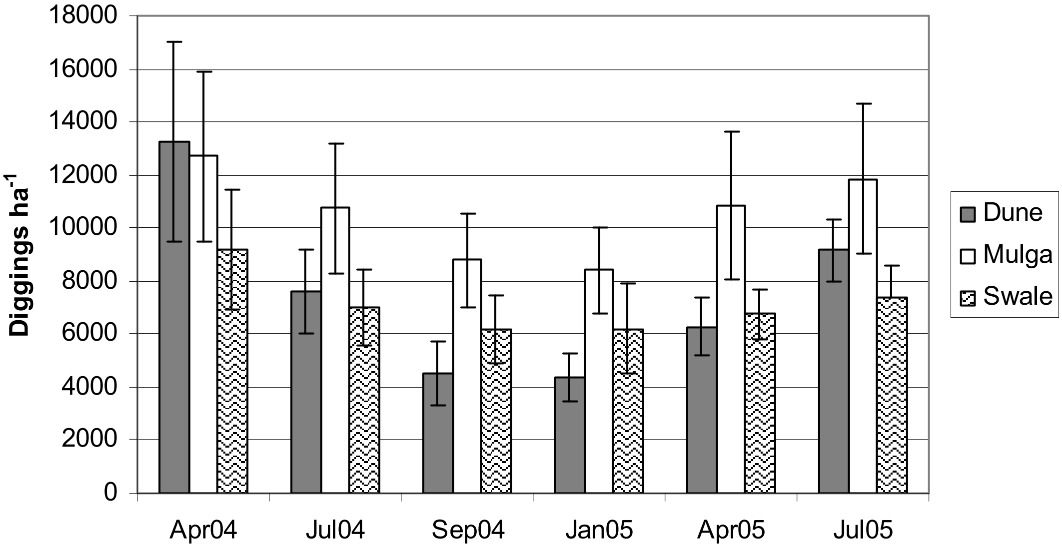


Figure 3.2: The average digging densities (diggings ha^{-1}) (± s.e.) recorded in the three habitat types over six sampling periods from April 2004 to July 2005. Dune: n = 14, Mulga: n = 5, Swale: n = 11 for each sampling period.

3.3.3.2 Disturbance

The area of disturbance was significantly different between the sampling periods ($F_{10,46}$=2.5, p=0.02). The temporal pattern was similar to that of digging densities with highest values in April 2004, and lowest in September 2004 and January 2005 (Figure 3.3). Variation of disturbance between sampling periods was six-fold over time in the Dune habitat type, again over twice the variation in Mulga and Swale. Area of disturbance was significantly correlated over time between all three habitats (Dune: Mulga: r = 0.88, Dune: Swale: r = 0.98 and Swale: Mulga: r = 0.88, all p <0.01; all n = 6).

At each sampling time, the area of disturbance was significantly correlated with the density of diggings for Dune and Swale (r values Dune: 0.88 to 0.97, n = 14, p <0.01; Swale: 0.83 to 0.97, n = 11, p <0.01). However for Mulga, disturbance and digging density were correlated in April and September 2004, but not at the other four sampling times (April 2004: r = 1, September 2004: r = 0.9 both p <0.01; other times r = 0.4 to 0.64, p = 0.22 to 0.5, all n = 5).

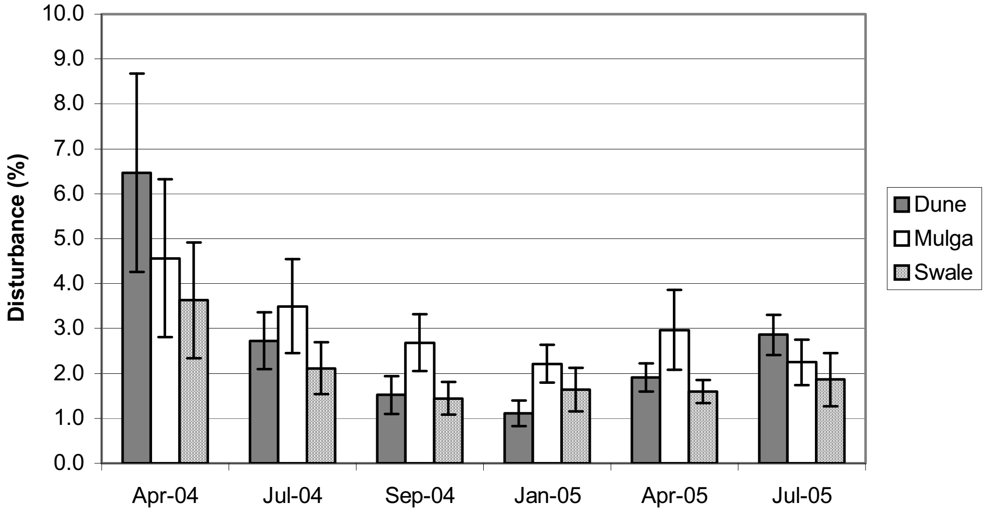


Figure 3.3: The average percent of surface area disturbed (± s.e.) by the diggings in the three habitat types over six sampling periods from April 2004 to July 2005. Dune n = 14, Mulga n = 5, Swale n = 11 for each sampling period.

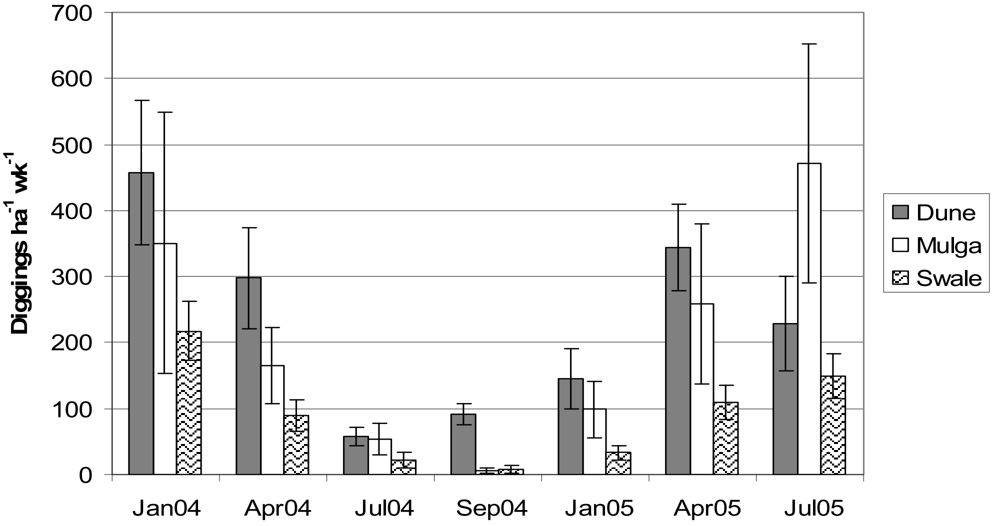


Figure 3.4: Average rate of diggings per hectare per week (±s.e.) recorded for the three habitat types over seven sampling periods from January 2004 to July 2005. Dune: n = 14, Mulga: n = 5, Swale: n = 11 for each sampling period.

3.3.3.3 Rate of digging

The rate of digging varied significantly between sampling periods ($F_{12,44}$=4.6, p<0.001) (Figure 3.4). The variation in the rate of digging between sampling periods was greater than the variation for both the digging densities and disturbance, with an 8-fold variation in Dune, 10-fold in Mulga and 18-fold in Swale. Rate of digging was significantly correlated over time between all three habitats (Dune: Mulga: r = 0.68, p <0.05; Dune: Swale: r = 0.89 and Swale: Mulga: r = 0.88, both p <0.01; all n = 7).

At each sampling time, rate of digging was not correlated with either digging or area of disturbance in any of the three habitat areas (r values: Dune: 0.07 to 0.37, n = 14, p = 0.8 to 0.18; Mulga: 0 to 0. 7, n = 5, p = 1 to 0.1; Swale: 0.01 to 0.32, n = 11, p = 0.97 to 0.33).

3.3.4 Habitat availability

The rate of digging in each of the habitat types was significantly different from the availability of these three habitat types in the study area (χ^2 = 34.0, d.f. = 2, p<0.001). Figure 3.5 suggests a marked preference for Dune and Mulga and an avoidance of Swale.

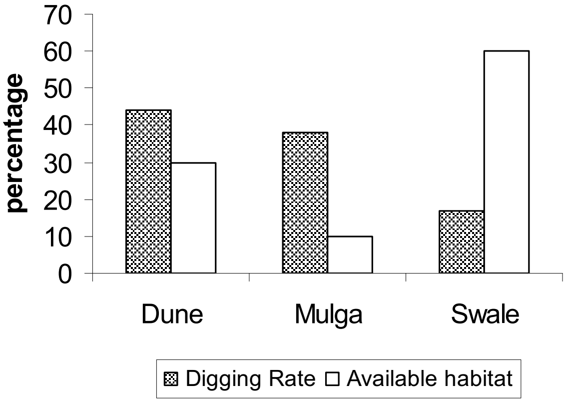


Figure 3.5: A comparison of the average relative rate of new diggings in each habitat type (Dune, Mulga and Swale) with the availability of each habitat type in the study area (percentage of total area). Relative rates of digging were calculated using average values of rates of digging over all sampling periods. Relative area of each habitat is from Moseby and O'Donnell (2003) and Finlayson and Moseby (2004).

3.3.5 Environmental factors

Correlations of rates of digging, digging density and disturbance over time with environmental factors, and with track and spotlighting counts are presented for Dune habitat only because of the likelihood of indirect correlations (Haig 2003) resulting from the high correlations between habitats over time for all these factors. Correlations with Mulga and Swale were similar to those presented for Dune for all these factors.

3.3.5.1 Temperature

The rate of bilby and bettong digging increased with increasing average monthly minimum temperatures, showing increased digging activity on warmer nights (Dune: r = 0.75, p = 0.05, n = 7). Areas of disturbance were not correlated with either the monthly minimum or maximum temperatures (minimum: Dune: r = -0.14, p = 0.79; maximum: Dune: r = -0.35, p = 0.50, both n = 7).

3.3.5.2 Rainfall

The rate of digging over the 19 month period of the study showed a negative correlation with recent rainfall but a weak positive correlation with the cumulative rainfall for the preceding six months before sampling (rainfall two months before: r = -0.75, p = 0.05; 6 months before: r = 0.57, p = 0.18; both n = 7). Other measurements of rainfall, e.g. rainfall 2 months preceding sampling time, resulted in similar patterns of correlations.

3.3.5.3 Moonlight intensity and duration

There was no correlation between the rates of digging and the moonlight intensity and duration during the study (Dune: r = 0.09, p = 0.85, n = 7).

3.3.6 Digging persistence

The persistence of diggings differed between the three habitat types, with the majority of the diggings in the Mulga (94%) and Swale (87%) persisting for over 12 months (Figure 3.6). However Dune diggings filled much faster, with only 15% persisting over 12 months.

The persistence of the Dune diggings was strongly dependent on the amount of shelter of the digging. Diggings in open areas filled in less than three to six months, or even overnight if it was especially windy or rainy. The rate of filling was not linear, as many diggings filled relatively quickly until about one to two centimetres deep and then remained for months as shallow depressions that often contained some litter.

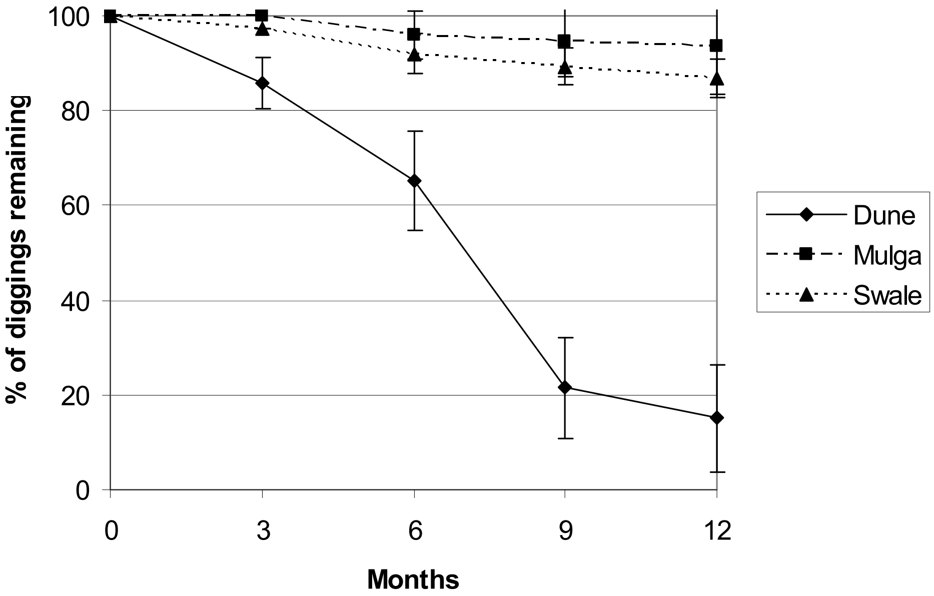


Figure 3.6: The percentage of diggings (±s.e.) that persisted over a 12 month period in each of the three habitat types (Dune, Mulga and Swale). n: Dune = 109, Mulga = 58, Swale = 36.

3.3.7 Seeds buried in diggings

The number of seeds buried in diggings that had filled-in and the depth at which they were buried varied with the amount of shelter at the location of the digging (Table 3.3). Significantly more seeds accumulated in the more sheltered (category B – shelter but minimal litter) diggings than those in the open (category C – no shelter and no litter) (χ^2 = 4.3, d.f. = 1, p = 0.04). The number of seeds that were in the control samples was also significantly different between the three shelter categories (χ^2 = 13.1, d.f. = 2, p = 0.001), with seed numbers decreasing with decreasing shelter. No filled-in diggings were available in category A (shelter and high litter).

Table 3.3: The number of seeds (±s.e.) that were found in the filled-in Dune diggings and the control samples, separated into three depths (surface, 0-2cm and deep) and overall. A – sheltered with litter, B – sheltered but minimal litter, C – no shelter and no litter.

Shelter category		Number of seeds (sample^{-1} or digging^{-1})			
		Surface	0-2 cm	Deep (2-20 cm)	Total
A (n=6)	Control	4.5 ± 1.9	11 ± 2.2	26.3 ± 10.9	41.8 ± 13.7
B (n=6)	Digging	12.8 ± 5.4	6 ± 2.7	17 ± 6.1	35.8 ± 8.1
B (n=6)	Control	3.8 ± 3.3	2.7 ± 0.8.	2 ± 0.8	8.5 ± 3.7
C (n=9)	Digging	1.7 ± 0.7	3.6 ± 0.6	7.9 ± 5.7	13.1 ± 6.4
C (n=6)	Control	0	0.2 ± 0.2	0.5 ± 0.3	0.7 ± 0.5

The filled-in diggings in both shelter categories B and C had significantly more seeds than the respective control samples (B: χ^2 = 5.9, d.f. = 1, p = 0.02; C: χ^2 = 10.0, d.f. = 1, p = 0.002) (Table 3.3). In shelter category B, numbers of seeds were statistically equal in diggings and controls for the surface, and 0-2 cm depths, though the 2-20 cm depth of the diggings had significantly more seeds than the controls (surface: χ^2 = 2.8, d.f. = 1, p = 0.1; 0-2 cm: χ^2 = 1.0, d.f. = 1, p = 0.33, deep: χ^2 = 8.4, d.f. = 1, p = 0.004). In shelter category C, the diggings had significantly more seeds than the control samples in the surface and 0-2 cm depths, but not in the deepest depth (surface: χ^2 = 5.8, d.f. = 1, p = 0.02; 0-2 cm: χ^2 = 10.3, d.f. = 1, p = 0.001, deep: (χ^2 = 3.6, d.f. = 1, p = 0.06).

All the diggings also contained leaf litter buried at all depths up to the original depth of the digging. The mass of litter in each digging was positively correlated with the number of seeds in that digging for category C diggings, but not for category B (C: r = 0.66, n = 9, p = 0.05; B: r = 0.09, n = 6, p > 0.5). Very little, if any, litter was found in any of the control samples.

3.3.8 Growth of seedlings in diggings

The number of seedlings growing in the diggings was measured in summer (January 2005, max. temp 36.3˚C), about a month after 25 mm rain, when the seedlings were approximately 3 to 5 cm tall. Diggings in Dune contained two times more seedlings than the surrounding soil matrix (Figure 3.7). However, the diggings in Mulga contained only half as many seedlings as the soil matrix, while diggings in Swale contained equal numbers of seedlings in the diggings as in the soil matrix.

A second set of measurements in winter (July 2005, max temp 18 ˚C), about two weeks after 14 mm of rain, when the seedlings were still only cotyledons and possibly two true leaves, showed greater differences between the number of seedlings inside and outside diggings with 1.8 times more seedlings growing in bilby and/or bettong diggings than in equivalent areas of the surrounding soil matrix in both the Dune and Mulga, and over 4 times more in the Swale diggings (Figure 3.7).

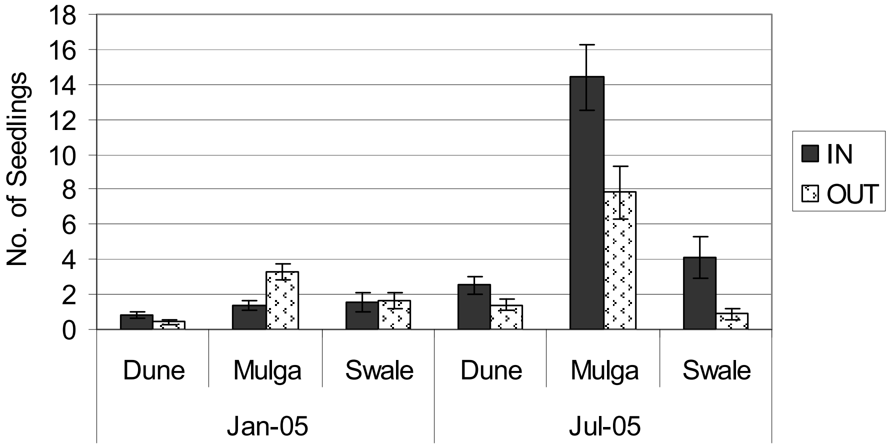


Figure 3.7: The average (± s.e.) numbers of seedlings in bilby and bettong diggings (IN) compared with seedling numbers in the surrounding soil matrix (OUT) in the three habitats. The January 2005 sampling was in summer, about one month after 25 mm rain, whereas the July 2005 sampling was in winter, about 2 weeks after 14 mm rain. Wilcoxon signed ranks tests: January 2005: Dune: $z = -2.0$, $p = 0.04$, $n = 29$; Mulga: $z = -4.9$, $p < 0.001$, $n = 63$; Swale: $z = -0.2$, $p = 0.9$, $n = 14$; July 2005: Dune: $z = -2.2$, $p = 0.03$, $n = 54$; Mulga: $z = -4.3$, $p = < 0.001$, $n = 71$; Swale: $z = -4.0$, $p < 0.001$, all $n = 32$.

3.3.9 Relationship between rate of digging and population estimates

Over the period of this study, the population estimates for the bilbies and bettongs by track transects varied over time (2.4-fold for bilbies and 1.9-fold for bettongs), less than the 8-fold variation in rate of digging in the Dune habitat, while the spotlighting counts varied (10.8-fold for bilbies and 21-fold for bettongs) (Figure 3.1). Overall variation in track transects over time may be an underestimate, as no data was available for July and September 2004 when spotlighting counts for bilbies were lowest.

The rate of digging in the Dune habitat was correlated with both the track transects and the spotlighting counts for bilbies but not bettongs (Figure 3.8). The percentage of area disturbed was correlated with the track transect counts but not spotlighting for bilbies (tracks: $r = 0.98$, $n = 4$, $p < 0.01$; spotlighting: $r = -0.01$, $n = 5$, $p > 0.5$), and not correlated to either population estimates of the bettongs (tracks: $r = 0.11$, $n = 5$, $p > 0.5$; spotlighting: $r = -0.62$, $n = 5$, $p > 0.2$).

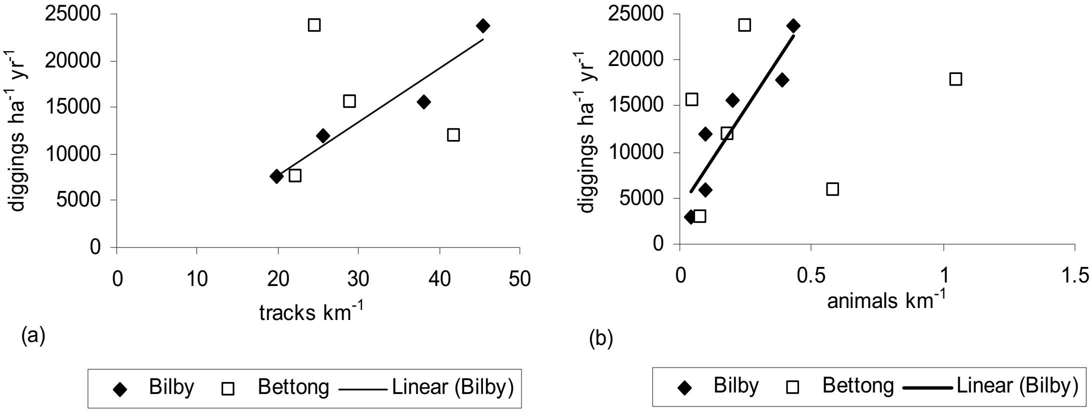
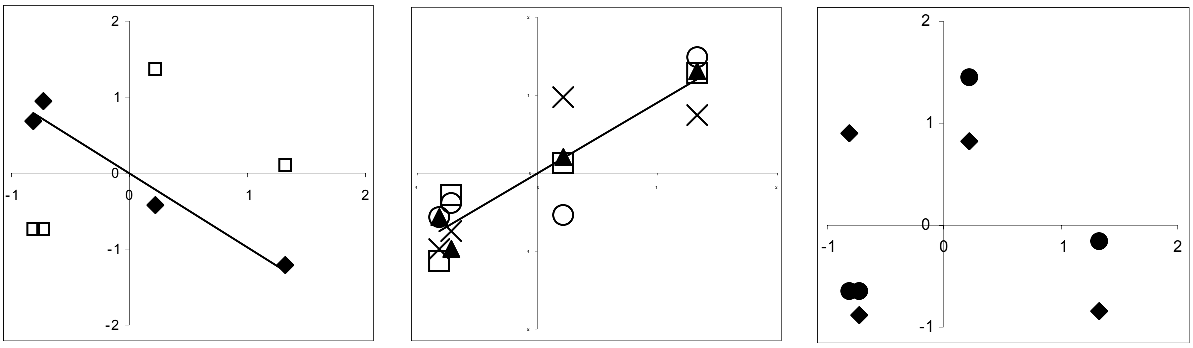


Figure 3.8: Relationship of (a) track numbers and (b) spotlight counts of bilbies and bettongs to the rate of digging. Only the comparisons with rate of diggings in Dune are presented as digging rates were highly correlated over time between all three habitats. Correlation of tracks to diggings: bilbies: $r = 0.91$, $n = 4$, $p = 0.03$, bettongs: $r = -0. 34$, $n = 4$, $p>0.5$; spotlight counts to diggings: bilbies: $r = 0.91$ $n = 6$, $p<0.01$; bettongs: $r = -0.35$, $n = 6$, $p>0.5$. Regression lines for bilby: Track: $y = 570x – 3700$; Spotlight: $y = 47600 x + 2185$. Track and spotlight data from Arid Recovery (Arid Recovery 2006 and Figure 3.1). Closed symbols – bilby; open symbols – bettong.

3.3.10 Relationship of rate of digging to diet

The rate of digging was negatively correlated to the percent of sand in bilby pellets but not correlated for bettong pellets (bilby: $r = -0.98$, $p < 0.01$, bettong: $r = 0.52$, $p > 0.5$, $n = 4$) (Figure 3.9a).



(a) Sand consumption (b) Grass seed consumption (c) *Dodonaea* and *Zygophyllum*

Figure 3.9: Relationship between rate of diggings and dietary consumption of (a) sand by bilbies and bettongs, and (b and c) different species of seeds by bilbies. X axis: standardised rate of digging and Y axis: standardised volume of sand/seeds consumed. (a) sand content of (◆) bilby and (☐) bettong faecal pellets. (b) Grass seeds: (☐) Aristida sp., (▲) Dactyloctenium radulans, (✕) Paractaenum sp., (○) Sporobolus actinocladus. (c) (◆) *Dodonaea viscosa* and (✱) *Zygophyllum ammophilum.* Diet data taken from Chapter 4.

By contrast, the rate of digging was positively correlated to percent grass seeds in bilby pellets (r = 0.99, n = 16, p <0.01), but not correlated with the consumption of two other main species of seeds in bilby diets: the forb *Zygophyllum ammophilum* and the shrub *Dodonaea viscosa* (Figure 3.9b and c). (*Z. ammophilum*: r = -0.35, *D. viscosa*: r = 0.46, both p > 0.5, n = 4). An estimate of the overall rate of digging for the study area was used for these correlations, as neither sand nor seed consumption could be related specific habitats. For bettongs, rate of digging was significantly correlated with invertebrate consumption (r = 0.93, n = 4, p <0.01).

3.4 DISCUSSION

3.4.1 Bilbies and bettongs as ecosystem engineers

The size, extent, and persistence of the foraging diggings of greater bilbies and burrowing bettongs at Arid Recovery indicated that these animals are ecosystem engineers (Jones *et al.* 1994) supporting the conclusions from another less extensive study of these foraging diggings at Arid Recovery by James and Eldridge (2007) shortly before the start of this study. The density of diggings, area disturbed, and volume of soil excavated per year measured in this study were all comparable to or higher than the same variables for two extensively studied porcupine species, the Indian crested porcupine (*Hystrix indica*) in Israel (Alkon and Olsvig-Whittaker 1989, Alkon 1999) and the Cape porcupine (*H. africaeaustralis*) in South Africa (Bragg *et al.* 2005). The rates of digging were also greater than those reported for other Australian species including brush-tailed bettong (*Bettongia pencillata*) (Garkaklis *et al.* 2004), Tasmanian bettong (*Bettongia gaimardi*) (Johnson 1994a), and long-nosed potoroo (*Potorous tridactylus*) (Claridge *et al.* 1993).

As historical records suggest that such foraging diggings were once a numerous and visible feature of Australia's arid regions, the ecosystem engineering effects of these diggings may once have been ecologically important throughout the region, but lost with the local disappearance of these mammals (Martin 2003). Although rabbits (*Oryctolagus cuniculus*), which are now relatively numerous throughout the region, create foraging diggings, these diggings are neither as numerous, nor as effective at accumulating litter as bilby and bettong diggings (Sparkes 2001, James and Eldridge 2007). In addition, damage to perennial species from browsing by rabbits probably offsets any positive effects of their diggings (Noble *et al.* 2007a). Diggings of goannas (*Varanus gouldii*), another semi-fossorial taxon at the study site, occur at only about one eighth of the density of bilby and bettong diggings, thus are not as potentially ecologically important as bilby and bettong diggings (James and Eldridge 2007).

The overall ecological impact of diggings is related to the length of time it takes for them to fill and disappear (Gutterman 1982). More than 85% of bilby and bettong diggings in the Dune habitat had disappeared within a year, with all the diggings in open areas filling within four months. By contrast, about 90% of the diggings in the higher clay soils of the Mulga and Swale were still present after one year, although they had all filled in nearly two years later (K. Moseby, personal communication, 2007). The life-spans of the diggings in the Mulga and Swale are similar to the life-spans of the diggings of both Cape porcupines in South Africa (Bragg *et al.* 2005), and Indian crested porcupines in Israel (Alkon and Olsvig-Whittaker 1989), although some of the Indian crested porcupines diggings in Israel have been shown to last for over 20 years (Alkon 1999).

Even the short-lived diggings in Dune would have a long-term impact on soil and vegetation due to the seeds and litter that become buried in the diggings. Buried litter decomposes faster than litter on the surface, and contributes more to soil nutrients (Whitford and Kay 1999). The soil turnover by diggings may also be an important ecological service (Bragg *et al.* 2005). As the majority of nutrients in soils in arid Australia are in the top 5 to 10 cm of the soil (Stafford Smith and Morton 1990), and the majority of diggings were in this depth category, soil turnover may be an important part of nutrient regeneration in these areas (Whitford and Kay 1999). The high spatial variability of soil turnover measured in this study may assist in maintaining the high spatial heterogeneity of arid landscapes (Jackson *et al.* 2003) which has been shown to be important for landscape resilience and increased growth responses of plants to rainfall events (Noy-Meir 1973, Holm *et al.* 2002, Holm *et al.* 2003).

Excavation of filled-in diggings showed that seeds had collected and become buried in the diggings. However, the great variability in the number of seeds buried in each digging and the depth of burial of these seeds with the amount of shelter of the digging makes it impossible to predict how this burial of seeds in diggings might affect the depth of seeds in the overall soil seed banks. Although some seeds may have been buried too deeply for germination, others may have been buried at depths that might facilitate their germination (Guo *et al.* 1998). Seeds collected in diggings may be eaten by granivores like bilbies and bettongs, that preferentially consume larger clumps of seeds (Gutterman *et al.* 1990, Chapter 6). The seeds that were recovered from the filled-in diggings may therefore not include all the seeds that were trapped in the diggings during their lifetime (Chapter 7). In this way, bilbies and bettongs may benefit directly from the effects of their diggings.

The two surveys of seedling numbers in old bilby and bettong diggings confirmed that these diggings do collect seeds (James and Eldridge 2007), and possibly enhance their rate of germination (Sparkes 2001). However the lower or equal numbers of older seedlings in diggings in Mulga and Swale than the surrounding soil matrix in January 2005 suggests that under some environmental conditions diggings may not increase plant growth, as the increased resources, including moisture within the diggings themselves (Eldridge and Mensinga 2007, James and Eldridge 2007), may be insufficient to result in increased plant establishment. In addition, herbivores, including bettongs and stick-nest rats (*Leporillus conditor*) may possibly preferentially forage on seedlings in diggings because of their increased density and higher palatability from the improved growing conditions within the diggings (Noble *et al.* 2007b).

Extensive studies of porcupine diggings in arid areas in Israel have found that the main effect of diggings on landscape level productivity and diversity is through increased productivity and diversity inside the diggings themselves (Gutterman *et al.* 1990, Alkon 1999). However, most previous research that has demonstrated effects of diggings by semi-fossorial species on plant productivity has been in higher rainfall areas than Arid Recovery (e.g. Whitford 1998), or in more arid regions where rocky areas have been shown to be important in enhancing surface flows to the diggings (e.g. Boeken *et al.* 1998). Thus further and more detailed studies of productivity and diversity in diggings at Arid Recovery would be essential in understanding the overall importance of these diggings in landscape functioning at the Reserve.

3.4.2 Relationships of diggings to diet

Although the possible ecological effects of diggings may be very important for the restoration of arid environments (Martin 2003), the most immediate importance of diggings for bilbies and bettongs is as a means of obtaining food. Many species like Indian porcupines, long-nosed potoroos, and several North American rodents are thought to dig almost exclusively for a single type of food such as underground bulbs and tubers, fungi, and seeds respectively (Claridge *et al.* 1993, Alkon 1999, Whitford and Kay 1999), making it relatively easy to relate these diggings to specific objectives. However, the reason that bilbies and bettongs dig is much less clear, as their omnivorous diet offers many possible reasons for digging. Observations of the shape and locations of diggings at Arid Recovery suggests that at least some of the diggings were for termites, spiders, root-dwelling larvae, seed-harvester ant nests, seeds and roots (Bice and Moseby 2008, Chapter 6, personal observation).

Negative correlations between the rate of digging and the bilbies dietary consumption of sand, and positive correlations with consumption of grass seed, suggest that at times of lower digging rates, bilbies were consuming more sand per digging or digging larger diggings to obtain fewer grass seeds. As bilbies are thought to obtain many of their seeds from seed caches of harvester ants (Gibson 2001, Chapter 4), they may be forced to utilise smaller and possibly deeper caches after the more readily accessible caches are used. As the rate of digging might then decrease because of the decreasing success rate, or because of resulting population declines, these correlations, like track transects and spotlighting counts (Bowen and Read 1998), are unable to separate changes in animal numbers from changes in overall activity. Such scenarios based on correlations of limited numbers of points over only a nine month time period must be considered speculative until confirmed by further studies, as it is easy to confuse correlation with causation (Johnson 2002).

3.4.3 Temporal variability of digging rates

The amount of variation in digging rates of the bilbies and bettongs with time was much greater than that found by studies of other semi-fossorial Australian mammals. The rate of digging varied 8-fold in Dune, 10-fold in Mulga and 18-fold in Swale over the 19 month period of the study, a much greater variation than the 3.2-fold variation measured by Garkaklis *et al.* (2004) for brush-tailed bettong (*Bettongia penicillata*) diggings, and 2-fold variation with season for diggings by long-nosed potoroo (*Potorous tridactylus*) (Claridge *et al.* 1993). Both brush-tailed bettongs and long-nosed potoroos dig mainly for subterranean fungi, while both bilbies and bettongs dig for a greater range of food types (Bice and Moseby 2008, Chapter 6). The greater variation in rates of digging found in this study may also relate to the shorter periods used for determining the digging rates – two weeks as compared to one month (Claridge *et al.* 1993) and three months (Garkaklis *et al.* 2004). The large variation in overall digging rates between sampling sites and between sampling times, and the considerable variations in diet of both bilbies and bettongs between three month sampling periods (Bice and Moseby 2008, Chapter 4) all suggest that higher rates of digging may occur in relatively short pulses as animals access seasonally available foods. This shorter-term variability may have been recorded more frequently by the shorter sampling periods used in this study resulting in the overall greater variability of digging rates.

The strong correlations of track transect and spotlighting counts of bilbies but not of bettongs with both the rates of digging and area of disturbance over the period of this study suggest that changes in bilby activity and/or numbers with time might be a factor in the variability in rates of digging over time. The high, but variable, percentage of sand by volume (5 to 76%) of bilby faecal pellets compared with on average only 5% sand in bettong pellets (Chapter 4) supports this suggestion that bilbies dug more frequently than bettongs. Correlation of track counts of bilbies with areas of disturbance was unexpected because of the lack of correlation over time between area of disturbance and rates of diggings. This correlation might be an artefact related to the small number of measures used for these correlations, or may indicate that bilbies are attracted to disturbed areas when foraging, and thus forage more widely when more areas are disturbed. Mallick *et al.* (1997) found that the number of diggings by eastern barred bandicoots (*Perameles gunnii*) was correlated with numbers of animals trapped at the monitoring site. However, digging rates for brush-tailed bettong were not correlated over time with animal numbers as determined by trapping at the digging monitoring sites (calculated from data in Garkaklis *et al.* (2004).

The calculated digging rate of 120 diggings individual $^{-1}$ night^{-1} is comparable to the 38 to 114 diggings individual^{-1} night^{-1} calculated by Garkaklis *et al.* (2004) for brush-tailed bettongs, considering the uncertainties of the estimates of the number of animals digging during the current study, and differences in species, and in habitat between studies. Soil turnover per ha was similar in both studies, though the estimated annual turnover per animal was six times higher in the current study partly because of the larger average volumes of bilby and bettong diggings.

The rates of digging were directly correlated with minimum overnight temperatures, suggesting that the animals dug more on warmer summer nights when the minimum temperature was highest. Subterranean termites, and possibly other invertebrates at Arid Recovery are more active on warmer nights (J. Read, personal communication, 2003), and thus may be easier for bilbies and bettongs to locate and access at these times.

The rates of bilby and bettong digging showed only limited correlation with rainfall, possibly because of the variability between plant species in their responses to different rainfall events (Noy-Meir 1973), and because bilbies and bettongs may forage by digging for invertebrates and roots as well as plant foods (Bice and Moseby 2008). In addition, bilbies may obtain many of their dietary seeds, especially the very small grass seeds, *Dactyloctenium radulans* and *Sporobolus actinocladus,* from ant seed caches (Gibson 2001, Southgate and Carthew 2006, Chapter 4) that might make seeds available for much longer periods than the limited periods of seed production (Bice and Moseby 2008, Chapter 4), and thus would lessen any correlation of digging rate to rainfall.

The calculated intensity and duration of moonlight was not correlated with the rate of digging. Some small rodents are known to change their foraging behaviour in response to moonlight, presumably to avoid visually-orienting predators (Bowers 1988, Abramsky *et al.* 2002), but this may be less important for the relatively large bilbies and bettongs that have fewer natural predators. However, the even larger Indian crested porcupines were found to be less active in moonlight in winter but not the summer (Alkon and Saltz 1988). It is thus possible that the calculated moonlight intensity was not sensitive enough to detect variations in the digging activity of bilbies and bettongs with moonlight that might only occur around the extremes of full and new moons. Alternatively, changes in moonlight might affect the total length of foraging, but not the rate of digging. Digging rates might be also be affected by cloud cover which would reduce the sensitivity of this analysis which did not include cloud cover as a variable.

The relative importance of these environmental factors and changes in seed availability and animal numbers in determining the considerable differences in rate of digging over time cannot be determined from these correlations. Causation can most confidently be ascribed to correlation by the presence of credible mechanisms (Johnson 2002). Logically, a change in animal numbers/activity would likely result in a change of the rate of digging. The much greater variation in digging numbers than in animals numbers/activity suggested by track transects suggests that other factors were also important. The correspondence of the lowest rate of digging in July and September 2004 with times of high consumption of plant foods and berries by both bilbies and bettongs, and low consumption of grass seed (Chapter 4) suggests that changes in diet were important in changing the rate of digging. Temperature and rainfall are most likely secondary factors, as they affect diet through changes in food availability.

3.4.4 Habitat use

Information on the differential use of habitats by bilbies and bettongs is important for evaluating the value of each habitat type for the maintenance of populations of these species, and to assist evaluation of possible new sites for their reintroduction. The relative rates of digging between the three main habitats were significantly different from the relative areas of these habitats, suggesting preferential use of Dune and Mulga habitats, and avoidance of Swale. However, the relative rates of digging in each habitat type may not directly reflect habitat use as bettongs, and to a lesser extent bilbies, consume considerable amounts of plant material and invertebrates that might not require digging, and therefore may spend considerable time in areas without digging. Information from rates of digging cannot be analysed by species between bilbies and bettongs, as bilby diggings could not be distinguished from bettong diggings, and frequently diggings appeared to have been explored and/or redug by a second animal of either species (personal observation).

Despite these limitations in determination of habitat use of both bilbies and bettongs by digging rates, diggings are a definite indication of the presence of an animal, and presumably of its attempts to obtain food. The relatively high use of Mulga is of interest, as it suggests that this relatively small habitat, about 12% of the study area, may be important as a source of food for bilbies and/or bettongs. At a finer scale, the relatively high frequency of digging at some of the digging monitoring sites, particularly one of the Mulga sites, suggests that some characteristic of these sites may be of particular value to bilbies and/or bettongs. Further surveys comparing sites that were comparatively digging-rich during this study with those where digging rates were consistently lower might give useful information on characteristics of “preferred” bilby and/or bettong habitat.

A comparison of habitat use based on rates of digging from this study with habitat use of both bilbies and bettongs based on radio-tracking during studies at Arid Recovery about three years earlier (Moseby and O'Donnell 2003, Finlayson and Moseby 2004) suggests a 50% decrease in use of Dune habitat and 6-fold increase in use of Mulga habitat by bilbies between the two studies, but very little change in habitat use for bettongs. However, because of the differences between the two monitoring methods, it is not possible to conclude that this comparison demonstrates a real change in habitat use. Further research comparing habitat use as shown by rates of digging directly with that shown by radio-tracking might lead to improved estimates of the relative importance of different habitats to both bilbies and bettongs.

Other studies have found that different methods of evaluating habitat selection give differing results. Claridge *et al.* (1993) found that the patterns of long-nosed potoroo foraging diggings differed somewhat from the distribution of the animals located by trapping. However as the relative habitat usage Claridge *et al.* (1993) measured for long-nosed potoroos by foraging diggings was opposite to that measured in a separate study on the closely related long-footed potoroo (*Potorous longipes*) by radio-tracking, the authors suggest caution is needed when interpreting habitat use data obtained by a single method.

3.4.5 Use of diggings for monitoring population levels

Monitoring of animal numbers is an important part of the management of a fenced reserve like Arid Recovery (Caughley and Sinclair 1994, Engeman 2005), but is especially difficult for bilbies as they are nocturnal and trap shy. At Arid Recovery, counting of the number of animal tracks crossing a walked transect has proved to be the best available method for obtaining relative population estimates, but this depends on calm, dry weather, suitable lighting, and skilled reading of tracks (Southgate *et al.* 2005) and can only be done on Dunes, as tracks are not visible on the harder Mulga and Swale soils. Smaller tracks of juvenile bilbies may be sometimes missed, or lost among tracks of spinifex hopping-mice (personal observation). Recently improvements to the monitoring technique by mechanically smoothing the transects to increase the range of potentially suitable weather conditions has made more regular monitoring possible (Arid Recovery 2007). Spotlighting is probably a less useful method of monitoring bilby and bettong numbers at Arid Recovery, as it appears to be even more influenced by variations in animal activity during the short period of time that animals are counted (Bowen and Read 1998, Edwards *et al.* 2000) and thus gives more variable results than the all-night counts from track transects. However, as spotlighting is applicable to all habitats, especially Mulga and Swale where track transects are not possible, it supplies worthwhile additional information on patterns of changes in animal activity and/or numbers.

The correlation of rate of digging and disturbance to track transects of bilbies suggests that regular surveys of either or both of these factors could be a useful additional tool for monitoring bilby populations and/or activity at Arid Recovery. Rate of digging can measure animal activity over longer periods than track transects, and thus reduce the influence of short-term fluctuations in activity on the monitoring. In addition, digging rate is able to provide comparative measures of habitat use in all three major habitats. Data on rates of digging can also be combined with dietary analysis of bilby faecal pellets to confirm trends in consumption of various dietary items suggested by dietary analysis. However, digging rates share many of the same limitations as tracks and spotlighting for monitoring animal numbers as they may vary with temperature, rainfall, and changes in levels of activity (Edwards *et al.* 2000).

3.4.6 Conclusion

This chapter presents four ways that monitoring the rate of digging and the effects of diggings have increased understanding of the overall role of bilbies and bettongs at Arid Recovery: (a) use of rate of digging for monitoring animal numbers, (b) relationships of rate of digging to dietary intakes, (c) the collection of seeds in diggings, and (d) the facilitation of seedling growth by diggings. Further research over longer time periods and different climatic conditions is needed to confirm the importance of these roles of diggings at Arid Recovery. Similar studies at other locations would be important to increase understanding the overall ecological roles of diggings along rainfall gradients, and the importance of diggings in maintaining landscape heterogeneity.

CHAPTER 4 The diet of reintroduced greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) in arid South Australia

4.1 INTRODUCTION

Greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) are medium-sized, semi-fossorial marsupials that were both once widely distributed over much of Australia. However, their ranges and abundance have declined dramatically since European settlement (Southgate 1990a, Short and Turner 1993). The distribution of the bilby is now less than 20% of its former range, where it survives only in relatively unproductive areas such as the Tamami, Gibson and Great Sandy Deserts (Southgate 1990a). The burrowing bettong persists only on three off-shore islands (Short and Turner 1993). Both species are classified nationally as vulnerable (Maxwell *et al.* 1996, Pavey 2005).

Bilbies and bettongs have been reintroduced to predator-free reserves within their former range, including the site of this study, Arid Recovery, in South Australia, as part of a national recovery effort for these species. Arid Recovery is a 60 km^2 reserve surrounded by a 1.8 m high predator-proof fence. All feral cats, foxes and rabbits have been removed from the Reserve, and four locally extinct species reintroduced, including bilbies and bettongs. One of the main objectives of Arid Recovery is to facilitate the ecological restoration of arid ecosystems through the removal of feral predators and herbivores, and the reintroduction of locally extinct species (Maxwell *et al.* 1996, Arid Recovery 2006). However, as bilbies and bettongs have been locally extinct for over 50 years, little is known about their ecological roles in these arid ecosystems, information which would assist in setting realistic restoration goals (Hobbs 2007).

Both greater bilbies and burrowing bettongs are omnivorous, with seasonally variable diets, probably depending on the availability of food resources (Gibson 2001, Robley *et al.* 2001). The diet of bilbies in remnant wild populations is often skewed towards either predominately insectivory or granivory depending on the locality and habitat (Smyth and Philpott 1968, Watts 1969, Southgate 1990b), while bettongs are largely herbivorous (Robley *et al.* 2001). Monitoring of the bilbies and bettongs diet at Arid Recovery for the first 18 months after their reintroductions showed these species had little dietary overlap and therefore indicates different dietary strategies for surviving in unpredictable and harsh environments (Bice and Moseby 2008).

As perameloids, bilbies have a simple gut, and hence limited fermentation capacity (Johnson 1989). They are therefore dependent on the availability of more nutritious foods like seeds and invertebrates (Southgate and Carthew 2006). Southgate and Carthew (2006) found that the decline in one bilby population was preceded by an increased intake of invertebrates possibly to compensate for decreased availability of plant material, including seeds. Bilbies have relatively low stores of body fat, and may therefore be vulnerable to periods of low food availability (Gibson and Hume 2000).

On the other hand burrowing bettongs, like other potoroids, have an enlarged sacciform forestomach in which microbial fermentation can take place, enabling them to digest fungi and fibrous vegetation like roots and bark (Johnson 1996, Strahan 2000). Thus, unlike bilbies, they are biologically suited to changing their diet to more continuously available fibrous plant material when seeds and digestible vegetation become difficult to obtain. However Noble *et al.* (2007a) suggests that bettongs probably specialised on juvenile foliage of seedlings when available, as the volume of their digesta might be insufficient to meet their energetic needs on more high fibre foods. Thus, like the closely-related rufous hare-wallaby (*Lagorchestes hirsutus*), the more fibrous diet available at times of low productivity might be sub-optimal for the needs of the bettongs (Lundie-Jenkins *et al.* 1993).

Populations of both bilbies and bettongs, like many other mammalian species in arid Australia, are thought to move to better habitat or decline during dry periods (Southgate 1990a, Short *et al.* 1998, Dickman *et al.* 1999, Finlayson 1958 in Noble *et al.* 2007b). The low reliance of bettongs on ephemeral foods, and its ability to store fat in its tail (Short and Turner 1999) may make bettongs more able to “sit out” droughts than bilbies (Bice and Moseby 2008). However, the relatively high breeding rates of both species make them able to respond quickly to the return of better conditions (Short and Turner 1999, Southgate *et al.* 2000).

This dietary study is part of a wider project on the role of reintroduced bilbies and bettongs in ecological restoration of arid ecosystems at Arid Recovery. This wider project focused on the interactions between these reintroduced species and soil seed banks, due to the ecological importance of arid seed banks, and as they are potentially affected by both trophic activities and the ecosystem engineering effects of bilbies and bettongs diggings. This dietary study therefore focused on the following questions: 1) What species of seeds are in the diets of bilbies and bettongs? 2) How does the consumption of these species of seeds vary with time? 3) How much dietary overlap is there between bilbies and bettongs?

This chapter also compares the diet of bilbies and bettongs during this study to their diet at Arid Recovery in 2000/2001 for the first 18 months after their reintroductions to the Reserve (Bice and Moseby 2008). This comparison was of particular interest since the populations of both species had increased three to seven-fold between the two studies (Arid Recovery 2005), and as confined populations, these animals are not free to seek new resources in response to environmental stress and decreased food availability.

4.2 METHODS

4.2.1 Study site

Arid Recovery (30°29'S, 136°53'E) is located approximately 20 km north of Roxby Downs in central South Australia. The Reserve is divided into four sections for ease of management, and the endangered species were first reintroduced into the 14 km^2 main enclosure, where this dietary study was conducted. Thirty burrowing bettongs (*Bettongia lesueur*) were reintroduced in September 2000 and nine greater bilbies (*Macrotis lagotis*) in April 2001. For further information on Arid Recovery, refer to Chapter 2.

The Reserve contains a range of habitats including longitudinal sand dunes dominated by sandhill wattle (*Acacia ligulata*) and sticky hopbush (*Dodonaea viscosa*), clay inter-dunal swales dominated by the chenopods bladder saltbush (*Atriplex vesicaria*) and low bluebush (*Maireana astrotricha*) and patches of mulga (*Acacia aneura*) woodlands sandy-clay soils.

Arid Recovery is located in the Australian arid zone with a long-term average rainfall of 166 mm, though this is very unpredictable and variable (Read 2002). Average monthly rainfall was very similar between the study of Bice and Moseby (2008) and this study (2000/01 – 15.6 ± 5.0 mm; 2003/04 – 15.2 ± 4.9 mm). However, the timing of the rainfall was quite different, with summer (December to March) rain much higher in 2000/01 than 2003/04 (72.3 and 21.5 mm respectively), and winter (May to August) totals slightly lower in 2000/01 (80.5 and 101.8 mm) (Figure 4.1).

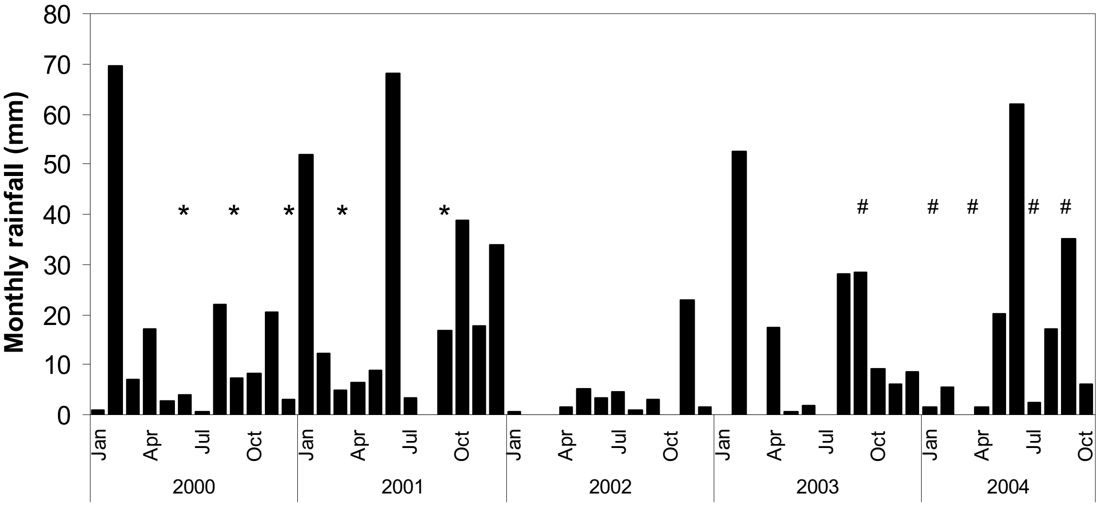


Figure 4.1: Monthly rainfall (mm) at Arid Recovery for 2000 to 2004. * indicates the 2000/01 sampling periods for Bice and Moseby (2008), # indicates the 2003/04 sampling periods for this study.

4.2.2 Bilby and bettong population monitoring

4.2.2.1 Population estimates

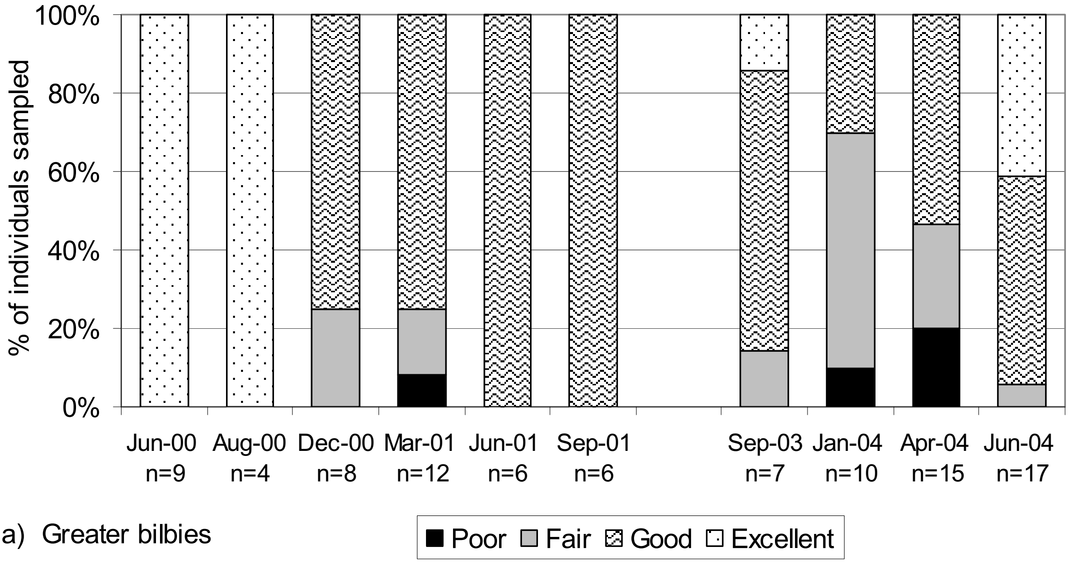
The bilby population in the 14 km^2 main enclosure of Arid Recovery, where this study was conducted, increased substantially from about 20 animals in September 2001 at the end of Bice and Moseby (2008) diet study, to an estimated 150 to 200 in 2003 and 2004 (Arid Recovery 2004, 2005). Bettong numbers increased from about 55 animals in September 2001 (Bice and Moseby 2008) to an estimated 150 to 200 in 2003 and 2004 (Arid Recovery 2004, 2005).

The regular monitoring by Arid Recovery of bilby and bettong track numbers in the main enclosure suggests that the bilby population was declining substantially over the period of this study, from a high in December 2003 to a low in November 2004 (Arid Recovery 2005). The size of the change is unknown as track transects only give a relative estimate that may be affected by changes in animal activity patterns (Edwards *et al.* 2000, Morris 2003, Robley *et al.* 2004) as well as changes in actual animal numbers. On the other hand, track numbers suggested the bettong population/activity increased over the period of this study from a low in December 2003 (Arid Recovery 2005).

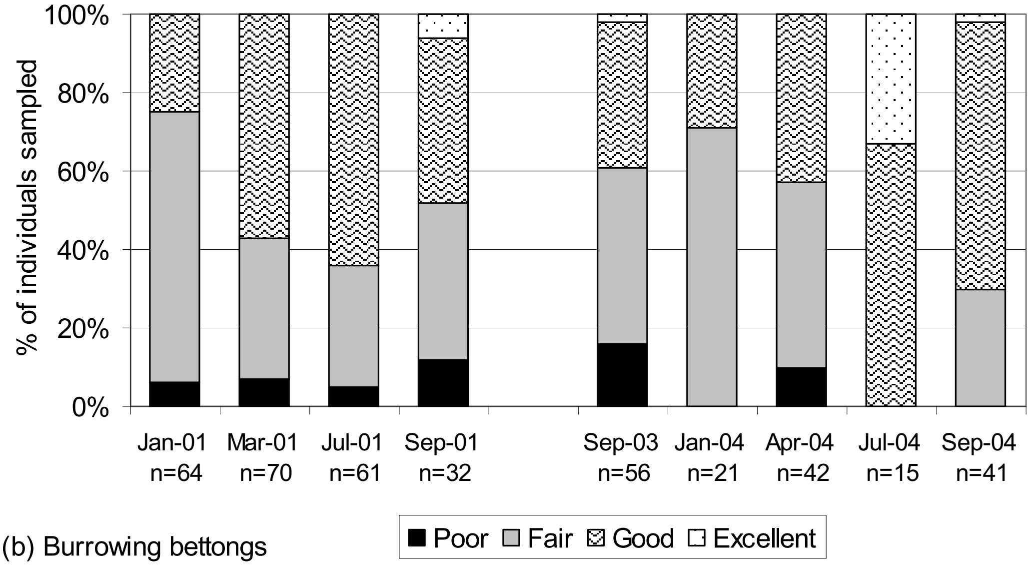
4.2.2.2 Body condition

The body condition of the bilbies and bettongs at the time of the 2000/01 (Bice and Moseby 2008) and this 2003/04 diet study were compared to determine if there were differences in the physical condition of the animals between the two studies (Figure 4.2). The condition of individuals of both species that were captured during Arid Recovery's regular monitoring (Arid Recovery, unpublished data) was assessed using a relative condition score of poor, fair, good or excellent determined by feeling the amount of fat present over the vertebrae and pelvis (Moseby and O'Donnell 2003). As this assessment is subjective, these comparisons of condition between the studies might have been affected by the use of different observers at the different times.

Body condition of bilbies decreased markedly after supplemental feeding was withdrawn in June 2000 (Moseby and O'Donnell 2003), and then remained relatively constant during the rest of the 2000/01 study (Figure 4.2). In 2003/04, bilby condition was relatively low in January 2004, when eight of the ten animals assessed were juveniles, which have significantly lower condition than adults (Arid Recovery, unpublished data). Both bilby and bettong condition increased markedly in July 2004 following 62 mm of rain in early June.



(a) Greater bilbies



(b) Burrowing bettongs

Figure 4.2: The body condition of individual (a) greater bilbies and (b) burrowing bettongs as determined during regular monitoring by Arid Recovery (unpublished data) for time periods approximating the 2000/01 (Bice and Moseby 2008) and this studies 2003/04 diet sampling periods. Body condition is a relative condition score of poor, fair, good or excellent determined by feeling the amount of fat present over the vertebrae and pelvis.

Table 4.1: The percentage of captured adult female bilbies and bettongs at Arid Recovery that were reproductively active (had an active pouch) by year of capture. Individual animals were only counted once per year, and were counted as reproductively active if they had an active pouch at any time during the year. n = total number of adult females captured.

	Percent adult females with active pouches				
	2000	2001	2002	2003	2004
Greater bilby	100% (n=5)	100% (n=9)	0% (n=15)	50% (n=2)	4% (n=23)
Burrowing bettong	60% (n=10)	95% (n=22)	32% (n=34)	71% (n=31)	18% (n=45)

4.2.2.3 Reproductive condition

The percentage of adult females of both bilbies and bettongs that were reproductively active was calculated from all bilbies and bettongs that were captured at Arid Recovery between 2000 and 2004 as a further indicator of the overall condition of the animal populations (Arid Recovery, unpublished data) (Table 4.1). All captured animals were weighed, and reproductive condition was assessed. Animals with pouch young or large lactating teats were considered to have active pouches (Moseby and O'Donnell 2003). Bilbies >600 g and bettongs >900 g were considered to be sexually mature (Short and Turner 2000, Southgate *et al.* 2000).

The percentage of adult female bilbies that were reproductively active declined considerably between 2000/01 and 2003/04 (Table 4.1). These figures might underestimate the reproductive activity in 2003/04, as female bilbies may be reluctant to leave cover when carrying young, similar to female western barred bandicoots (Short *et al.* 1998), and thus were underrepresented by hand netting surveys (personal observation). Breeding rate for bettongs was considerably lower in 2004 than during 2000/01.

4.2.3 Collection of faecal pellets

Fresh faecal samples were collected during sampling periods in September 2003, January 2004, April 2004, July 2004 and September 2004. These samples were collected opportunistically from either in front of active burrows, the spoil heaps of new diggings, or for bettongs, from animals captured in cage traps. During a single sampling period, samples were collected from different areas of the Reserve to assure they were as independent as possible. Only one pellet was collected from any single location. The faecal pellets of bilbies and bettongs were easily distinguished, as bettong pellets are relatively long and narrow with a pointed end and contain predominately vegetation, while bilby pellets are broader, shorter and with relatively broad ends and a high sand content.

4.2.4 Faecal analysis

The faecal samples were analysed using similar methods to Gibson (2001), Southgate and Carthew (2006) and the macroscopic method used by Bice and Moseby (2008). The microhistological analysis used by Bice and Moseby (2008) and Robley *et al.* (2001) to further identify leaf and stem material to species level was not used in this study as the identification of individual plant species was not required.

Ten bilby and six bettong pellets were analysed for most sampling periods, except for September 2003 (six bilby and six bettong) and September 2004 (eleven bilby and seven bettong). The pellets were sub-sampled to 0.6 g and then soaked overnight in water. The samples were then teased apart and suspended in water in a petri dish. A numbered 1 cm x 1 cm grid was attached under the petri dish to aid quantification, and the sample was examined under a dissecting microscope at 10x magnification.

Fifty-two grid squares were examined for each sample. The number and percentage area occupied by each item in each grid square was estimated and recorded (Gibson 2001).

Food items were classified as invertebrates, plant material (other than seeds), fungi, seeds or fruit using a reference collection established during Bice and Moseby's (2008) study. Seeds were identified to genus or species level where possible, using a reference collection of known seed species (maintained at Arid Recovery), and reference books: Cunningham *et al.* (1981), Jessop (1981), Kutsche and Lay (2003) and Sweedman and Merritt (2006). Most seeds were identified from seed coats or parts of seeds, though a few whole seeds were found. Seeds of *Enchylaena tomentosa* were classified as berries, as the single sampling time that these seeds were found in the faecal pellets coincided with a high fruiting period of this species (personal observation).

Faecal analysis was used to determine the diet of bilbies and bettongs as samples are easy to collect and the method does not involve killing or disturbing the study animals (Norbury and Sanson 1992). However, faecal samples may not reflect the proportions of dietary items ingested by the study animals due to the differential digestion (Norbury and Sanson 1992). Some dietary items, such as soft-bodied invertebrates, may be either completely or almost completely digested and therefore not detected (Dickman and Huang 1988), while, harder, less digestible particles, such as hard seed coats, may be overestimated in comparison to more easily digested items (Luo *et al.* 1994).

4.2.5 Endozoochory

As intact seeds were found in some faecal pellets of both bilbies and bettongs, the viability of these seeds was assessed to determine whether these animals could potentially be dispersal agents for these seeds (endozoochory). Six pellets, which had been stored in a refrigerator, from each of the four later sampling periods (January, April, July and September 2004) were broken up and spread over the surface of trays of potting mix. The samples were kept in an unheated greenhouse and regularly watered for three months (January to March 2005). Seedlings were then counted and identified. No seedlings germinated from the four control seed trays that contained only potting mix.

4.2.6 Data analysis

Dietary composition was expressed as both the frequency of occurrence in individual faecal pellets and proportional abundances (% volume of faecal pellets). Percentage volumes were calculated separately for the food components of the pellets and for sand so the data could be compared between species, and with data from the earlier dietary study of Bice and Moseby (2008).

Changes in diet by dietary category over time were compared using non-parametric Kruskal-Wallis tests. Spearman's rank correlations were used to test for correlations between rainfall patterns and consumption of different food categories. Chi-squared analyses were used to test for differences in percentages of different classes of seeds between this study and that of Bice and Moseby (2008). The analysis was carried out using JMPIN 4.0.4 (SAS Institute 2001) software.

Dietary overlap for seed consumption between the bilbies and bettongs, and between this study that of Bice and Moseby (2008) was estimated with the Proportional Similarity Index (PSI):

$$\mathrm{PSI} = 1 - 0.5\,\Sigma\,(\,|P_i - Q_i|\,)$$

where P_i is the proportion of species *i* in the diet of the animal P, and Q_i is the proportion of species *i* in the diet of animal Q. The PSI, expressed as a percentage, ranges from 0 (no overlap) to 100% (identical diets) (Feinsinger *et al.* 1981).

4.3 RESULTS

4.3.1 Overall dietary composition

A total of 47 bilby and 33 bettong faecal pellets collected over five sampling periods in 2003 and 2004 at Arid Recovery were analysed for their basic dietary components excluding sand (Table 4.2). Both species were omnivorous throughout the year, consuming a wide variety of both invertebrate and plant food items.

Table 4.2: Overall dietary composition of bilbies and bettongs expressed as frequency of occurrence in faecal pellets (%) and average volume of faecal pellets (%) occupied by each dietary category. The volume of sand in the pellets was not included in this analysis.

Dietary Categories	Greater Bilby (n = 47)		Burrowing Bettong (n=33)	
	Freq. of Occur. (%)	Volume (%)	Freq. of Occur. (%)	Volume (%)
Invertebrates	100	37.4	57.6	5.1
Plant material	89.4	18.5	100	64.3
Seeds	85.1	19.7	57.6	15.7
Berries	21.3	4	27.3	13
Fungi	36.2	6.5	0	0
Unidentified	91.5	13.8	12.1	1.9

Invertebrates occurred in all bilby faecal pellets, and formed the largest volume of all the dietary categories (Table 4.2). The largest component of this dietary category consisted of remains of termites, which occurred in 95% of the pellets. Traces of ants were recorded in 66% of the pellets. A sample of the few whole ants found in the pellets were identified as either *Monomorium D* or *Pheidole black* (John Read pers. comm., 2005), both genera that include some seed-harvesting species (Vander Wall 1990). Other invertebrates present included beetles and larvae.

Seeds and other plant material were the next largest dietary categories in bilby pellets, both present in similar frequency and volume. The plant material was mainly soft tissues.

The largest food category in bettong pellets was plant material, occurring in all of the pellets and occupying an average of 64% of the faecal volume (Table 4.2). This material included considerable amounts of coarse material that appeared to be bark and woody fragments. The remaining volume of bettong pellets was mostly seeds, including seeds from *Enchylaena tomentosa* berries, and a smaller proportion of invertebrates, which were predominately beetles and larvae, with only traces of termites and ants.

Fungal spores were found in 36% of bilby faecal pellets. Over half of these pellets contained 20% to 46% spores by volume, excluding sand. No fungal spores were found in bettong pellets.

Large amounts of sand (average 47% volume - range 27 to 76%, with 1 pellet with only 5%) were present in all of the bilby pellets. Only an average of 4.7% by volume sand (maximum of 6.9%) was present in 66% of the bettong pellets during the first 3 sampling times, while no sand was found in bettong pellets in the last two sampling times in July and September 2004.

4.3.2 Seasonal variation

The proportions of foods by dietary category in bilby faecal pellets did not vary significantly seasonally, except for plant material ($H = 21.8$, d.f. = 4, $p < 0.001$) that was high in July 2004 and then low in September 2004 (Figure 4.3a). Although the seasonal changes in the fungal content of the pellets were not significant ($H = 8.1$, d.f. = 4, $p = 0.09$), fungal content dropped to very low levels during the driest sampling period (April 2004). Very few spores were detected in July 2004 despite good rain six weeks before sampling. The proportion of invertebrates was fairly constant except for a peak in April 2004. The proportion of seeds was also fairly constant between sampling times except for September 2004, when the animals were eating large quantities of *Enchylaena tomentosa* berries, and consumption of other seeds dropped markedly.

The proportions of foods by dietary category in bettong pellets showed greater seasonal variation than those of bilbies (Figure 4.3b). Plant material, other than seeds and berries, showed the greatest variations, from a high of 100% of the faecal volume in July 2004 to a low of 28% in September 2004 ($H = 23.1$, d.f. = 4, $p < 0.001$). Seeds also varied significantly between sampling periods ($H = 23.1$, d.f. = 4, $p < 0.001$) with the highest percentage volumes during September 2003 and September 2004. Invertebrate volume also varied significantly between a high of 15% faecal volume in January 2004 to none in July 2004 ($H = 11.3$, d.f. = 4, $p = 0.02$).

4.3.3 Consumption of seeds

More seed species were found in bilby faecal pellets (22 species, Table 4.3a) than those of bettongs (13 species, Table 4.3b). Overlap between the seed species that were recorded in the pellets of bilbies and bettongs was very low (Proportional similarity index, PSI: 0.10), with even less overlap for each sampling period (PSI: 0 to 0.06). If *Enchylaena tomentosa* is included with seeds, the PSI for September 2004 was very high at 0.8, as both bilbies and bettongs fed on large quantities of the fleshy berries of this plant at this time.

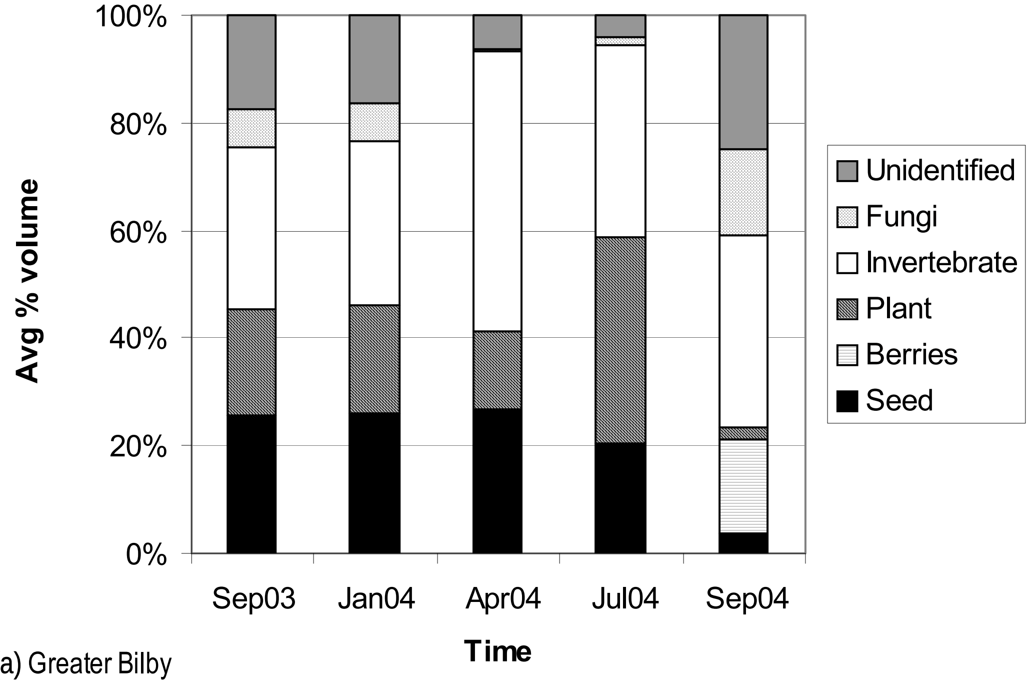
The species of seeds consumed varied between sampling periods for both bilbies and bettongs. For the bilbies, the highest number of seed species recorded from a sampling period was in January 2004 (16 species), while only four seed species were recorded in July 2004. The seeds of only two species, both grasses (*Paractaenum novae-hollandiae* and *Sporobolus actinocladus*), were recorded during all sampling periods. Only five species of seed were recorded occupying over 20% of the volume of any single bilby faecal pellet: two grass (*Dactyloctenium radulans* and *Sporobolus actinocladus*), one forb (*Zygophyllum ammophilum*) and two shrub species (*Dodonaea viscosa* and *Enchylaena tomentosa*).

For bettongs, the highest number of seed species recorded from a sampling period was also in January 2004 (8 species), while no seeds were recorded for July 2004. Four shrub and tree species (*Acacia* spp.*, Alectryon oleifolius*, *Dodonaea viscosa* and *Enchylaena tomentosa*) and one unknown seed species were recorded occupying over 20% of the volume of single faecal pellet.

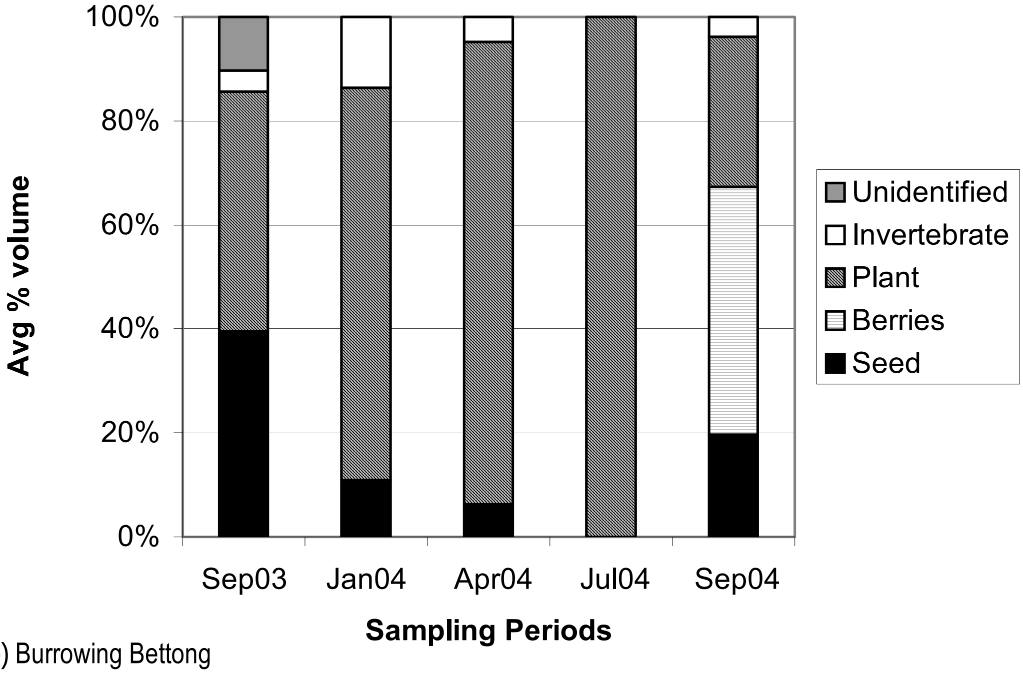
4.3.4 Endozoochory

Two plant species, both of which had been observed as seed fragments in bilby pellets from the relevant time point, germinated from bilby pellets. Eleven seedlings of *Dactyloctenium radulans* grew from four faecal pellets collected in January 2004, and one seedling from one pellet collected in July 2004. Two *Enchylaena tomentosa* seedlings grew from two pellets collected in September 2004.

Only *Enchylaena tomentosa* seedlings grew from bettong faecal pellets, four seedlings from three pellets collected in September 2004, a time when all surveyed pellets contained *E. tomentosa* seed fragments.



(a) Greater Bilby



(b) Burrowing Bettong

Figure 4.3: Seasonal comparison of the percent of each dietary category for (a) greater bilbies and (b) burrowing bettongs. The berry component consisted solely of *Enchylaena tomentosa* seeds, which would have been consumed as ripe berries. Bilbies: n = 10 (except for September 2003 n = 6, and September 2004 n = 11); bettongs: n = 6 (except for September 2004 n = 7).

Table 4.3: The species of seed and berries (*Enchylaena tomentosa*) recorded in the faecal pellets of (a) greater bilbies and (b) burrowing bettong during the five sampling periods (shown as the percent frequency of occurrence for each sampling period and the average overall total percent volume of the faecal pellets over all sampling periods). The seed species are classified according to the plants life form (grass, forb, shrub and tree) (Kutsche and Lay 2003), and seed size (Sm - smaller than 1 mm in at least 2 dimensions or Lg – larger than 1mm in at least 2 dimensions).

(a) Greater Bilby

Seed Species	Seed Size (mm)	Frequency of Occurrence (%)					Total (avg. % faecal vol.)
		Sept03 n=6	Jan04 n=10	Apr04 n=10	Jul04 n=10	Sept04 n=11	
Grasses							7.1
Aristida sp.	Sm	50%	30%	20%		18%	<1.0
Chloris sp.	Lg	33%					<1.0
Dactyloctenium radulans	Sm	17%	60%	30%	20%		3.3
Enneapogon sp.	Lg			10%			<1.0
Eragrostis dielsii	Sm		20%				<1.0
Paractaenum novae-hollandiae	Lg	33%	40%	20%	10%	9%	<1.0
Sporobolus actinocladus	Sm	50%	100%	10%	10%	36%	2.8
Forbs							9.7
Calandrina eremaea	Sm	33%	20%			18%	<1.0
Portulaca sp.	Sm		10%				<1.0
Sida ammophila	Lg	17%	10%				<1.0
Swainsona sp.	Lg		10%				<1.0
Zygophyllum ammophilum	Lg	67%	50%	70%	70%		8.9
Shrubs and Trees							5.9
Alectryon oleifolius	Lg			10%			<1.0
Dodonaea viscosa	Lg	50%	40%	10%			<1.0
Enchylaena tomentosa	Lg					91%	4.1
Gunniopsis sp.	Sm		10%				<1.0
Halosarcia pergranulata	Sm	67%	10%				<1.0
Unknowns							0.0
Unknown sp. 1	Sm	33%	10%				<1.0
Unknown sp. 2	Sm	33%					<1.0
Unknown sp. 3	Lg	33%					<1.0
Unknown sp. 4	Sm		10%				<1.0
Unknown sp. 5	Sm		10%	10%		55%	<1.0
Number of species		13	16	9	4	6	22

(b) Burrowing Bettong

Seed Species	Seed Size	Frequency of Occurrence (%)					Total (avg. % faecal vol.)
		Sept03 n=6	Jan04 n=6	Apr04 n=6	Jul04 n=6	Sept04 N=9	
Grasses							0.0
Sporobolus actinocladus	Sm		17%				<1.0
Forbs							0.2
Portulaca sp.	Sm	17%	17%				<1.0
Zygophyllum ammophilum	Lg					11%	<1.0
Shurbs and Trees							24.1
Acacia spp.	Lg	67%					5.5
Alectryon oleifolius	Lg	33%	17%	33%			2.8
Dodonaea viscosa	Lg		50%			44%	2.7
Enchylaena tomentosa	Lg					100%	13.0
Halosarcia pergranulata	Sm		17%				<1.0
Maireana sp.	Lg					11%	<1.0
Unknowns							0.0
Unknown sp. 6	Sm		33%				<1.0
Unknown sp. 7	Sm					56%	<1.0
Unknown sp. 8	Sm		17%			44%	<1.0
Unknown sp. 9	Lg		17%				<1.0
Number of species		3	8	1	0	6	13

4.3.5 Changes in diet since reintroduction

The overall composition of the bilby and bettong diets at Arid Recovery was similar between 2000/01 (Bice and Moseby 2008) and 2003/04 (Table 4.4). The greatest differences in the composition of the bilbies' diets between these two studies were a lower proportion of seeds and a higher proportion of fungi in 2003/04. The variation in the proportion of each of the dietary categories between the sampling periods was less for bilbies and greater for bettongs in 2003/04 than 2000/01.

Table 4.4: Comparison of overall dietary composition of bilbies and bettongs at Arid Recovery in 2000/01 and 2003/04, expressed as average volume of faecal pellets (%) occupied by each dietary category and range over sampling periods. The volume of sand in the pellets was not included. Number of sampling periods for both 2000/01 and 2003/04 was 5. Numbers of pellets analysed in each study: 2000/01: bilby –60, bettong – 71; 2003/04: bilby – 47, bettong – 33.

Dietary Categories	Greater Bilby				Burrowing Bettong			
	2000/01		2003/04		2000/01		2003/04	
	Average	Range	Average	Range	Average	Range	Average	Range
Invertebrates	38.1	16.4 - 88.7	37.4	30.1 - 52.2	6	0.3 - 9.8	5.1	0 - 13.2
Plant material	23.2	2.4 - 42.2	18.5	2.2 - 38.3	58.2	38.5 - 81.9	64.3	28.9 – 100
Seeds and berries	33.2	8.6 - 52.6	23.7	20.4 - 26.9	32.4	10.3 - 47.8	28.7	0 - 67.3
Fungi	1.1	0 - 3.6	6.5	0.2 - 7.4	trace	0 - 0.1	0	0
Unidentified	3.6	0 - 9.8	13.8	4.2 - 24.8	5	0 - 6.9	2	0 - 10.3

Differences in seed species found in bilby and bettong faecal pellets between the two studies were greater for bilbies (PSI = 0.21) than for bettongs (PSI = 0.50). The interspecies overlap in seed and berry consumption between bilbies and bettongs in 2000/01 (PSI = 0.36) (unpublished data, Bice and Moseby 2008) was greater than in 2003/04 (PSI = 0.16).

More seed species were recorded from bilby faecal pellets in 2003/04 (22 species), than in 2000/01 (16 species), although the sampling effort was lower (47 pellets compared with 60 pellets) (Table 4.5). In 2003/04, the faecal volume of grass seeds consumed was lower (though species numbers higher), while the volume of forb and shrub seeds were higher than in 2000/01 (F = 22.7, d.f. = 2, P <0.001). Overall seed consumption, including *Enchylaena tomentosa*, at all sampling times in 2003/04 was between 20 and 26% of total faecal volume, while consumption varied greatly with time in 2000/01, with three sampling times greater than 40% and one, January 2001, at only 9% when beetles and termites formed 89% of the bilby diet.

Average consumption of *Dactyloctenium radulans*, the major grass seed in bilby diet in 2000/01, was 3-fold (10.3% to 3%) lower in 2003/04 than 2000/01, while the average consumption of the second most common grass seed *Paractaenum novae-hollandiae* was 12-fold (8% to 0.6%) lower. The season of peak consumption of *D. radulans* differed between studies. Peak consumption of *D. radulans* in 2000/01 was in March 2001 following rain in January 2001, while consumption in 2003/04 was highest in January 2004 following rain in September 2003. *Paractaenum novae-hollandiae* consumption was high in the June and October 2000 sampling periods (14 and 20% respectively) following 70 mm rain in February, while the highest consumption in 2003/04 was in September 2003 (1.7%) following 50 mm rain in February. These measured peak times are only approximations of actual peaks because dietary intakes were measured at approximately three month intervals.

In 2003/04, the seed species with the highest overall frequency of occurrence, and the highest faecal volume in the bilby faecal pellets was the ephemeral forb, *Zygophyllum ammophilum,* which was not recorded for bilbies in 2000/01 (Table 4.5). *Zygophyllum ammophilum* was consumed during the first four sampling periods in 2003/04, with the highest amounts (17 and 18% by volume) in the two driest sampling periods, April 2004 and July 2004 (Table 4.2). Consumption of *Z. ammophilum* was low in January 2004 (when consumption of seeds from the grasses *Sporobolus actinocladus* and *Dactyloctenium radulans* was highest) and not recorded in September 2004 (coinciding with high consumption of *Enchylaena tomentosa* berries).

Fewer seed species were recorded from bettong faecal pellets in 2003/04 (13 species) than in 2000/01 (15 species) (Table 4.5), possibly related to a considerably lower sampling effort (33 pellets compared with 71 pellets). In 2003/04, almost all of the seeds recorded were shrub or tree species, with only traces of forb and grass species, which was significantly different from 50% shrub and tree species and 24% forb and 24% grass seeds recorded two years earlier (F = 53.6, d.f. = 2, P <0.001).

Table 4.5: Comparison of the percentages faecal volume of seed species, including *Enchylaena tomentosa*, found in pellets from bilbies and bettongs in 2000/01 and 2003/04 (this study). The percentages are averages of the five sampling times for each study. Data based on the dietary components of faecal volume – i.e. total faecal volume less volume of sand in pellets. Data from 2000/01 from Bice and Moseby (2008).

Seed Species	Bilby		Bettong	
	2000/01 n=60	2003/04 n = 47	2000/01 n=71	2003/04 n=33
Grasses				
Aristida sp.	1.2	<1.0		
Chloris sp.		<1.0		
Dactyloctenium radulans	10.3	3.3	3.8	
Enneapogon sp.		<1.0		
Eragrostis dielsii	<1.0	<1.0	<1.0	
Paractaenum novae-hollandiae	8.0	<1.0	<1.0	
Sporobolus actinocladus		2.8		<1.0
Total Grasses (excluding traces)	20.3	7.1	4.5	<1.0
Forbs				
Amaranthus sp.	1.2		3.2	
Boerhavia coccinea	<1.0			
Calandrina eremaea		<1.0	<1.0	
Citrillus sp.			<1.0	
Lotus cruentis	<1.0			
Portulaca sp.	3.1	<1.0	2.3	<1.0
Sida ammophila		<1.0		
Swainsona sp.		<1.0		
Zygophyllum ammophilum		8.9		<1.0
Total Forbs (excluding traces)	4.8	9.7	6.3	0.2
Shrubs				
Alectryon oleifolius	<1.0	<1.0	3.0	2.8
Atriplex sp.			1.3	
Acacia spp.				5.5
Chenopod sp.			<1.0	
Dodonaea viscosa	<1.0	<1.0	1.9	2.7
Enchylaena tomentosa	<1.0	4.1	9.2	13.0
Eremophila longifolia	<1.0			
Gunniopsis sp.		<1.0		
Halosarcia pergranulata	6.2	<1.0	<1.0	<1.0
Maireana sp.				<1.0
Sclerolaena sp.	<1.0		<1.0	
Total Shrubs (excluding traces)	7.2	5.9	16.1	24.1
Unidentified				
Unidentified	1.1		1.7	
Unknown sp. 1		<1.0		
Unknown sp. 2		<1.0		
Unknown sp. 3		<1.0		
Unknown sp. 4		<1.0		
Unknown sp. 5		<1.0		
Unknown sp. 6				<1.0
Unknown sp. 7				<1.0
Unknown sp. 8				<1.0
Unknown sp. 9				<1.0
Total Unid. (excluding traces)	1.1	<1.0	1.7	<1.0
Total % seeds	33.5	23.8	28.6	28.7
Total number species	15	22	15	13

4.4 DISCUSSION

Although bilbies and bettongs were both omnivorous, their diets were distinctly different, reflecting the large dietary differences between perameloids like bilbies that focus on higher energy, more easily digested foods like seeds and invertebrates (Johnson 1989, Gibson *et al.* 2002), and potoroids like bettongs which are able to use coarser, lower energy plant materials (Johnson 1996, Strahan 2000).

4.4.1 Greater bilbies (*Macrotis lagotis*)

The overall diet of the bilbies in this study was broadly similar to that of other bilby populations in arid and semi-arid Australia (Smyth and Philpott 1968, Watts 1969, Southgate 1990b, Gibson 2001, Southgate and Carthew 2006), and to their diet documented three years previously at Arid Recovery just after the bilbies were reintroduced to the Reserve (Bice and Moseby 2008). The bilby is considered an opportunistic generalist as its diet varies in response to the temporal availability of resources (Gibson 2001, Southgate and Carthew 2006). The bilby is unusual among the members of the family Peramelidae in its substantial use of seeds and other plant material, as the diet of other perameloids is generally dominated by invertebrates (reviewed in Southgate and Carthew 2006).

Seeds form an important but variable part of the diet of most bilby populations (Gibson 2001, Southgate and Carthew 2006), including those at Arid Recovery in 2000/01 (Bice and Moseby 2008), and in 2003/04 during the present study. However, the bilbies relative consumption of seeds was a third lower in 2003/04 than in 2000/01, with an overall reduction in the relative consumption of seeds of grasses, and increase in the seeds of forbs.

Seeds of grass species are considered particularly important to the bilby diet (Southgate and Carthew 2006). The relative consumption of grass seeds by the bilbies at Arid Recovery during this study was only a third of that in 2000/01. Although the number of species of grasses consumed was greater in 2003/04, the relative consumption of each species was markedly lower. This decrease in grass seed consumption may be related to decreases in seed availability due to differences in rainfall patterns, especially summer rainfall, between the studies and to increased trophic pressure from increased populations of granivores. Trophic pressure on seeds increased over the two years between the studies, as the populations of bilbies, bettongs and the omnivorous spinifex hopping-mouse (*Notomys alexis*) all increased from three to ten-fold (Arid Recovery 2005).

The differences between the bilbies consumption of all seeds including grass species in 2000/01 and 2003/04 resulted in a very low similarity coefficient of 0.21. Three of four main species consumed were not detected in previous study, or were detected in only trace amounts, while all of the four major species in the earlier study were consumed in much reduced amounts three years later. *Sporobolus* *actinocladus* and *Zygophyllum ammophilum,* two species of seed that by volume together formed nearly half of the bilbies' seed consumption in 2003/04, were not detected in 2000/01.

The consumption in 2003/04 of *Sporobolus actinocladus,* a tiny grass seed that is released from the plant on ripening (Latz 1995), may reflect a difference in productivity of this grass between the two study periods, and/or that the bilbies have learnt over time how to access this tiny seed, possibly from ant seed caches. Bice and Moseby (2008) give a similar example of bilbies learning to exploit new food sources as bilbies only began accessing root-dwelling larvae at Arid Recovery some months after their reintroduction. *Sporobolus actinocladus* was recorded by the annual vegetation monitoring at Arid Recovery at similar densities since 1999 (Arid Recovery unpublished data). Although this does not mean that productivity was similar during the two study periods, it is unlikely that these seeds would not have been available in 2000/01.

Zygophyllum ammophilum was eaten by bilbies mainly when the consumption of grass seeds or *Enchylaena tomentosa* berries was low, suggesting that *Z. ammophilum* was only consumed in the absence of these other species of seeds. There are no other available records of mammalian consumption of *Z. ammophilum* seeds. However, Johnson (1980) reported that two of nine bilby colonies observed consumed up to 35% of the seed of the annual forb *Stylidium desertorum*, showing that the observed high consumption of seeds of an annual forb by bilbies was not an isolated occurrence.

Some species of seeds were consumed by bilbies for all or most of the year during both 2000/01 and 2003/04 and Gibson's (2001) study in southwest Queensland, despite the discontinuous, and rainfall-dependent pattern of seed production for most species in arid areas (Noy-Meir 1973, Lundie-Jenkins *et al.* 1993). This suggests that the bilbies were obtaining these seeds from long-lasting sources including soil seed banks (Reichman 1975), ant seed caches (Johnson 1989, Gibson 2001, Southgate and Carthew 2006), depressions (Reichman 1975) and foraging diggings where seeds have accumulated (Gutterman *et al.* 1990, Chapter 7). At Arid Recovery the soil seed banks do not appear to be important sources of many seeds for bilbies, as no direct relationship was found between amounts of the major dietary seeds consumed by bilbies and the densities of these seed species in the soil seed bank at the different sampling times (Chapter 5).

Mycophagy is widespread among Australian mammals (Claridge and May 1994), and most reported bilby diets include fungi, although in lower amounts than found in this study (Gibson 2001, Southgate and Carthew 2006). In this study, fungal spores were found in 36% of bilby faecal pellets, with the highest content during the sampling periods with the highest prior rainfall. This may reflect temporal variation in food availability, as fungi are rainfall dependent. Although some of the spores may have been accidentally ingested while digging, the very high spore content of some pellets suggests that the fungi, most likely hypogenous species (Southgate and Carthew 2006), were intentionally foraged (Murray and Dickman 1994).

An average of 6.4% by volume of bilby pellets in 2003/04 consisted of fungal spores, distinctly higher than the 1.1% found in 2000/01. This increase in consumption of fungi could represent an increase in availability of fungi due to an increased dispersal of fungal spores through bilby faecal pellets and their foraging diggings (Claridge and May 1994, Johnson 1996). As bilbies, like other bandicoots, have a simple gut, and hence limited fermentation capacity (Johnson 1989), the nutritional value of fungi for these animals is probably limited (McIlwee and Johnson 1998).

4.4.2 Burrowing bettongs (*Bettongia lesueur*)

Burrowing bettongs at Arid Recovery in 2003/04 had a seasonally variable diet that was dominated by plant material, similar to that in 2000/01, and in broad agreement with the diet of reintroduced burrowing bettongs on Heirisson Prong, Western Australia (Robley *et al.* 2001). Like bilbies, bettongs vary their diet opportunistically throughout the year (Short and Turner 1999). Bettongs consumed small amounts of sand during the first three sampling periods, which were all relatively dry, suggesting that they may have been accessing roots and root coverings by digging (Bice and Moseby 2008). However, during the last two sampling periods, after good rain in early June 2004, bettongs consumed chiefly plant material and no sand at all suggesting they were consuming mainly new vegetation and berries. This change in diet was accompanied by a marked increase in body condition.

Differences in the species of seeds consumed by bettongs in 2003/04 compared with 2000/01 suggest that availability of seeds for bettongs, like bilbies, decreased between the two study periods. The decrease in both the relative volume and the number of species consumed was smaller than that for bilbies. However, the consumption by bettongs of larger hard-coated seeds of the shrubs *Acacia* spp., *Dodonaea viscosa* and *Alectryon oleifolius* in 2003/04 was more than twice that in 2000/01. Over half these seeds consumed in 2003/04 were *Acacia* seeds, which were not present in the 2000/01 pellets, and which were consumed at a single sampling period, September 2003. All three of these species of hard-coated seeds were either not recorded or recorded only in trace amounts in the diet of the bilbies in both 2000/01 and 2003/04. Such larger, hard-coated seeds have not been reported in the diet of any other bilby populations (Gibson 2001, Southgate and Carthew 2006), suggesting that bilbies may be reluctant to consume these seeds, either because of their size, or because of the difficulty of chewing the harder coats compared with ingesting other seeds. Captive bilbies were observed to fill their cheeks until bulging with budgerigar seeds, then move around audibly masticating the food (Johnson and Johnson 1983), a behaviour that might be incompatible with larger, harder seeds.

There are no other reports of the species of seeds consumed by bettongs, or by other *Bettongia* species, so it is not possible to determine if the consumption of larger, hard-coated seeds occurs in other bettong populations. Nutritionally, the increase in consumption of these seeds may be advantageous, as *Acacia* seeds, in particular, are highly nutritious (Latz 1995). The increased consumption of this group of hard-coated seeds by bettongs in 2003/04 might reflect differences in availability of these seeds between studies. Seeding times and productivity of Australian arid-zone shrubs have been shown to vary greatly between species, and to depend on subtle interactions between temperature, day length and moisture levels (Friedel *et al.* 1993).

No fungal spores were found in the faecal pellets of the bettongs in 2003/04 and only traces of spores were found in 2000/01. Robley *et al*. (2001) found that at Heirisson Prong, Western Australia, burrowing bettongs relied quite heavily on fungi during winter (19-23% volume) though not during the drier summers (0-2% volume). Fungi have also been shown to be a major component of the diet of other bettong species including *Bettongia gaimardi* (Taylor 1992, Johnson 1994b), and *B. penicillata* (Lamont *et al.* 1985), and *B. tropica* (Johnson and McIlwee 1997). The reason that the burrowing bettongs are not utilising this resource at Arid Recovery, despite fungi being found in 36% of bilby faecal pellets, is unknown, but it is possible that the bilbies are out-competing the bettongs for this odoriferous food source, even though bilbies may be physiologically less suited to fungal consumption than the bettongs (Claridge and May 1994, McIlwee and Johnson 1998).

4.4.3 Endozoochorous dispersal of seeds and fungi

Two plant species, the annual grass, *Dactyloctenium radulans,* and the shrub, *Enchylaena tomentosa,* germinated from bettong and bilby pellets. These pellets had been stored refrigerated for up to a year. More species may have germinated from fresh pellets, or under different germination conditions (Facelli *et al.* 2005). Both bilbies and bettongs could be important seed dispersers as female bilbies travel up to 1 km on their nightly foraging, male bilbies travel up to 3 km, and bettongs up to 750 m (Moseby and O'Donnell 2003, Finlayson and Moseby 2004). Seed ingestion has been shown to enhance the germination of some seed species (Traveset 1998). Germination of *D. radulans* is promoted by fire (Latz 1995) and seed scarification improves germination of both this species, and *Sporobolus actinocladus* (Silcock *et al.* 1990). Thus, in areas such as Arid Recovery where fire is rare, ingestion by bilbies may be important in enhancing the germination of these seeds.

As over a third of bilby pellets contained fungal spores, these pellets may also be important in spreading mycorrhizal fungi, which have the potential to greatly increase productivity and drought resistance of many plant species (Johnson *et al.* 1996). Many mycorrhizal fungi produce their sporocarps under ground and so rely on animals for the dispersal of their spores, either as a direct consequence of their foraging digging activity or through ingesting of the spores (Reddell *et al.* 1997). Spores of some fungal species may also require to be ingested by a mycophagist for germination (Johnson 1996). Information on the importance of mycorrhizal fungi in arid Australia is limited, although mycorrhizal associations have been found in three quarters of both annual and perennial species of plants surveyed in the Simpson Desert (O'Connor *et al.* 2001a), and both annual and perennial grasses in the Namibian Desert (Jacobson 1997).

4.4.4 Diet and population dynamics

The high reproduction rate and good body condition of bilbies at the time of the 2000/01 study suggests that the diet of the animals was easily adequate to support a viable breeding population shortly after the animals were reintroduced to Arid Recovery. The almost complete cessation of reproduction by bilbies before and during this study is more difficult to interpret, as the relationships between cessation of population growth and food availability are complex, poorly understood, and vary between species (Dickman *et al.* 1999). The considerable differences in the bilby diet between 2000/01 and 2003/04, and the lower body condition January and April 2004 both suggest that a sub-optimal diet may have been an important factor in reducing reproductive activity of bilbies at this time, and thus the bilby population may at least in part be limited by food availability. Although availability of different foods was not measured during this study, it is most likely that many of these dietary changes represent changes in food availability (Reichman 1975, Lundie-Jenkins *et al.* 1993, Gibson 2001, Cooke *et al.* 2006). Gibson and Hume (2000) suggested that bilbies might be vulnerable to such periods of low food availability as they have a relatively high field metabolic rate for a mammal living in arid areas. However, although bilby numbers at Arid Recovery since the end of this study have continued to decline during drier months, numbers recover during wetter months (Arid Recovery 2007), suggesting that the population is coping adequately with current food availability.

These rapid declines in bilby population numbers during even relatively short dry periods as in 2003/04 could be important in facilitating long-term persistence for populations at Arid Recovery as this minimises the possibility of lasting environmental damage by the surviving animals (Petrides 1975). However, the greater drought resistance shown by bettongs may result in sufficient environmental damage through their browsing on perennial shrubs, particularly juveniles, during dry periods to adversely affect food supplies for all taxa (Arid Recovery 2007, Noble *et al.* 2007a).

As there is only one other detailed study on the diet of a bettong population (Robley *et al.* 2001) other than that at Arid Recovery (Bice and Moseby 2008), it is difficult to assess the suitability of Arid Recovery as bettong habitat from the perspective of diet. Previous reported bettong diets include tubers, bulbs, seeds, nuts and green herbage (Short 1998), roots, seeds, fruits and grass (Burbidge *et al.* 1988), and roots, tubers, underground fungi, and invertebrates, fruit, flowers, and leaves of forbs and shrubs (Short and Turner 1994), all suggesting a greater utilisation of more moisture-dependent foods like bulbs, and tubers that are not available to bettongs at Arid Recovery except following periods of unusually heavy rainfall. Bettongs on Heirisson Prong (average rainfall 203 mm yr^{-1}) altered their diet between relatively moist winters and hot dry summers by changing from fungi and forbs to seed and stems (Robley *et al.* 2001). The bettong diet in 2000/01 at Arid Recovery included foliage from *Gunniopsis quadrifida* and *Atriplex* sp. (Bice and Moseby 2008) in addition to a much larger and more consistent intake of root coverings and fibrous material than reported by Robley *et al.* (2001). Noble *et al.* (2007a) suggested that a high fibre diet might be energetically insufficient for bettongs. As bettong numbers at Arid Recovery are much more stable than bilby numbers (AR 2005), the relatively high consumption of fibrous materials by bettongs appears sufficient to maintain a successful breeding population (Arid Recovery 2007).

4.4.5 Conclusion

This study has demonstrated that dietary monitoring could be a useful monitoring tool to monitor the long-term viability of an animal's population. Dietary analysis, especially to the detail of specific species of seeds consumed, could be a useful tool to monitor changing utilisation of different foods in relationship to changes in population sizes and environmental changes like droughts. As such dietary changes might be measurable while the animal populations are still viable, as in the current studies, information from such comparative dietary studies would enable management to institute proactive actions such as control of population numbers.

Collection and storage of faecal samples for use by future researchers if time and resources do not permit immediate analysis of the samples should be an important part of population monitoring for reintroduced species. For example, Lundie-Jenkins *et al.* (1993) found that analysis of stored samples from three to ten years before their main study increased their understanding of the response of rufous hare-wallabies to periods of food scarcity. Dietary analysis also enables vegetation studies to be focused on species of seeds and plants most likely to be damaged by over-exploitation by trophic activities.

Since diet measures changes from the animal’s perspective (Southgate and Carthew 2006), information on dietary changes over time or in response to climatic changes could assist monitoring and assessment of environmental changes. However interpretation of changes in seed consumption requires adequate information on phenology and productivity of key species to be able to evaluate relative contributions of differences in seed production and changes in animal numbers. Dietary monitoring is especially important in reserves like Arid Recovery where confined populations are not free to disperse to new territory when food supplies become limited, increasing the possibility of environmental damage from foraging.

CHAPTER 5 Effects of granivory and diggings by reintroduced semi-fossorial omnivores on soil seed banks in arid Australia

5.1 INTRODUCTION

Soil seed banks are important in arid areas as buffers against drought (Kerley and Whitford 1994), as a source of regeneration for ephemeral species that are present only in seed banks when conditions are unfavourable (Chambers and MacMahon 1994, Moles *et al.* 2003) and as stores of concentrated nutrients for granivores (Janzen 1971). Some perennial plants also rely on soil seed banks to enable populations to re-establish after long periods of drought (Kinloch and Friedel 2005). The significant role of soil seed banks in arid ecosystems means that maintenance of the diversity and density of seed banks is important for both the plant communities and the many animal species for which seeds are an important food resource (Brown *et al.* 1979, Kemp 1989).

Greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) are medium-sized, semi-fossorial, omnivorous marsupials that were both once widely distributed over much of Australia. However, their ranges and abundance declined dramatically since European settlement (Southgate 1990a, Short and Turner 1993). Historical records suggest that the overall productivity of arid Australian landscapes decreased after the local extinctions of these species (Martin 2003). The loss of the soil disturbance through these species foraging diggings may have been an important factor in this landscape deterioration since diggings have been shown to have reinvigorating effects on soil quality, distribution of beneficial soil microorganisms, and hence on plant communities (Alkon 1999, Whitford and Kay 1999, Martin 2003).

In recent years, both bilbies and bettongs have been reintroduced to predator-free reserves within their former range, including Arid Recovery, in South Australia, as part of a national recovery effort for these species. Arid Recovery provided the opportunity to study the effects of the reintroduction of bilbies and bettongs on arid ecosystems, as the Reserve has three different management areas suitable for assessing both the effects of the removal of feral cats (*Felis catus*), foxes (*Vulpes vulpes*) and rabbits (*Oryctolagus cuniculus*) when establishing the Reserve, and the effects of reintroducing bilbies and bettongs. The three areas are: with bilbies and bettongs (Inside), with no bilbies and bettongs (Control) and with no bilbies and bettongs but with rabbits (Outside). This study focused on the effects of the reintroduction of bilbies and bettongs on soil seed banks, as seed banks would possibly be affected by both the feeding and digging activities of these animals.

Both greater bilbies and burrowing bettongs are omnivorous, consuming considerable but varying amounts of seeds (Southgate 1990b, Gibson 2001, Southgate and Carthew 2006, Bice and Moseby 2008, Chapter 4). Both species have been shown to forage on buried seeds, particularly when shallowly buried (Chapter 6). Other studies suggest that bilbies obtain seeds from seed-harvester ant seed caches (Gibson 2001, Southgate and Carthew 2006) and by licking individual seeds from the soil surface (Johnson 1980). The effects of granivory by these animals would thus be expected to be greatest in the shallow seed banks.

Granivory has been shown to have a significant influence on the dynamics of the distribution and abundance of arid soil seed banks and plant communities (Brown *et al.* 1979). Many studies have found that granivores decrease the density of seeds in seed banks (Nelson and Chew 1977, Brown *et al.* 1979, Ghermandi 1997, Anderson and MacMahon 2001, Marone *et al.* 2004), consuming up to 95% of seed production for some plant species (Chew and Chew 1970, Auld and Denham 1999, Montiel and Montana 2003). However, the effects of granivory on seed banks may not be measurable when the amount of seeds removed by granivory, germination and decay are similar to the amounts entering the seed bank through seed rain (Price and Joyner 1997, Marone *et al.* 1998). Seed consumption might also not cause measurable decreases in seed bank density if the quantity of seed consumed were small relative to the total amount of seed present. The level of granivory has also been shown to be dependent on many factors including seed size, with larger seeds preferred by many rodents (Davidson *et al.* 1984), species of seed (Reichman 1975, Marone *et al.* 1998), microsite (Mull and MacMahon 1996, Schnurr *et al.* 2004), size of clumps of seeds (Reichman and Oberstein 1977, Reichman 1979, Marino *et al.* 2005), and depth of burial of seeds (Reichman and Oberstein 1977, Christian and Stanton 2004).

Herbivory affects the distribution and abundance of seeds in seed banks through the reduction of biomass and available resources for the production of seeds (Maron and Crone 2006), and more directly through foraging on the floral parts of plants (Crawley 1990). The impacts of bilby and bettong herbivory are unknown though grazing by rabbits has resulted in changes in the composition and species diversity of plant communities (Crawley 1990, North *et al.* 1994) and soil seed banks (Edwards and Crawley 1999).

The reintroduction of bilbies and bettongs could also affect soil seed banks through the effects of their diggings on soil formation and health (Martin 2003) and hence on plant productivity (Boeken *et al.* 1995). Diggings have been shown to increase the abundance of soil micro-arthropods (Eldridge and Mensinga 2007), incorporation of litter into soil (James 2004), and water infiltration (Garkaklis *et al.* 1998), and to act as colonisation sites for seedlings (Boeken and Shachak 1994). Ground-foraging mammals like bettongs and bilbies may spread mycorrhizal fungi (Johnson 1996) and microbial endophytes (Lucero *et al.* 2006) that enhance the growth of many plants (Sarre 1999, Martin 2003, Plenchette and Duponnois 2005). As Australian soils are generally of very low fertility (Stafford Smith and Morton 1990), small changes in nutrient pools related to diggings may possibly have large effects on productivity (James and Eldridge 2007).

Diggings also have the potential to affect soil seed banks through trapping seeds (Alkon 1999, Sparkes 2001, Chapter 3, Chapter 7), thus creating concentrated seed sources for granivores (Gutterman 1987, Claridge and Barry 2000), and redistributing the seeds in the seed bank (Chambers and MacMahon 1994). In addition, diggings bury some seeds (Chapter 3), and bring others to the surface (Chapter 6), thus changing the probabilities that they will be eaten or germinate successfully (Hulme and Borelli 1999).

The objective of this chapter is to determine the effects of the reintroduction of semi-fossorial omnivores on soil seed banks by comparing seed banks in three different management areas of Arid Recovery: with bilbies and bettongs (Inside), with no bilbies or bettongs (Control) and with no bilbies or bettongs but with rabbits (Outside). The discussion considers how this research increases our overall understanding of the ecological roles of bilbies and bettongs and assists the management of populations of these animals.

5.2 METHODS

5.2.1 Study area

This study was conducted at Arid Recovery (30°29'S, 136°53'E), located approximately 20 km north of Roxby Downs in central South Australia. This 60 km^2 reserve is surrounded by a 1.8 m high predator-proof fence (Moseby and Read 2006). All feral cats (*Felis catus*), foxes (*Vulpes vulpes*) and rabbits (*Oryctolagus cuniculus*) have been removed from the Reserve, and four locally extinct species reintroduced: greater bilbies (*Macrotis lagotis*), burrowing bettongs (*Bettongia lesueur*), greater stick-nest rats (*Leporillus conditor*) and western barred bandicoots (*Perameles bougainville*). For further information on Arid Recovery see chapter 2.

In order to determine the effects of the removal of rabbits, cats and foxes, and of the reintroductions, three management areas at Arid Recovery were compared, Inside the Reserve (reintroduced species), Outside the Reserve (cats, foxes and rabbits) and a Control area (neither reintroduced species or rabbits, cats and foxes). The mammal species that were present in each of the management areas are shown in Table 5.1.

Table 5.1: The mammals present in the three management areas in which this study was conducted. Shaded cells show presence of those species, and 'low' and 'high' indicate relative population numbers. The small native mammals present were predominately spinifex hopping-mouse (*Notomys alexis*) with smaller numbers of Bolam's mouse (*Pseudomys bolami*).

Management areas	Mammals present in the management areas				
	Reintroduced Species	Cats and Foxes	Rabbits	Kangaroos	Small native Mammals
Inside	▨				High
Control				Low	High
Outside		▨	▨	▨	Low

The three main habitats are low longitudinal sand dunes dominated by sandhill wattle (*Acacia ligulata*) and sticky hopbush (*Dodonaea viscosa*) (Dune), clay inter-dunal swales dominated by the chenopods bladder saltbush (*Atriplex vesicaria*) and low bluebush (*Maireana astrotricha*) (Swale), and patches of mulga (*Acacia aneura*) woodlands with sandy clay soil (Mulga). Mulga patches in Control were the smaller than those Inside and Outside, and hence some of the sampling sites were nearer the ecotones.

The climate of the area is characterised by hot summers (mean daily maximum 37°C and minimum 21°C in January) and mild winters (mean maximum of 19°C and minimum of 4°C in July) (Read 2002). The 10-year average rainfall at Arid Recovery is 154 mm (CV 45%), with greatest variability in summer (Arid Recovery unpublished data). For further details refer to Chapter 2.

There was average to above average annual rainfall during the study period (2003: 152 mm, 2004: 193 mm) (Figure 5.1). The first sampling period, September 2003, followed a dry winter (30 mm rain including 28 mm within a month before sampling). The summer preceding the second sampling (April 2004) was also relatively dry, with only 30 mm rain. The third sampling period (September 2004) followed 82 mm of rain in May and June 2004, which resulted in a burst of winter flowering not seen in the region for 10 years (Arid Recovery 2005). The September 2004 sampling period was undertaken during this burst of flowering, and therefore before many species had seeded.

NOTE:
This figure is included on page 81 of the print copy of
the thesis held in the University of Adelaide Library.

Figure 5.1: The monthly rainfall at Arid Recovery preceding and during the seed bank sampling study (Arid Recovery, unpublished data). The seed bank sampling periods are represented by *.

5.2.2 Seed bank sampling

Soil seed banks were sampled in each of the management areas (Inside, Outside and Control) in each of the three habitat types (Dune, Mulga and Swale). Sampling sites were located near Arid Recovery's permanent vegetation monitoring sites, which wherever possible, provide cross-fence comparisons with a 500 m buffer zone between the fence and the sites (Arid Recovery, unpublished data). Extra sites were established in both the Control and Outside areas to obtain sufficient sites for this study.

Each sampling site was a 40 m diameter circular plot (1,260 m^2) marked with a central post. Ten samples were taken per site by sampling at 4 m intervals along a 40 m transect following a compass bearing either side of a permanent central post. The samples were obtained using a 20 cm long piece of bore pipe (inner diameter 15 cm), which was hammered into the ground and then the soil scooped out. The samples were sub-sampled to three depths: surface, 0-2cm and 2-10 cm (Mulga and Swale) or 2-20 cm (Dune). The surface sub-samples were carefully collected using a paintbrush, while a ruler was used to determine the depths of the other sub-samples. The soil was sieved on-site using a 1 mm mesh sieve and the seeds identified using a reference collection for the Reserve (maintained at Arid Recovery) and plant identification books including Cunningham *et al.* (1981) and Kutsche and Lay (2003).

The soil depth to which the seed banks at Arid Recovery were sampled was determined by a pilot survey of one site (10 samples) in each of the three habitat types. Each sample was sub-sampled at nine depths (surface, 0-1 cm, 1-2 cm, 2-5 cm, 5-10 cm, 10-15 cm, 15-20 cm, 20-30 cm, and 30-40 cm). The resulting cumulative percentage of seeds in each depth sub-sample is shown in Figure 5.2.

Many soil seed bank studies sample to 2 cm deep as this contains at least 80% of the seed bank in many areas (Marone and Horno 1997). The Mulga and Swale were similar to this (Mulga 85%, Swale 87%), but only 45% of the Dune soil seed bank was less than 2 cm deep (Figure 5.2). Therefore for this survey, it was decided to sample to 10 cm deep in Mulga and Swale, and 20 cm in Dune. These samples were sub-sampled to surface, 0-2 cm and 2-10 or 2-20 cm deep to enable comparisons to be made with other studies.

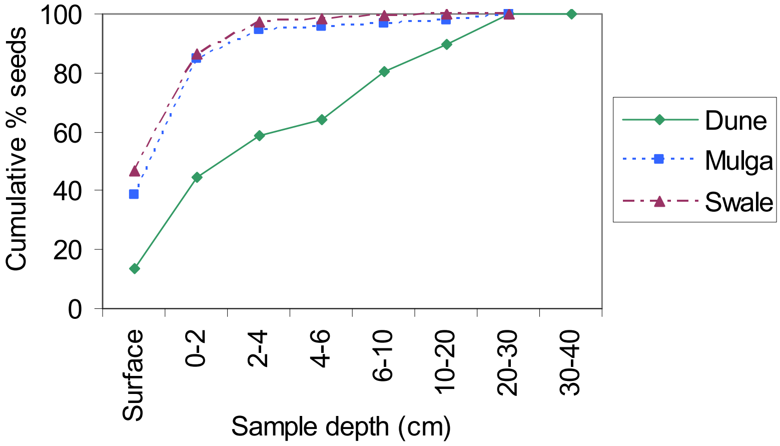


Figure 5.2: The cumulative number of seeds in the sub-sampled depths taken during the pilot study from one site Inside the Reserve in each of the three habitat types. n = 10 for each habitat.

The soil seed banks were sampled three times: a pilot study in September 2003 (north-south transect of the sampling site), the main study in April 2004 (east-west transect), and a follow-up study in Dune habitat in September 2004 (north east – south west transect). The number of sites and depth sampled differed between these sampling periods due to time and weather constraints as show in Table 5.2. For example, in September 2004, the sand in the Dunes was too wet to be able to sieve deeper samples.

Table 5.2: The soil seed sampling protocol for each sampling period (September 2003, April 2004 and September 2004).

	September 2003	April 2004	September 2004
Management areas	Inside, Outside and Control	Inside, Outside and Control	Inside, Outside and Control
Habitat types	Dune, Mulga and Swale	Dune, Mulga and Swale	Dune
Sampling sites	2 sites per treatment per habitat type	5 sites per treatment per habitat type	5 sites per treatment
Samples per site	10	10	10
Depth of sub-samples	Surface-2 cm; 2-10 cm (Mulga and Swale) or 2-20 cm (Dune)	Surface; 0-2 cm; 2-10 cm (Mulga and Swale) or 2-20 cm (Dune)	Surface, 0-2 cm

The term ‘seed’ is used here to refer to the diaspore of a species, the unit of the plant that is actually dispersed (Howe and Smallwood 1982). The grass *Dactyloctenium radulans* was sampled as spikelets with the seeds firmly held by the glumes (Latz 1995, Clayton *et al.* 2006), as the seeds themselves are too small to have been retained by the sampling sieve. Therefore *D. radulans* seeds separated from their spikelets would not have been sampled.

5.2.2.1 Comments on seed bank sampling method

This sieving technique was chosen for this study rather than other sampling methods such as germination (e.g. Kinloch and Friedel 2005) or flotation (eg. Gross 1990) as it is a simple technique, and allows the processing of numerous samples relatively quickly. The 1 mm mesh sieve used was the finest possible for use with the Dune sand (approximate grain size 0.1 to 0.5 mm). As sieving determines actual seed numbers and not just the seeds able to germinate at a particular time under a particular set of growth conditions (Facelli *et al.* 2005), it better assesses availability of seeds to granivores than a method based on germination.

The possibility that some seeds were small enough to pass through the sieve was assessed by watering samples of sieved soil for three months to obtain germinants. Only a few seedlings grew from these samples, including two species that were sampled in the seed banks (*Dactyloctenium radulans,* and *Eragrostis setifolia*) as well as four species that were not sampled in the seed banks (*Calandrina* sp., *Portulaca oleracea*, *Eragrostis kenadia and Eragrostis dielsii*). Soil seed banks in many arid areas in North America contain up to 80% very small seeds (Price and Reichman 1987, Marone and Horno 1997). There is however no readily available data on the size distribution of seeds in seed banks in arid Australia. As over 80% of the seeds in the diet of bilbies and bettongs at the study site were within the size range collected during this study (Bice and Moseby 2008, Chapter 4), the size range of seeds sampled is representative of most of the seeds in the bilby and bettong diets.

5.2.3 Monitoring *Enchylaena tomentosa*

As another measure of the effects of removal of rabbits and reintroduction of bilbies and bettongs on a food resource, the sizes of *Enchylaena tomentosa* bushes and the number of ripe berries were measured in the Dune habitat in the three management areas in September 2004. Fifty bushes were selected using a wandering quadrat (Tongway and Hindley 2004) at each of the five seed sampling sites in each of the management areas. The length, width, and height of each bush, its location on the dune (crest, slope or base) and in relationship to living or dead bushes were recorded. The number of ripe berries was counted using a 25 x 25 cm quadrat randomly placed once horizontally on the top and once vertically at the side of each bush. Berries were counted from both the top and side of the bushes as predation was predicted to be greater on the side of the bush where they could be more easily reached.

5.2.4 Data analysis

As the three management areas of Arid Recovery are not replicated, randomised, or the treatments and control interspersed, this comparative study could be considered an experimental event, and pseudoreplicated (Hurlbert 1984, Oksanen 2004). The resulting lack of statistical independence of the sampling sites means that inferential statistics are inappropriate for determining differences between the management areas (Hurlbert 1984). Therefore the comparisons of seed bank densities between both vegetation types and management areas are presented as 95% confidence intervals around the mean (Fidler *et al.* 2006, Stephens *et al.* 2007), and the results are presented graphically to permit visual evaluation of differences between the areas. The analysis was carried out using StatsDirect (2005) software.

The similarity in the species composition of the soil seed banks and standing vegetation was determined using the Sorenson index of similarity, based on presence/absence of species (Greig-Smith 1983 in Kinloch and Friedel 2005). A value of 1 indicates complete similarity while a value of 0 indicates complete dissimilarity. Simpson's Diversity Index was used to compare the number of species of seeds between management areas as this index gives a measure of both richness and evenness (the distribution of seeds between species). The variability between the management areas and habitat types of both the soil seed banks and standing vegetation was further explored using multi-dimensional scaling (MDS) using PRIMER (Clarke and Warwick 1994) software.

5.3 RESULTS

5.3.1 Differences between habitat types

Soil seed banks of the three habitat types in April 2004, the most comprehensive of the three sampling times, differed in both seed abundance and species composition. Mulga seed bank density was nearly twice that of Dune and Swale (Mulga: 4750 ± 1880 (95% confidence interval) seeds m^{-2}, Dune: 2480 ± 1400 seeds m^{-2}; Swale: 2460 ± 1580 seeds m^{-2}).

A total of 71 species of seeds were found across all three habitats and all three sampling times (Appendix 5.1). Thirteen of these species were represented by fewer than ten seeds. In April 2004, Mulga had more species than Dune or Swale (Dune: 39; Mulga: 46; Swale: 35). Forty-three percent of species were found in all three habitats, and 29% in two habitats (18% in Dune and Mulga; 9% in Mulga and Swale; and 2% in Dune and Swale). Twenty-eight percent of species occurred in only one habitat: 7% in Dune, 12% in Mulga and 9% in Swale.

The species composition of the April 2004 seed banks was relatively dissimilar to that of the standing vegetation at each site, as determined using Sorenson index of similarity. Dune seed banks were more similar to the standing vegetation than Mulga and Swale seed banks (range of Sorenson index - Dune: 0.33 – 0.61; Mulga: 0.20 – 0.50; Swale: 0.22 – 0.45).

5.3.2 Differences between management areas

5.3.2.1 Seed density

The differences in density of seeds in the soil seed banks between the management areas showed different patterns in each habitat type (Figure 5.3). In Dune, Inside seed densities were lower in the shallow (surface + 0-2 cm) sampling depth than in the other two management areas at all three sampling times, though there was no overall difference between seed densities in the deeper seed banks. In the Mulga, Inside seed densities were higher than in the Control at both sampling times and both sampling depths. However Mulga seed densities Outside relative to the other two management areas were distinctly different between sampling times especially for shallow seeds, as densities were similar to the Control in September 2003, but higher in than the Control in April 2004. Swale seed banks also had distinctly different patterns at the two sampling times, with lower densities Inside at both depths in September 2003, but similar numbers in all areas in April 2004.

The differences between soil seed banks in the three management areas are shown in more detail by separating the April 2004 seed banks into the basic plant life forms (grass, forbs and shrubs) (Figure 5.4). In Dune, the lower seed densities Inside were most pronounced for grasses, followed by forbs. However, densities of shrub seeds in the deep seed bank were highest Inside. Mulga had higher seed numbers both Inside and Outside compared with the Control for shrubs, and the 0-2 cm and deep sampling depths for forbs. Grass seeds showed a different pattern, with seed banks of both Inside and Control areas higher than Outside. In Swale, grass (0-2 cm and deep) and shrub (surface) seed densities in the Inside and Outside areas were both higher than in the Control, showing a similar pattern to that of forb and shrub seeds in Mulga.

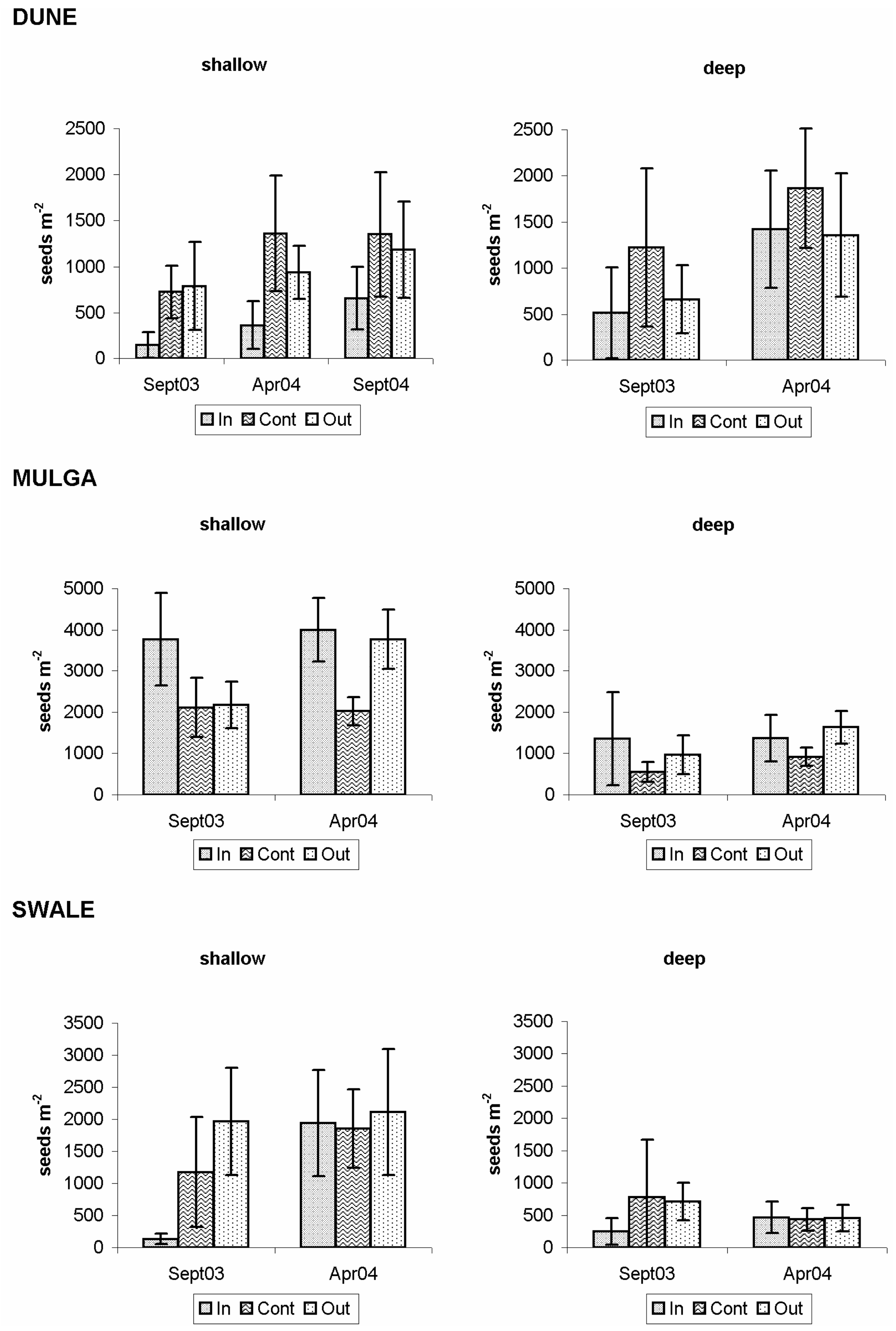


Figure 5.3: The seed density (average number of seeds m^{-2} ± 95% confidence intervals) of the soil seed banks for each depth (shallow (surface + 0-2 cm) and deep (2-20 cm for Dune, 2-10 cm for Swale and Mulga)) in each management area and habitat type for the three sampling periods. September 2003: n = 20; April 2004 and September 2004: n = 50.

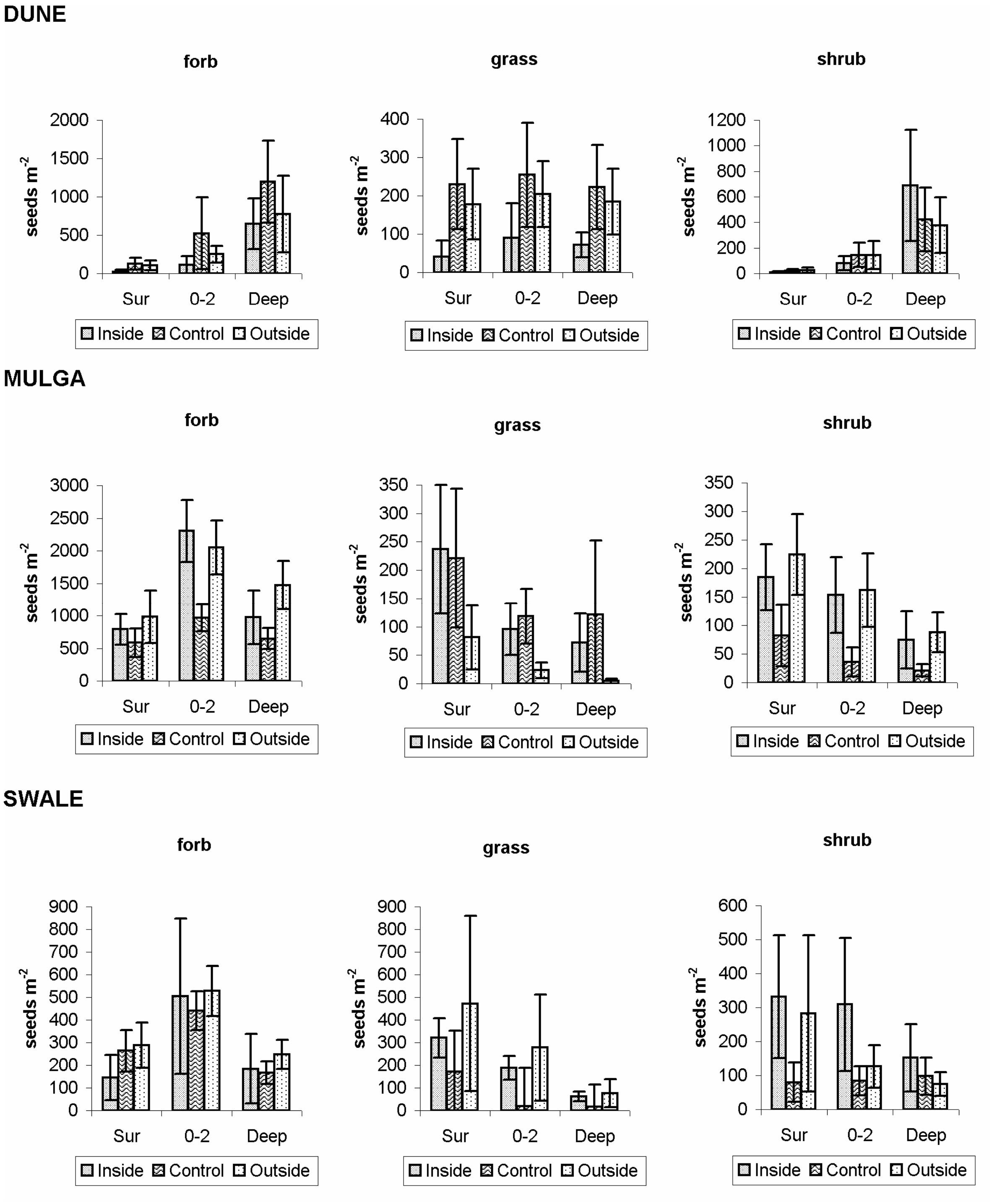


Figure 5.4: The April 2004 soil seed bank densities (average number of seeds m^{-2} ± 95% confidence intervals) for the forb, grass and shrub seeds, for each depth (surface, 0-2 cm and deep (2-20 cm for Dune, 2-10 cm for Swale and Mulga)) in each management area and habitat type. Total number of species: Dune - forbs 27, grass 6, shrub 6; Mulga - forbs 31, grass 7, shrub 8; Swale - forbs 20, grass 8, shrub 8. n = 50.

5.3.2.2 *Spatial heterogeneity*

The soil seed banks in all the habitat types were highly heterogeneous at both sample and site levels. The number of seeds in individual samples varied between 0 and 287 seeds (equivalent of 16,000 seeds m^{-2}) in Dune; 4 and 497 seeds (200 to 27,000 seeds m^{-2}) in Mulga; and 0 and 343 seeds (19,000 seeds m^{-2}) in Swale. The number of seeds per sample also varied between management areas (Figure 5.5). The largest differences between the areas were the lower number of samples with higher numbers of seeds Inside both in Dune and in the Control in Mulga.

Multi-dimensional scaling (MDS) of April 2004 species occurrence and abundance of the soil seed banks and species occurrence of the standing vegetation at each sampling site showed a similar degree of separation between the management areas and high variability between sampling sites within management areas for both seed banks and the standing vegetation (Figure 5.6).

5.3.2.3 *Species composition*

The density of the nine most abundant species of seeds in each habitat type in April 2004 are shown in Table 5.3, and compared with their densities at the other two sampling times. A complete list of all the species of seeds collected and their abundance is included in Appendix 5.1.

In the Dune habitat, the numbers of seeds for five of these nine species were at least two times lower Inside than in the Control area during all three sampling periods (Table 5.3). Of these, three species (*Paractaenum novae-hollandiae*, *Boerhavia* sp. and *Aristida contorta*) are known to be consumed by bilbies while two species (*Brassica tournefortii*, *Euphorbia drummondii*) are not known to be consumed by either bilbies or bettongs (Chapter 4). The seed of the forb, *Zygophyllum ammophilum*, made up less than 1% of the Dune seed banks in both September 2003 and April 2004, but 51% of the shallow seed banks in September 2004 (Inside: 332 seeds m^{-2}, Control 454 seeds m^{-2}, Outside 494 seeds m^{-2}).

In the Mulga habitat, numbers of all of the nine most abundant species in April 2004, and six of the nine in September 2003 were higher Inside than the Control area (Table 5.3). The numbers of most of these seeds were also higher Outside than in the Control, though these differences were less pronounced for some species.

In the Swale habitat, the differences between the management areas in seed numbers for individual species varied considerably between September 2003 and April 2004 (Table 5.3). Of particular interest is *Dactyloctenium radulans*, a major dietary seed for bilbies (Chapter 4), for which seed numbers were lowest Inside compared to the other management areas in September 2003, but then in April 2004 numbers Inside were equal to Outside and higher than in the Control.

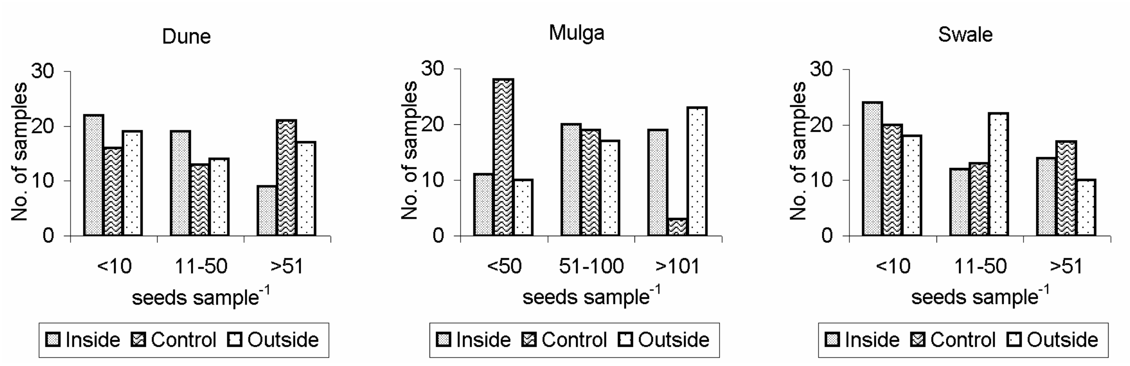


Figure 5.5: The size class frequency distributions (number of seeds per sample) for the April 2004 soil seed bank sampling for the three management areas. Larger size classes were used for Mulga because of the higher number of seeds in this habitat.

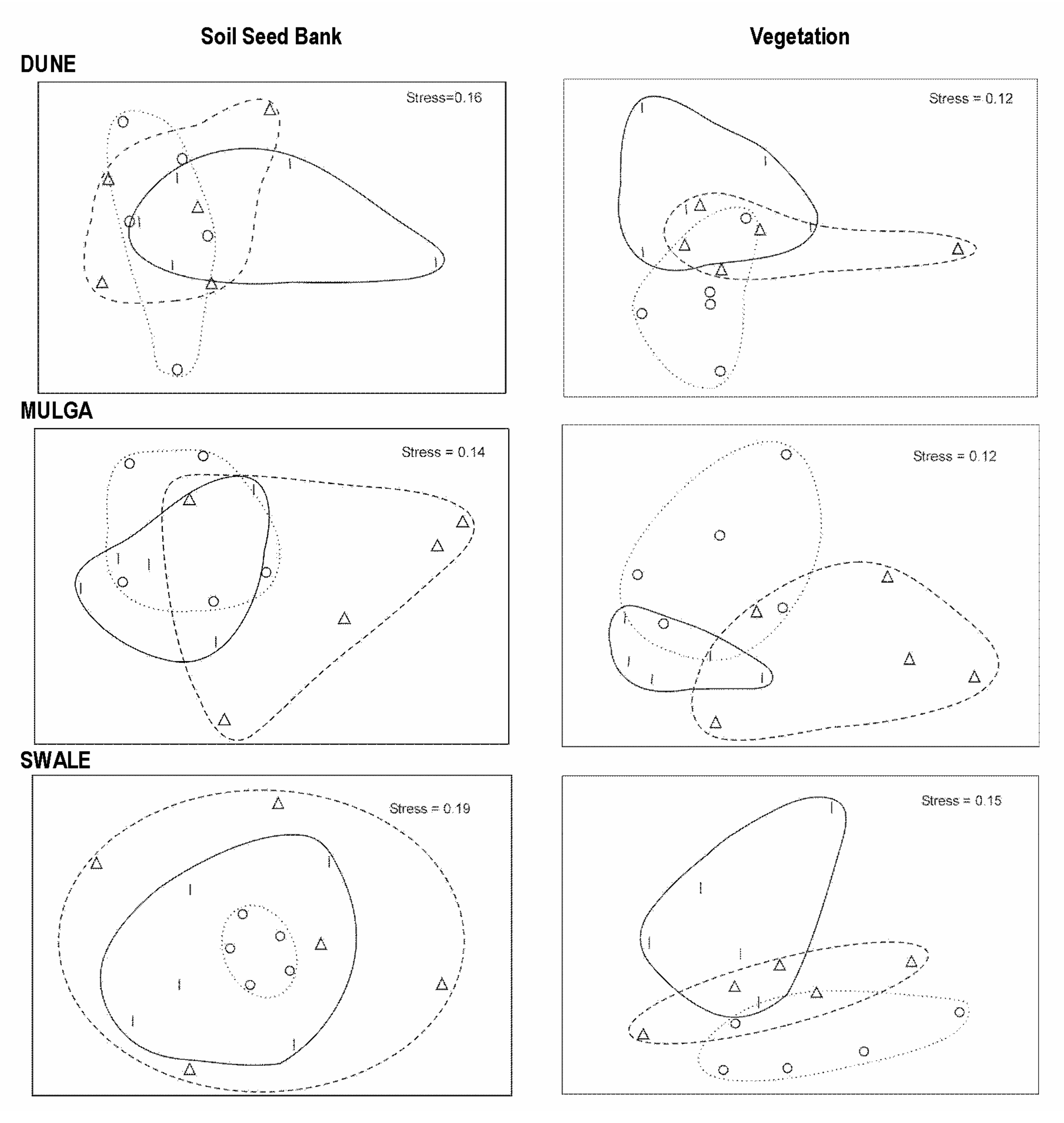


Figure 5.6: MDS of the species richness and abundance of the April 2004 soil seed banks (left) and the standing plant by species occurrence at April 2004 (right) for each of the seed sampling sites within each habitat type. Inside management area = I (solid line), Control area = Δ (dash line); Outside area = O (dotted line).

Table 5.3: The total number of seeds (as seeds m^{-2}) collected from each management area at each sampling period for the nine most abundant species of seeds in each habitat, listed in descending order of abundance. Sampling protocols for each sampling time are given in Table 5.2. ✶ indicates species known to be consumed by either bilbies or bettongs at Arid Recovery (Bice and Moseby 2008, Chapter 4). The trends between the management areas (I:C – comparison of Inside with Control; C:O – comparison of Control with Outside) are represented by: >> or << at least 2x greater than or less than; > or < 1.25x to 2x greater than or less than; = equal or less than 25% difference. For the Simpson D diversity index * indicates significant trends based on non-overlapping 95% confidence intervals. *Par.* – *Paractaenum*, *Enne*. - *Enneapogon*, *Dact*. - *Dactyloctenium*, *Sclero*. - *Sclerochlamys*.

Seed Species	Life Form	Sept 2003					April 2004					Sept 2004				
		Seeds m^{-2}			Trends		Seeds m^{-2}			Trends		Seeds m^{-2}			Trends	
		In	Cont	Out	I:C	C:O	In	Cont	Out	I:C	C:O	In	Cont	Out	I:C	C:O
DUNE																
Brassica tournefortii	F	58	122	42	<<	>>	430	1110	780	<<	>	76	204	127	<<	>
Dodonaea viscosa ✶	S	392	172	431	>>	<<	750	510	410	>	>	54	26	40	>>	<
Par. *novae-hollandiae* ✶	G	3	292	222	<<	>	105	520	310	<<	>>	21	359	134	<<	>>
Euphorbia drummondii	F	3	172	117	<<	>	95	410	120	<<	>>	4	144	90	<<	>
Boerhavia sp. ✶	F	0	25	283	<<	<<	20	90	140	<<	<	2	64	52	<<	=
Enne.avenaceous ✶	G	3	6	6	=	=	55	90	80	<	=	11	1	26	=	<<
Sida ammophila ✶	S	86	83	6	=	>>	145	35	40	>>	=	13	11	3	=	=
Aristida contorta ✶	G	3	33	28	<<	=	15	80	90	<<	=	13	77	11	<<	>>
Acacia ligulata ✶	S	19	106	28	<<	>>	20	10	126	=	<<	1	1	3	=	=
Total no. of seeds		661	1950	1456	<<	>	1802	3262	2318	<	>	657	1467	1130	<<	>
Total no. of species		18	27	22			26	36	31			24	29	24		
Simpson D		0.63	0.89	0.83	<*	>*	0.76	0.81	0.82	<*	=	0.71	0.82	0.78	<*	>*
MULGA																
Tetragonia sp.	F	853	197	575	>>	<<	1420	965	1520	>	<					
Erodium cygnorum	F	1428	597	822	>>	<	1360	625	1540	>>	<<					
Calotis hispidula	F	6	14	142	=	<<	440	160	650	>>	<<					
Brassica tournefortii	F	33	3	47	>>	<<	200	55	510	>>	<<					
Tribulus terrestris	F	936	314	292	>>	=	365	115	140	>>	=					
Sclerolaena sp. ✶	F	483	467	344	=	>	165	7	375	>>	<<					
Enne. cylindricus ✶	G	89	94	44	=	>>	285	75	60	>>	=					
Sida ammophila ✶	F	92	6	8	>>	=	308	20	15	>>	=					
Dissocarpus paradoxa	F	233	47	8	>>	>>	160	15	45	>>	<<					
Total no. of seeds		5114	2536	3131	>>	=	5586	3088	5457	>	<					
Total no. of species		22	27	24			33	38	30							
Simpson D		0.83	0.87	0.86	<*	=	0.85	0.84	0.81	=	>*					
SWALE																
Calotis hispidula	F	3	128	294	<<	<<	350	545	375	<	>					
Sclerolaena sp. ✶	F	69	217	408	<<	<	720	230	250	>>	=					
Unknown 2	-	0	0	83	=	<<	65	680	225	<<	>>					
Erodium cygnorum	F	6	122	428	<<	<<	175	255	350	<	<					
Enne. avenaceous ✶	G	111	183	186	<	=	270	130	300	>>	<<					
Dact. radulans ✶	G	67	792	872	<<	=	235	65	240	>>	<<					
Schlero. brachyptera	F	0	111	142	<<	<	285	35	110	>>	<<					
Unknown 3	-	0	331	11	<<	>>	120	180	25	<	>>					
Tetragonia sp.	F	0	0	39	=	<<	25	12	235	=	<<					
Total no. of seeds		381	1950	2678	<<	<	1931	1628	1835	=	=					
Total no. of species		14	12	19			27	28	26							
Simpson D		0.82	0.77	0.82	>*	<*	0.84	0.82	0.90	=	<*					

5.3.3 Relationship of seed banks to diet

Only ten of the 71 species of seeds found in the soil seed banks were known to be consumed by bilbies and/or bettongs (Southgate and Carthew 2006, Bice and Moseby 2008, Chapter 4). Only three (*Paractaenum novae-hollandiae*, *Boerhavia* sp. and *Aristida contorta*) of these dietary species were consistently in lower numbers Inside than Control, while seed numbers of five species were higher at least one sampling time (*Dodonaea viscosa*, *Sida ammophila, Sclerolaena* sp.*, Enneapogon cylindricus,* and *Dactyloctenium radulans*), one species was variable depending on habitat type (*Enneapogon avenaceous)* and one variable over time (*Acacia ligulata*).

Comparing the relative percentage volumes of seeds of particular species consumed by bilbies (Chapter 4) with the seed densities of the same species in the soil seed banks at the three seed bank sampling times showed that there was no direct relationship between relative consumption of a particular seed and its density in the seed bank for any species of seed (Figure 5.7). One possible exception is *Dactyloctenium radulans*, although data available are limited to two time periods. The greatest difference between seed consumption and seed bank densities was found for the forb *Zygophyllum ammophilum*, the most abundant seed in the bilby diet during this study (Chapter 4).

The only species of seeds shown in Figure 5.7 that was consumed by bettongs was *Dodonaea viscosa*, which formed 5% of bettong pellets by volume in January 2004, and 6% in September 2004 (unpublished data).

5.3.4 Differences in *Enchylaena tomentosa* between management areas

In September 2004, *Enchylaena tomentosa* bushes on the Dunes Inside were distinctly larger, and had higher numbers of ripe berries on both the top and side of the plants than in Control or Outside areas (Figure 5.8).

Proportionally more of the *E. tomentosa* plants surveyed were on the crest of the Dune Inside than the other areas, while the location of the surveyed plants in relationship to perennial bushes was more even between areas (Figure 5.8). Inter-area differences in location of plants on the Dunes are indicative of only plants sampled and not of general distribution of *E. tomentosa* on the Dunes, as the sampling protocol used was not designed to measure distribution at this scale.

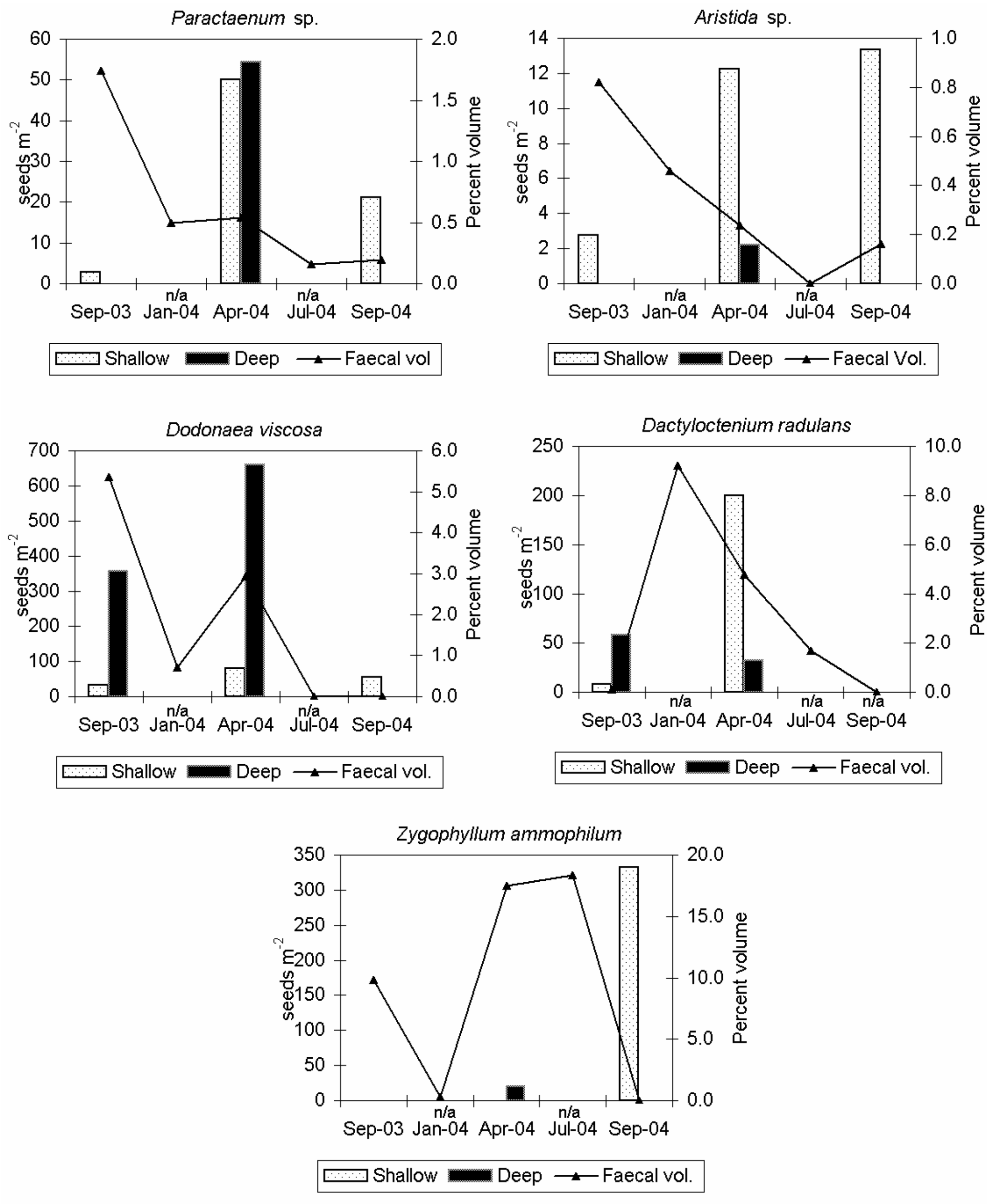


Figure 5.7: Relationship of seed densities in Inside soil seed banks to consumption of these seeds by bilbies over the period of the study. Seed densities are in seeds m^{-2}, and seed consumption in percent faecal volume. *Paractaenum* sp., *Aristida* sp., *Dodonaea viscosa*, and *Zygophyllum ammophilum* all occur mainly in the Dune, and are compared with Inside Dune seed bank densities, while *Dactyloctenium radulans* occurs mainly in Swale, and is compared with Inside Swale seed bank densities. n/a – seed bank density not available for this sampling period. Deep seeds were not sampled in September 2004. Data on seed consumption from Chapter 4, and seed densities in September 2003 and September 2004 seed banks are in the Appendix 5.1.

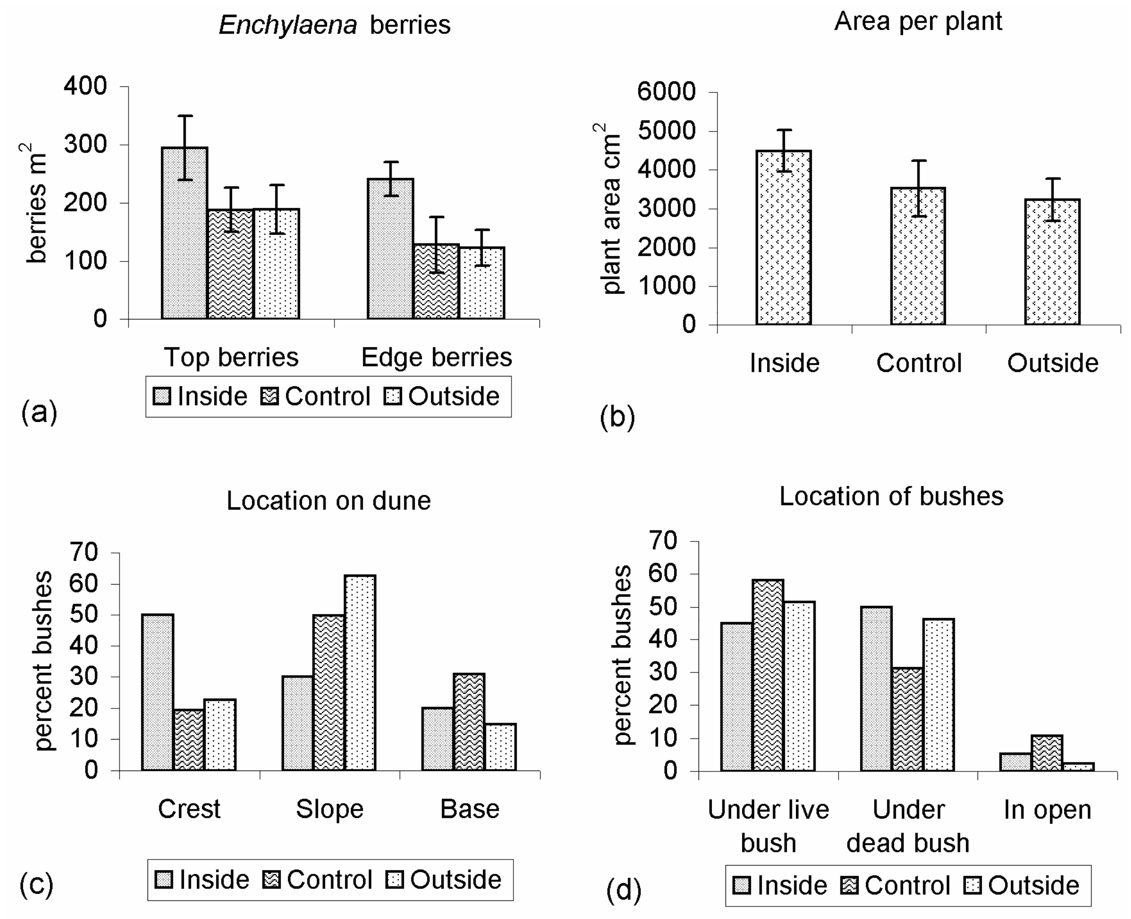


Figure 5.8: (a) The density of ripe *Enchylaena tomentosa* berries on the top and side of these bushes (mean ± confidence intervals), (b) average area per plant of the bushes in the three management areas (mean ± 95% confidence intervals), (c) location on the Dunes of these bushes in the three management areas, and (d) the location of these bushes in relation to the standing vegetation. n = 250.

5.4 DISCUSSION

This study found differences in the seed densities of specific species and the overall soil seed banks between the three management areas at Arid Recovery in Dune and Mulga habitats, and to a lesser extent in Swale. Overall, the largest differences were between the Inside and the Control areas, with smaller differences between the Control and the Outside. The measured differences were likely to be the result of effects of both the different management protocols, and the natural variability between the areas (Oksanen 2001, 2004).

Soil seed bank densities represent the net result of increases from seed production, and decreases from herbivory, granivory, germination, decay, and redistribution of seeds (Figure 5.9). Interactions between plant species, such as competition and facilitation, can be important factors in determining the overall productivity of the plant species (Hastwell and Facelli 2003, Brock and Kelt 2004, Holzapfel *et al.* 2006, Brooker *et al.* 2008). Thus, although the conceptual model (Figure 5.9) shows the seed bank and vegetation both as single entities, both consist of many species, each of which would respond differently to the other factors in the model. Furthermore, ascribing causality to differences between soil seed banks is difficult, as similar patterns might result from different combinations of factors (Belovsky *et al.* 2004).

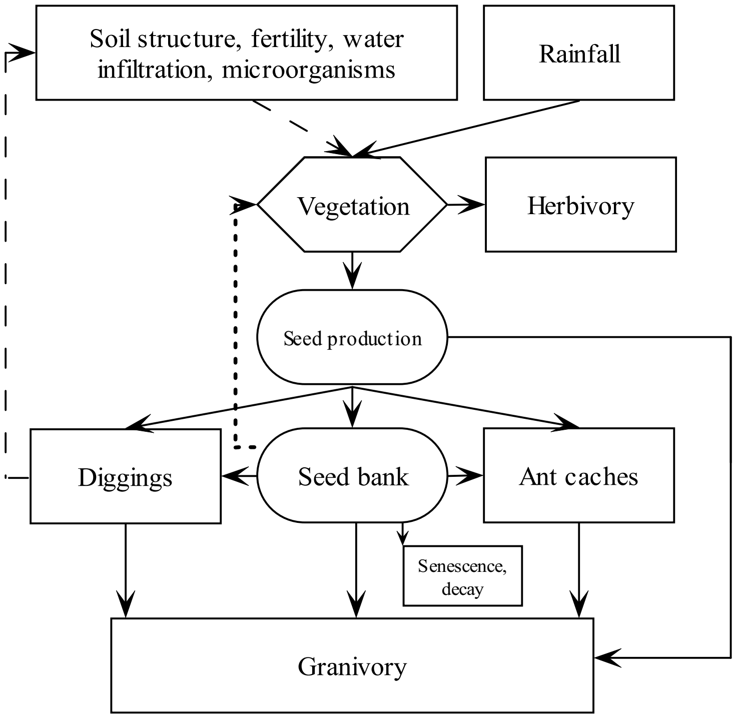


Figure 5.9: A conceptual model of how the soil seed banks at Arid Recovery could be affected by the factors of granivory, digging and herbivory by the reintroduced greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*). The long dashes indicate possible ecosystem engineering effects of the diggings, and the shorter dashes indicate regeneration of vegetation from seed bank through germination.

The high heterogeneity of arid areas means that all areas differ significantly at least at some scales (Ludwig and Tongway 1995, Oksanen 2001). Small differences in soils and rainfall between areas could result in differences in vegetation, and hence seed production and seed bank densities over time (Shachak *et al.* 2008). While multivariate analysis of standing vegetation at the seed sampling sites confirmed the existence of inter-area differences in vegetation, the contributions of the removal of rabbits, and of the reintroduction of bilbies and bettongs to creating and maintaining these vegetation differences is unknown.

The length of time since establishment of the management areas (four to five years) at Arid Recovery is probably sufficient for differences between areas to be measurable in the standing vegetation, as the length of time for a measurable response in seed bank densities or vegetation to occur after the removal of granivores and/or herbivores in other studies in arid areas ranges from two to three years (Guo *et al.* 1995, Gutierrez *et al.* 1997). However, as seed crops in arid areas are highly unpredictable, and may be separated by several years (Brown *et al.* 1979), rainfall patterns, including frequency and timing of extraordinary events (Noy-Meir 1973, Stafford Smith and Morton 1990, Facelli *et al.* 2005), might be more important then calendar time in determining the length of time for the effects of management changes to be measurable.

The pattern of the differences in seed densities between the management areas in Dune was very similar over the three sampling times. This consistency suggests that the differences between the areas were real and just not random variation (Carpenter *et al.* 1998). The trends to higher seed densities Inside, and to smaller differences in seed densities between Inside and Control over time coincide with significant decreases in the rate of digging between April 2004 and September 2004 (Chapter 3). The decreased rate of digging was related to decreases in bilby numbers/activity as determined by track transects (Chapter 3). In addition, seed consumption by bilbies was distinctly lower in September 2004 than in April 2004 (Chapter 4). It therefore is possible that seed consumption and/or digging by bilbies and/or bettongs were causal factors in the lower seed bank densities in Inside than the Control in Dune habitat.

By contrast, the seed densities of Outside Mulga compared with the Mulga in the other management areas, and of the Inside Swale compared with the Swale in the other areas, differed between the two sampling periods (Figure 5.3). For Outside Mulga, possible seasonal differences in diet and habitat use of rabbits (Robley *et al.* 2001, Martin *et al.* 2007), could account for the variations in impact on seed banks at the two sampling periods. The very low seed density in the Inside Swale in September 2003 was similar to the low density in Dune at this time, and could have resulted from a depletion of seeds by the bilbies and bettongs following a relatively dry winter. Although it is possible to suggest such credible mechanisms for observed differences between the management areas, the importance of these mechanisms cannot be evaluated from the available data. The inability to confirm the extent of these mechanisms does not mean they did not occur during this study, but points to the need for further research in order to estimate their importance relative to background variation between the management areas.

5.4.1 Contribution of diggings

The foraging diggings by the bilbies and bettongs could be a causal factor in the differences in seed densities Inside compared with the Control, particularly in the Dune habitat. The density of diggings, area disturbed, and volume of soil excavated per year measured for bilby and bettong diggings at Arid Recovery (Chapter 3) were all comparable to or higher than the same variables for two extensively studied porcupine species, *Hystrix africaeaustralis* (Alkon and Olsvig-Whittaker 1989, Alkon 1999) and *H. indica* (Bragg *et al.* 2005). Although diggings by bilbies and bettongs at Arid Recovery have been shown to capture litter and seeds (Sparkes 2001, James and Eldridge 2007, Chapter 3), and more seeds germinated within diggings than in the nearby matrix (Chapter 3), much more data is needed determine the effects of diggings on the growth, productivity and survival of plants in the different habitats. The location of diggings (Shachak *et al.* 1991), their size, shape (Sparkes 2001), density (Boeken *et al.* 1998, Chapter 7), and position in relationship to depressions, vegetation, litter, shelter and soil types (Alkon 1999, Whitford and Kay 1999) would all be important factors in determining the overall biotic effect of an individual digging. The spatial distribution of diggings and annuals in relationship to shrub patches, and comparison of growth of biomass and/or seed production of annuals growing in these patches with those growing in interpatch areas, with and without foraging diggings present, would be of particular interest because of the importance of facultative interactions between plants on productivity in arid areas (Hastwell and Facelli 2003, Holzapfel *et al.* 2006, Brooker *et al.* 2008).

Seed capture by diggings has the potential to lower the measured density of shallow seeds in the seed banks (Chapter 7). In addition, diggings act as concentrated sources of seeds, known as the treasure effect (Gutterman 1987, Claridge and Barry 2000). As bilbies and bettongs, as well as granivorous rodents forage large clumps of seeds in preference to smaller clumps (Reichman and Oberstein 1977, Reichman 1979, Cabin *et al.* 2000, Chapter 6), the treasure effect could increase the number of seeds eaten, as seeds eaten from diggings might not have been eaten when more scattered on the soil matrix between diggings.

5.4.2 Contribution of diet

Granivory by bilbies and bettongs could be another causal factor in the lower seed densities Inside compared with the Control, particularly in Dune habitat. The lower abundance of the grass *Paractaenum novae-hollandiae* Inside the Reserve compared to the Control was the most consistent difference at all three sampling periods. Semi-quantitative data from Arid Recovery's annual (August) vegetation surveys at the seed sampling sites in 2003 and 2004 indicated that overall cover of *P. novae-hollandiae* Inside was equal to or greater than the Control (Arid Recovery, unpublished data). Though plant cover cannot be equated with seed production, the large differences between Inside and Control seed banks but not the standing vegetation suggests that the low densities of *P. novae-hollandiae* seeds Inside were related to consumption by bilbies. As one of the larger grass seeds at Arid Recovery, *P. novae-hollandiae* could be particularly attractive to bilbies, which show a high dietary preference for grass seeds (Southgate and Carthew 2006, Chapter 4).

The seed densities for two other major Dune species, *Brassica tournefortii* and *Euphorbia drummondii,* which are not known to be consumed by bilbies and/or bettongs, were also distinctly lower Inside than the Control. These species of seeds may have been eaten, but not detected in faecal pellets, either because of insufficient sampling, or because the seed remnants were not recognised in the pellets, or because they were consumed at different times than the sampling times. In addition, the animals could have eaten either the plants, or immature seeds. The data from Arid Recovery's semi-quantitative vegetation surveys recorded similar abundances of both species in all three management areas in both 2003 and 2004 (Arid Recovery, unpublished data), further supporting the possibility of inter-area differences in granivory and/or herbivory affecting the seed banks.

The relationship between seed bank densities and the percentage faecal volume of individual species at each sampling period was variable between species, with both high consumption at times of lower seed density and low consumption at times of higher seed density. Bilbies are thought to obtain seeds from harvester ant caches (Gibson 2001, Southgate and Carthew 2006), which may not have been adequately sampled during seed bank sampling. More data would be needed on the amount, distribution and timing of seed rain to be able to evaluate the relationship of seed consumption to the availability of seeds, whether from seed rain, seed bank or ant seed caches.

A clear example of this lack of correlation between level of consumption of a seed and its density in the seed bank is the forb, *Zygophyllum ammophilum*. This species was the main seed consumed by bilbies in September 2003 and April 2004, despite being almost absent from the soil seed banks. However, *Z. ammophilum* was not consumed at all in September 2004, when it formed over half of the Inside Dune seed bank. Reichman (1975), in his study of granivory by four species of heteromyid rodents, recorded similar cases of high seed consumption of seed species at times when the seeds were not present in the soil seed banks. He did not note if the seeds of these species were available from aboveground seed banks, but this possibility is unlikely for *Z. ammophilum*, a small prostrate forb that did not maintain above ground seed banks for the period over which it was foraged (personal observation).

5.4.3 Productivity of *Enchylaena tomentosa*

Confirmation of the possibility that diggings might have increased plant growth and hence seed production (Boeken and Shachak 1994, Martin 2003) would require direct measurements of productivity differences between management areas that were not possible during this study. However the study of *Enchylaena tomentosa* in September 2004 provides evidence of such inter-area differences in productivity for one plant species at one time at Arid Recovery. Plant size of *E. tomentosa* was larger, and berries numbers were higher Inside compared with both Control and Outside despite high levels of consumption by both bilbies and bettongs at the time of sampling (Chapter 4). These differences were probably not related to the location of the bushes on the dunes, as more bushes in the Control and Outside areas than Inside, were at the dune bases where they could have benefited from the higher water infiltration and storage capabilities of these areas (Moseby and Bice 2004). Growth of *E. tomentosa* has been shown to be facilitated by shade (Hastwell and Facelli 2003), and the enriched soil under live bushes (Facelli and Brock 2000). The difference between the management areas in location of *E. tomentosa* bushes in relationship to other bushes was small, though more bushes in the Control were under live bushes. Another factor that could have influenced the growth of *E. tomentosa* bushes in the Inside area was the diggings of the bilbies and bettongs, though more detailed information on the spatial distribution of the diggings and their ecological impacts would be required to support this suggestion. Although a priori differences between management areas could be an important factor in the higher densities of *E. tomentosa* berries Inside than the other management areas, this is unlikely, as this pattern is opposite that documented for inter-area differences in seed bank densities.

Further surveys of *E. tomentosa* berries at Arid Recovery in November 2005 and April 2006 (Gerlach 2006), found inter-area differences discussed above. These found over ten times as many ripe berries were found on the plants Outside as in either Inside or the Control, while plant cover Inside and Control was only half that Outside. The similar levels of both berries and plant density in the Inside and the Control suggests that frugivores and herbivores common to both areas, possibly the omnivorous spinifex hopping-mice (*Notomys alexis*), and reintroduced stick-nest rats (*Leporillus conditor*) may have been consuming both *E. tomentosa* berries and foliage. Stick-nest rats have been observed to forage frequently on both the foliage and berries of *E. tomentosa* (Ryan *et al.* 2003), and had become established in small numbers in the Control between the two studies on *E. tomentosa* (personal observation). Although a few bilbies and bettongs had managed to cross the fence into the Control area during this period (Arid Recovery 2007), it is thought to be unlikely that this would have been sufficient to equal the level of frugivory and herbivory on *E. tomentosa* Inside.

5.4.4 The way forward

This study is a first step in describing the effects of reintroductions of bilbies and bettongs on soil seed banks, and includes tantalising suggestions of possible increases in productivity related to the effects of diggings of these animals (Martin 2003, Eldridge and Mensinga 2007). This possibility of positive effects of the reintroduction of bilbies and bettongs on the productivity of arid ecosystems is important both for understanding of the ecology of these ecosystems (Martin 2003), and for supporting future reintroductions of these species. Since several studies suggest that as productivity in arid areas is limited more by resource flows than by trophic interactions, the overall effectiveness of bilbies and bettongs in ecological restoration will depend on the restorative functions of diggings (Crain and Bertness 2006, James and Eldridge 2007) being greater than the trophic impacts of these species.

Overall, the relative contributions of the management protocols and natural variation to the differences reported here could best be evaluated by replicating the study at different locations (Johnson 2002, Belovsky *et al.* 2004) where bilbies and/or bettongs, or other semi-fossorial mammals like brush-tailed bettongs (*Bettongia penicillata*) (Garkaklis *et al.* 2004, Pizzuto *et al.* 2007) and long-nosed potoroo (*Potorous tridactylus*) (Claridge *et al.* 1993) have been reintroduced or occur naturally. Such replication would be the best way of gaining confidence in the importance and generality of the mechanisms suggested by this study.

Further research at Arid Recovery would also provide useful supporting data for this research. Although vegetation studies alone might be less labour intensive than seed bank studies, they might not detect possible effects of granivory on species such as *Paractaenum novae-hollandiae* which showed large differences in soil seed bank densities, but not in the standing vegetation (Arid Recovery, unpublished data). However, since such decreases in seed bank densities might become apparent in standing vegetation over time (Maron and Gardner 2000), vegetation studies could still provide valuable information on the eventual impact of seed bank changes. The possibility that seed bank studies could be able to detect such changes before they are evident in vegetation deserves further study.

Focusing seed bank studies on a finer scale, such as stratification of sampling by microsite (Marone and Horno 1997, Cabin and Marshalll 2000, Facelli and Temby 2002, Johnson 2002) might lessen uncertainties related to natural variation between areas. Relating seed densities to characteristics of microsites, such as litter, shelter and nearby vegetation, could detect differences between management areas that could be clearly related to granivory and/or diggings. Such a study could be supported by direct measurements of productivity such as seed rain or biomass production. Narrowing the focus of the study to selected species might also increase its ability to discriminate between a priori, random, or management effects. Species, such as the grasses *Paractaenum novae-hollandiae* and

Dactyloctenium radulans, which showed the largest differences in seed densities in the current study between the Inside and Control, and were consumed by bilbies and/or bettongs, could be suitable foci for such a study.

An alternative approach to evaluate impacts of bilbies and bettongs on soil seed banks would be a well-structured, long-term experiment, such as that of Brown and Heske (1990). The use of interspersed exclosures in the different habitats (Hurlbert 1984) would support detailed statistical evaluation of the data. The monitoring of seed banks for evaluating differences in such an experiment could be replaced or supplemented by vegetation studies, provided these studies were timed to record ephemeral species when they were present in the standing vegetation. Measurements of biomass production and/or seed rain would be needed to evaluate the possibilities of differences in productivity between areas.

This chapter provides a benchmark against which any further changes in soil seed bank densities Inside could be measured. Continued monitoring of vegetation, animal numbers, and soil seed banks will help management take proactive action to prevent detrimental ecological effects of the reintroduced animals.

APPENDIX 5.1: LIST OF SPECIES OF SEEDS IN SEED BANKS

Table 5.4: The total number of seeds by species sampled from soil seed banks at three sampling times. Species are listed in alphabetical order followed by unknowns. The results for all three habitat areas are combined for each sampling date. Habitat notes the habitats in which seeds of the noted species were found in decreasing order of abundance: D – Dune, M – Mulga, S – Swale. Habitats with relatively few seeds of that species are noted in brackets. Sampling protocols for each date are given in Chapter 5. Note: September 2003, 2 sites were sampled for each area and habitat; other times, 5 sites were sampled for each area and habitat.

Species of Seed	Area	Depth	Total Seed Numbers								
			September 2003			April 2004			September 2004		
			In	Out	Cont	In	Out	Cont	In	Out	Cont
Abutilon otocarpum	D	Surface				0	0	0	0	0	0
		0-2	0	0	11	0	0	32	0	0	1
		Deep	0	0	0	0	3	0			
Acacia aneura	M	Surface				0	2	0			
		0-2	3	0	1	2	2	0			
		Deep	1	19	10	34	12	6			
Acacia ligulata	D M	Surface				0	1	0	0	0	0
		0-2	0	1	1	1	7	1	1	4	1
		Deep	7	9	73	17	104	10			
Acacia ramulosa	D	Surface				0	0	2	0	0	0
		0-2	0	1	12	0	0	2	0	2	1
		Deep	1	2	144	0	0	0			
Aristida contorta	D M S	Surface				6	8	17	0	1	5
		0-2	1	12	18	7	63	98	12	40	64
		Deep	0	0	4	4	14	17			
Atriplex vesicaria	D S	Surface				50	30	29	73	0	2
		0-2	7	5	24	15	1	3	0	0	4
		Deep	3	1	4	10	0	3			
Boerhavia sp.	D M (S)	Surface				17	37	16	0	1	2
		0-2	5	99	63	13	149	84	2	47	56
		Deep	1	16	6	15	64	46			
*Brassica tournefortii**	D M (S)	Surface				7	53	3	25	33	56
		0-2	32	23	42	60	181	114	43	93	108
		Deep	2	9	3	492	917	926			
Calotis hispidula	M S (D)	Surface				237	324	281	0	6	0
		0-2	165	187	32	346	429	249	2	9	2
		Deep	6	21	20	123	163	101			
*Citrullus colocynthis**	M	Surface				2	0	1			
		0-2	0	1	6	0	0	0			
		Deep	0	47	3	1	0	0			
Crotaloria eremaea	D	Surface				0	2	2	0	2	0
		0-2	1	0	0	5	1	1	1	0	0
		Deep	13	3	9	10	2	12			
Dactyloctenium radulans	S M (D)	Surface				124	190	99	0	0	0
		0-2	10	207	238	88	24	15	1	0	0
		Deep	31	125	140	36	29	6			
Dissocarpus paradoxa	M (S)	Surface				106	39	12			
		0-2	67	48	4	33	4	1			
		Deep	90	43	17	6	0	1			
Dodonaea viscosa	D (M S)	Surface				2	20	4	1	1	0
		0-2	13	51	8	69	120	89	48	35	22
		Deep	129	110	57	594	230	370			

Species of Seed	Area	Depth	Total Seed Numbers								
			September 2003			April 2004			September 2004		
			In	Out	Cont	In	Out	Cont	In	Out	Cont
Eremophila sp.	D S	Surface				6	0	0			
		0-2				3	0	4			
		Deep				0	0	0			
Enchylaena tomentosa	D M	Surface				6	22	12	2	40	27
		0-2	0	0	19	6	4	5	12	42	35
		Deep	0	0	0	9	13	11			
Enneapogon avenaceous	D M S	Surface				214	272	232	3	3	0
		0-2	26	49	46	97	39	40	7	21	1
		Deep	15	25	24	29	34	27			
Enneapogon cylindricus	D M S	Surface				172	79	19	0	1	0
		0-2	23	12	18	67	69	5	0	1	2
		Deep	11	1	16	54	23	10			
Eregrostis setifolia	S	Surface				6	0	4			
		0-2	0	0	15	2	0	0			
		Deep	1	0	0	1	0	0			
Erodium cygnorum	(D) M S	Surface				10	19	19	0	1	0
		0-2	368	257	193	1120	1288	622	1	5	3
		Deep	149	218	66	236	379	189			
Euphorbia drummondii	D (M)	Surface				2	30	39	2	2	7
		0-2	1	33	32	50	62	244	2	79	123
		Deep	1	14	35	32	23	99			
Hibiscus krichauffianus	D	Surface									
		0-2	0	0	2						
		Deep	0	0	3						
Lepidium sp.	D	Surface							0	0	0
		0-2							0	0	8
		Deep									
Maireana sp.	S	Surface				1	8	5			
		0-2				1	5	1			
		Deep				0	0	0			
Minuria cunninghamii	D	Surface							0	0	1
		0-2							0	0	0
		Deep									
Paractaenum nove-hollandiae	D (M S)	Surface				6	57	161	2	15	96
		0-2	2	63	76	40	93	178	17	106	227
		Deep	24	38	29	49	126	248			
Phyllanthus lacunarius	D M	Surface				0	3	0			
		0-2				0	0	1			
		Deep				0	7	12			
Polycalymma stuartii	D (S)	Surface				0	2	63	3	3	1
		0-2				0	0	3	2	2	0
		Deep				0	0	3			
Ptilotus pessifolius	D M (S)	Surface				0	11	115	0	0	0
		0-2	0	0	19	0	9	66	0	4	0
		Deep	0	0	30	1	0	4			
Salsola kali	D M	Surface				4	2	30			
		0-2	0	6	8	3	8	20			
		Deep	0	1	0	2	4	7			
Schlerolamys brachyptera	S	Surface				30	24	5			
		0-2	0	45	4	160	41	24			
		Deep	0	6	36	62	34	3			

Species of Seed	Area	Depth	Total Seed Numbers								
			September 2003			April 2004			September 2004		
			In	Out	Cont	In	Out	Cont	In	Out	Cont
Sclerolaena sp.	S M (D)	Surface				291	218	56	1	0	0
		0-2	163	174	200	346	224	74	0	0	0
		Deep	36	98	48	153	117	82			
Sclerolaena sp. 1	S	Surface				11	3	45			
		0-2				12	2	26			
		Deep				0	1	2			
Sclerolaena sp. 2	S	Surface				0	135	0			
		0-2				0	20	0			
		Deep				0	5	1			
Sida ammophila	M D (S)	Surface				10	6	5	0	0	3
		0-2	35	5	14	125	4	17	12	3	5
		Deep	29	0	18	270	36	32			
Swainsona sp.	S	Surface				0	2	0			
		0-2				0	0	0			
		Deep				0	0	0			
Trachymene glaucifolia	D	Surface				0	0	1	2	0	0
		0-2	0	0	3	3	4	2	8	0	4
		Deep	0	0	0	48	9	18			
Tragus australianus	M S	Surface				3	2	12	0	0	0
		0-2	1	6	1	23	3	15	0	1	1
		Deep	2	0	0	12	1	12			
Tetragonia sp.	M (D)	Surface				387	638	251	0	0	0
		0-2	231	216	66	619	345	294	2	2	2
		Deep	79	5	6	284	584	329			
Tribulus terrestris*	M (D)	Surface				163	92	75	0	0	1
		0-2	224	93	71	127	31	14	0	0	5
		Deep	113	12	42	36	18	28			
Triraphis mollis	M D	Surface				8	50	16	2	1	0
		0-2				12	24	4	0	1	5
		Deep				4	11	4			
Zygophyllum ammophilum	D	Surface				0	0	2	202	241	228
		0-2	0	0	6	1	1	1	97	204	100
		Deep	0	0	0	18	11	9			
Zygophyllum eremaeum	D	Surface							0	1	0
		0-2	2	0	0				0	7	1
		Deep	2	1	0						
101	D S	Surface							1	0	0
		0-2							0	0	0
		Deep									
14	D	Surface									
		0-2	0	0	0						
		Deep	0	1	60						
16	S	Surface									
		0-2	0	1	0						
		Deep	0	0	1						
25	D M	Surface				0	0	0			
		0-2	0	0	1	2	2	0			
		Deep	2	0	1	1	8	1			
33	D	Surface									
		0-2	0	0	0						
		Deep	0	0	3						

Species of Seed	Area	Depth	Total Seed Numbers								
			September 2003			April 2004			September 2004		
			In	Out	Cont	In	Out	Cont	In	Out	Cont
44	D M	Surface				5	3	2			
		0-2	0	2	116	56	16	142			
		Deep	0	3	3	46	10	24			
51	M	Surface									
		0-2	0	0	1						
		Deep	0	0	2						
62	D M	Surface				9	19	2			
		0-2	9	48	0	7	21	5			
		Deep	0	1	0	2	0	16			
63	D	Surface									
		0-2	0	0	0						
		Deep	1	0	0						
67	D M	Surface				64	125	316	0	2	0
		0-2	31	70	6	61	117	189	1	1	4
		Deep	0	1	0	31	53	104			
70	D	Surface									
		0-2	0	0	0						
		Deep	3	0	0						
74	M	Surface									
		0-2	0	0	3						
		Deep	0	0	0						
75	D	Surface									
		0-2	0	1	1						
		Deep	8	3	0						
8	M	Surface									
		0-2	0	0	0						
		Deep	0	1	0						
87	D M	Surface				33	47	1			
		0-2	34	48	1	170	56	6			
		Deep	1	0	0	69	20	1			
88	M	Surface				1	0	0			
		0-2	0	0	6	0	0	0			
		Deep	0	0	2	0	0	0			
95	D M	Surface				2	4	2			
		0-2	0	0	9	7	5	26			
		Deep	0	0	4	1	0	3			
C	D	Surface				0	0	1	0	0	0
		0-2				0	3	2	0	0	1
		Deep				0	1	6			
H	D	Surface				0	4	0			
		0-2	0	0	1	0	2	0			
		Deep	0	0	0	1	0	0			
J	M	Surface				1	1	7			
		0-2				6	1	26			
		Deep				5	0	35			
K	D M	Surface				0	2	3			
		0-2				0	0	11			
		Deep				0	1	2			
L	D M	Surface				0	0	3			
		0-2				1	0	55			
		Deep				0	2	39			

Species of Seed	Area	Depth	Total Seed Numbers								
			September 2003			April 2004			September 2004		
			In	Out	Cont	In	Out	Cont	In	Out	Cont
M	M	Surface				1	0	0	0	0	0
		0-2				17	0	2	1	0	0
		Deep				122	16	7			
G11	S	Surface									
		0-2	1	6	0						
		Deep	0	4	0						
G21	S	Surface									
		0-2	0	1	0						
		Deep	0	0	0						
N	D	Surface				0	0	0	0	0	0
		0-2				0	0	0	0	2	1
		Deep				0	4	1			
O	D	Surface				0	0	0	0	0	0
		0-2				0	0	0	0	1	0
		Deep				0	0	4			
P	M	Surface				0	0	0			
		0-2				0	0	0			
		Deep				0	0	22			

CHAPTER 6 Foraging of greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) on buried seeds and ant seed caches

6.1 INTRODUCTION

Granivores are one of the major consumer groups in arid regions and can have substantial impacts on the abundance, distribution and species richness of soil seed banks (Reichman 1979, Andersen 1982, Anderson and MacMahon 2001), and therefore vegetation communities (Turnbull *et al.* 2000, Folgarait and Sala 2002, Orrock *et al.* 2006). In arid Australia, seed-harvesting ants have been found to be the primary granivores (Predavec 1997), in contrast to North American deserts where rodents are usually the dominant granivores (reviewed in Morton 1985). However, since many medium-sized Australian mammals, such as greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*), have been extinct or locally rare for much of the last century, they may have formerly played important roles as granivores in these ecosystems (Martin 2003, Noble *et al.* 2007a).

Bilbies and bettongs have been reintroduced to predator-free reserves within their former range, including the site of this study, Arid Recovery, in South Australia, as part of national recovery efforts for these species. One of the main objectives of Arid Recovery is to facilitate the ecological restoration of arid ecosystems through the removal of feral predators and herbivores and the reintroduction of locally extinct species (Arid Recovery 2006).

The foraging abilities and preferences of granivores, including the depths and size of seed caches that they access, determines how they affect soil seed banks and plant communities (Reichman and Oberstein 1977). The ability of many species of granivorous rodents to find buried seeds has been shown to decrease with increasing depth and decreasing cache size, and to be lower in dry sand than moist sand (Lockard and Lockard 1971, Reichman and Oberstein 1977, Vander Wall 1998, Geluso 2005). Australian mammals (excluding bilbies and bettongs and other rare, endangered species) differ from mammals in many other ecosystems, especially in Israel (Abramsky 1983) and North America (Morgan and Price 1992), in that they tend not to dig for buried seeds of any size, even when the depth of burial is relatively trivial (C. Dickman, pers. comm. in Murray and Dickman 1994, Moles *et al.* 2003). Buried seeds could thus be an under-utilised resource available to the reintroduced bilbies and bettongs.

Both bilbies and bettongs are omnivores, with seeds forming an important, though variable part of their diets (Gibson 2001, Robley *et al.* 2001, Southgate and Carthew 2006, Bice and Moseby 2008, Chapter 4). Both species create numerous foraging diggings, although the specific purpose of these diggings is unknown. Bilbies have been reported to forage on the underground seed caches of seed-harvester ants (Smyth and Philpott 1968, Johnson 1989, Gibson 2001, Southgate and Carthew 2006), and ants and remains of ant nests have been found in diggings at Arid Recovery (personal observation). Surveys of the soil seed banks at Arid Recovery approximately four years after the reintroductions of both bilbies and bettongs found that in one of the major habitat types, sand dunes, seed densities in the shallow (up to 2 cm deep) seed bank Inside the reserve were significantly lower than those in a control area where no bilbies or bettongs were present (Chapter 5).

This chapter presents the results of two experiments designed to examine the foraging abilities of the bilbies and bettongs and to consider the potential effects of their granivory on the soil seed banks. The first experiment explored whether bilbies and bettongs at Arid Recovery could locate and dig for buried seeds, and if so, whether the size and depth of the seed caches influenced the probability that the cache would be dug. The second experiment involved excavating the nests of seed-harvester ants (*Pheidole* sp.) to determine the depth and size of their seed caches, and then testing whether bilbies and/or bettongs would dig for seeds cached by harvester ants in their nests.

6.2 METHODS

6.2.1 Study area

This study was conducted at Arid Recovery (30°29'S, 136°53'E), located 20 km north of Roxby Downs in central South Australia. Arid Recovery is a 60 km^2 reserve surrounded by a 1.8 m high predator-proof fence. All feral cats (*Felis catus*), foxes (*Vulpes vulpes*) and rabbits (*Oryctolagus cuniculus*) have been removed from the reserve, and four locally extinct species reintroduced. For a more detailed description of the study site and the reintroduced species see Chapter 2. This chapter focuses on greater bilbies and burrowing bettongs as both species create numerous foraging diggings (Chapter 3) and were the most numerous of the reintroduced species at the time of this study (Arid Recovery 2005). The other granivores present at Arid Recovery include seed-harvester ants, rodents (principally spinifex hopping-mice (*Notomys alexis*) and Bolam's mice (*Pseudomys bolami*)), and birds.

Arid Recovery is located in the arid zone where the summers are hot (mean daily maxima exceeding 35°C in January and February) and winters are mild (mean minimum of 4.3°C in July) (Read 2002). The long-term average rainfall for this region is 166 mm, though this is very unpredictable and variable.

The three main habitat types within the reserve are longitudinal sand dunes dominated by sandhill wattle (*Acacia ligulata*) and sticky hopbush (*Dodonaea viscosa*); clay inter-dunal swales dominated by the chenopods, bladder saltbush (*Atriplex vesicaria*) and low bluebush (*Maireana astrotricha*) and patches of mulga (*Acacia aneura*) woodlands with sandy clay soils.

6.2.2 Seed foraging experiment

An experiment using caches of buried rice was designed to determine the influence of cache size and depth on the probability that a cache would be dug by either a bilby or bettong. Four sites inside the reserve on relatively flat vegetation-free areas on sand dunes were used for this experiment, as the sand was relatively easy to dig and animal tracks could be clearly seen. The sites were at least 2 km apart so that they were as independent as possible as only male bilbies are likely to move this far between adjacent sites in one night (Moseby and O'Donnell 2003, Finlayson and Moseby 2004).

Uncooked brown rice was used for this experiment as dish-feeding trials had shown that it was eaten by both bilbies and bettongs (unpublished data) and that it was clearly visible in the red sand. Eight treatments were compared: two quantities of brown rice (small – 3 grains; large – approx 50 grains) at four depths (2 cm, 5 cm, 10 cm, and 20 cm), plus a control treatment with no rice. The rice was not handled but placed in the diggings using a teaspoon to minimise experimental bias resulting from human smell on the seeds (Duncan *et al.* 2002, Wenny 2002).

At each site, four replicates of each of the treatments were arranged in a 9 m x 4 m grid, consisting of 4 parallel transects each with the 8 treatments and 1 control placed in random order at 1 m intervals. For each sample, a 20 cm deep hole was dug (approx. 15 cm diameter), and the appropriate treatment was placed in the hole at the appropriate depth while the hole was being filled. The control samples were dug and filled without adding rice. The locations of each sample were then marked with paddle-pop sticks and then the whole site was swept to allow identification of animal tracks.

This experiment was repeated over three consecutive nights. Each morning animal activity as determined by tracks and diggings, and whether each sample had been dug up were recorded using the classification in Table 6.1. Some examples are shown in Figure 6.1. All rice that had been consumed was replaced, and the sites were reswept.

This experiment was first conducted in September 2004, and repeated at the same sites in April 2005. Temperatures were higher in April 2005 (max: 30.8°C, min: 13.2°C) than September 2004 (max: 24.1°C, min: 8°C) (Olympic Dam Meteorology Station, 20 km south of Arid Recovery, Bureau of Meteorology, Canberra). Rainfall at Arid Recovery in the two months preceding the experiment was lower for April 2005 (4 mm) than for September 2004 (19.5 mm), though the rainfall was equal for the four months before the experiments began (67 and 65 mm respectively).

Table 6.1: The classification used to record the bilby and bettong activity at each sample.

Activity Class	
Not Visited	There were no bilby and/or bettong tracks near the sample.
Knocked (Knk)	The paddle pop stick marking the sample was knocked over and tracks showed that a bilby and/or bettong had walked over the sample.
Small digging (Sm Dig)	There was a small exploratory digging (<3 cm deep) at or close to the paddle pop stick marking the sample, but the rice was not disturbed.
Sample dug (DUG)	A bilby and/or bettong had dug up the rice sample and some or all of the rice had been removed.

The data from all three nights in each trial were combined for analysis as the overall digging activity did not differ significantly between the three consecutive nights. Combining the data over the three nights also avoided problems with temporal non-independence of the data (Edwards *et al.* 2000). The influence of cache size and/or depth of burial on foraging of the bilbies and bettongs was assessed using two-way ANOVA (SPSS software (2007)) and logistic regression (Microsoft Excel (Microsoft Corporation 2003)).

6.2.2.1 Foraging for native seeds

A further foraging experiment was conducted in July 2005 to test whether bilbies and bettongs would dig for native seeds in addition to rice. The seed species tested were *Acacia ligulata, Brassica tournefortii, Dactyloctenium radulans, Dodonaea viscosa*, and rice. The native seeds were harvested in the local area or collected during soil seed bank sampling.

This experiment used a similar site layout as that of the previous seed foraging experiment, but at different locations within the reserve. Two sites were located on two dunes about 500 m apart with two replicates of the five seed species and a control sample at each site. For each sample, a 5 cm deep hole was dug (approximately 15 cm diameter), the appropriate treatment (10 seeds or small pinch of the small seeds of *B. tournefortii* and *D. radulans*) was placed in the hole, and then the hole filled in. The control samples were dug and filled in without adding any seeds.

The sites were monitored the day after they were prepared and whether each sample had been dug up was recorded using the same classification as the previous experiment (Table 6.1). These sites were again monitored two days after replacement of the samples consumed on the first night. Rain on the second day and night prevented access to the sites on the following day.

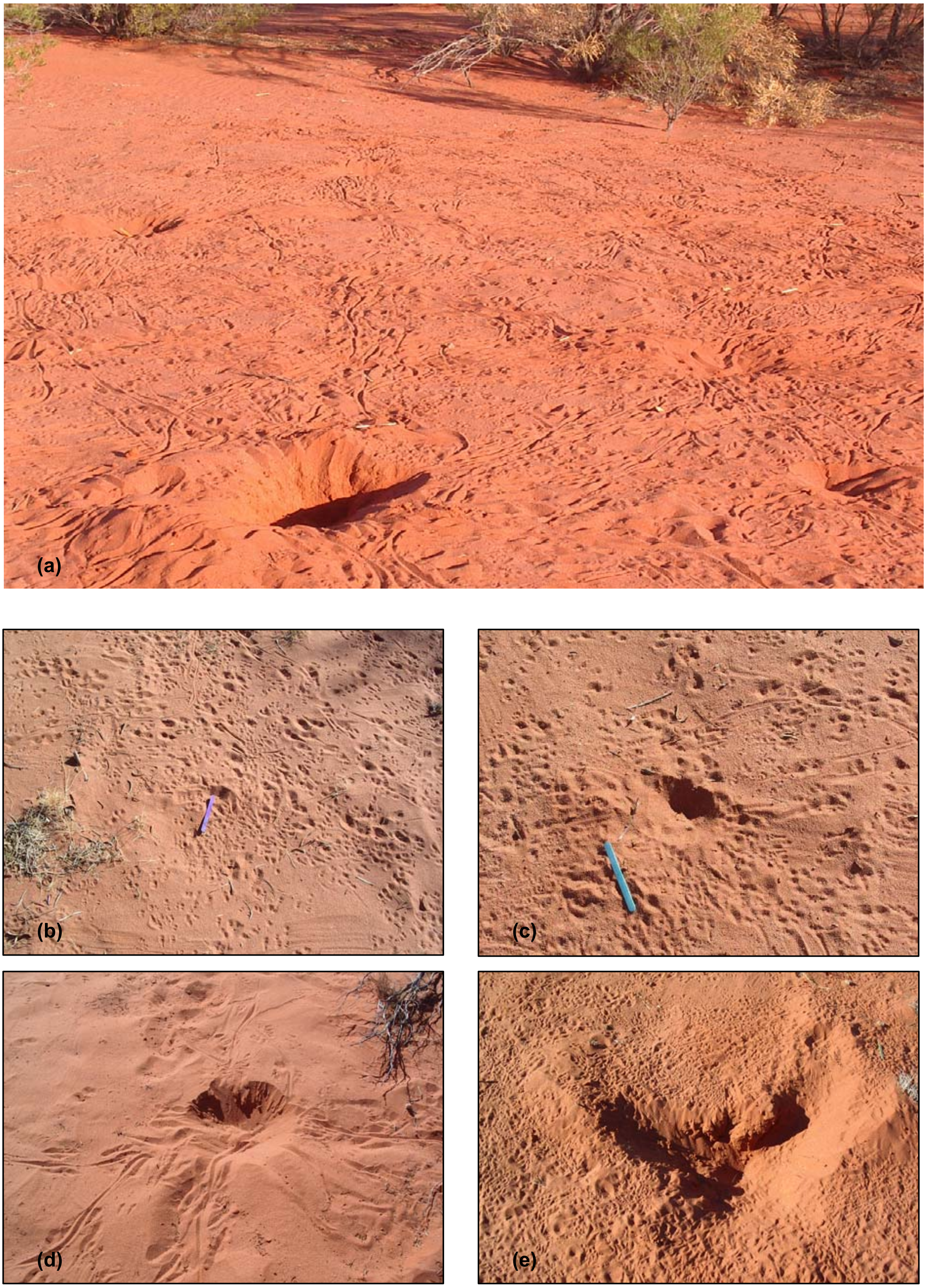


Figure 6.1: (a) A foraging trial site (April 2005) at time of monitoring, showing diggings and animals tracks, (b) a control sample at which the marking post had been knocked over, (c) a control sample with a small exploratory digging, (d) a 5 cm sample DUG, (e) a 20 cm sample DUG. Bilby and bettong tracks are clearly visible in these photos, as well as numerous small animal tracks from spinifex hopping-mice (*Notomys alexis*).

6.2.3 Seed-harvester ant experiments

6.2.3.1 Location of seed caches

In order to determine the sizes, depths and distribution of seed caches of harvester ants at Arid Recovery, eight *Pheidole* sp. ant nests, one of the most conspicuous of the seed-harvester ant nests at the reserve, were excavated systematically. The selected nests were located outside the reserve so they would not be disturbed by bilbies or bettongs.

These nests occurred in clay soil in or near the edges of patches of mulga (*A. aneura*) woodlands, with each nest consisting of a group of 2 to 5 entrances at distances ranging from 2 to 5 m apart (personal observation). Only one nest entrance from each group was chosen for this study, and was at least 100 m from other groups of entrances. As little is known about the structure of ant colonies at Arid Recovery, it is not known whether or not this distance between colonies would ensure independence of observations.

Active *Pheidole* sp. ant nests were ‘fed’ rice for 24 to 48 hours before excavating so that the ants would cache this rice in their underground seed caches, thus making the caches more visible during excavation (Figure 6.2). The rice used was uncooked brown rice that had been lightly blended with a food processor to decrease the grain size so the ants would have a range of grain sizes to harvest, and coloured with blue food colouring to make it easier to distinguish from light-coloured seeds. About 225 ml (195 g) of this rice was left within 0.5 m of the ant nest entrance and covered with 1 cm wire mesh to prevent it from being eaten by other granivores.

The ‘fed’ nests were excavated in the afternoon when the ants were not active above ground. Any rice that remained on the soil surface was collected and weighed to determine how much rice the ants had taken. A sample of the spoil at the nest entrance was also taken to determine what seed species were deposited there. The nest entrance was then marked with a peg and a 1 m^2 area around it swept to remove any surface seeds. The nest entrance and the surrounding 1 m^2 area were then carefully excavated to approximately 1 m deep, or when there was no further sign of ant activity. The location of ant tunnels was noted and any caches of blue rice or other seeds collected. The depth of the cache and its distance from the centre peg was recorded, as well as other features of the nests. Contents of caches were sieved with a 1 mm mesh sieve then sorted to determine amount of rice and the numbers and species of other seeds present. Some seeds may have been missed during excavation if they were in caches that did not contain rice and thus were not noticed, or if they were small enough to pass through the 1 mm sieves.

Six *Pheidole* sp. ant nests were excavated in April 2005 when the soil was dry, and a further two in July 2005 shortly after rainfall. In April the ants were observed to be active above ground in the morning and inactive by noon, whereas in July the ants were active from mid-morning until late afternoon.

Figure 6.2: The nest of a Pheidole sp. seed-harvester ant next to the blue dyed brown rice covered by wire mesh to prevent predation by other granivores 24 to 48 hours before excavating.

6.2.3.2 Foraging at ant nests

Other nests of the same harvester ant *Pheidole* sp., this time inside the Arid Recovery Reserve with bilbies and bettongs present, were 'fed' rice and then monitored for bilby and bettong activity the following morning to determine whether bilbies and/or bettongs dug for seeds cached by harvester ants. For the purpose of this experiment, a *Pheidole* sp. ant nest was considered a cluster of two to three entrances that were separated from any other entrances by at least 20 m in order to increase the possibility that adjacent nests would be visited by similar numbers of foraging bilbies and/or bettongs. Pairs of adjacent nests (one fed, and one as a control) were located at six sites separated by at least 100 m in July 2005. The soil was moist during this experiment as there had been rain the previous week.

The nests were ‘fed’ by placing 225 ml (195 g) of blue rice (prepared as for the previous experiment) within 0.5 m of each of the nest entrances in the morning before the ants became active. The rice was placed on paper plates so that all unused rice could be easily removed. Empty plates were also placed near the entrances of the control ant nests to control against any disturbance the plates might cause. The edges of all the plates were buried to give the ant’s easy access to the rice.

In the late afternoon of the same day, after the ants had become inactive above ground, the plates and any remaining rice, including any rice which the ants had deposited on the spoil heaps, were removed so that bilbies and bettongs would not be attracted to the area by rice on the soil surface. The total amount of rice harvested by the ants was recorded.

The nests were monitored the next morning for any bilby or bettong diggings at or near the nests. Any diggings were measured, and searched for blue rice both in the digging and in the spoil heap. The location of all diggings relative to the nest entrance was also noted, along with any bilby or bettong tracks and/or fresh scats on the spoil around the diggings.

6.2.4 Bilby and bettong body condition

In order to compare the physical condition of bettongs at the time of the two seed foraging experiments (September 2004 and April 2005) a body condition index (BCI) was calculated for animals that were captured during regular monitoring at these times (Arid Recovery, unpublished data). BCI was calculated using the ratio of the cube root of body mass (g) divided by the length of pes (mm) (Short and Turner 2000). Only data from adult animals (> 900 g) (Short and Turner 2000) were used, as the BCI of juvenile animals was significantly lower than that of adult animals. Too few bilbies were captured at these times to determine condition indices for this species (Arid Recovery, unpublished data).

A subjective body condition was determined at the same time by feeling the amount of fat present on the vertebrae and pelvis, and assigning a relative condition score of poor, fair, good or excellent (Moseby and O'Donnell 2003).

The BCI for the bettongs was lower, though not significantly so, in September 2004 than April 2005 (September 2004: BCI = 0.107 ± 0.001 n = 43; April 2005: 0.110 ± 0.002 n = 17; t-test: t = - 0.18, d.f. = 23, p = 0.18). This trend was supported by the subjective body condition (% of animals): September 2004: Excellent: 3, Good: 67, Fair: 30; compared with April 2005: Excellent: 29, Good: 59, Fair: 12 (Sept 04: n= 43; Apr 05: n = 17).

6.3 RESULTS

6.3.1 Seed foraging experiment

Bettong tracks were recorded at all sites on each night of both experimental trials, except for one site on one night in April 2005. Bilby tracks were less frequent and recorded at all sites for the first night, and then three of the four sites on each of the following nights in September 2004, and at only three sites for two nights at each site in April 2005. One site had no detectable sign of being visited by bilbies during this later trial.

It was not always possible to determine which species had made the diggings since many were visited by both bilbies and bettongs. However, some of the diggings at all treatments, including the controls, could be ascribed to either bilbies or bettongs as they had tracks of only one species. The size and shape of most of the 20 cm deep diggings suggested that they were dug by bilbies and only later visited by bettongs (personal observation). However, since two of the large 20 cm deep caches were dug at a site that was not visited by bilbies, bettongs did dig this deep at times. The tracks of spinifex hopping-mice were present on all the sites, often in large enough numbers to make distinguishing the bilby and bettong tracks difficult, particularly during the April 2005 experiment.

The probability of a rice cache being DUG decreased with increasing depth, and was lower for smaller caches (Figure 6.3). The size and depth of the samples both had a significant effect on whether the rice was DUG in both September 2004 (cache size: $F = 31.2$, $p < 0.001$, depth: $F = 37.5$, $p < 0.001$, size*depth: $F = 0.1$, $p = 0.96$, d.f. = 1,3) and April 2005 (cache size: $F = 85.1$, $p < 0.001$, depth: $F = 34.8$, $p < 0.001$, size*depth: $F = 3.5$, $p = 0.02$). The difference in the size*depth interaction term between studies shows that in September 2004 depth of cache and size of cache independently determined whether a cache were DUG, whereas in April 2005 the size of a cache affected whether it would be DUG at any given depth.

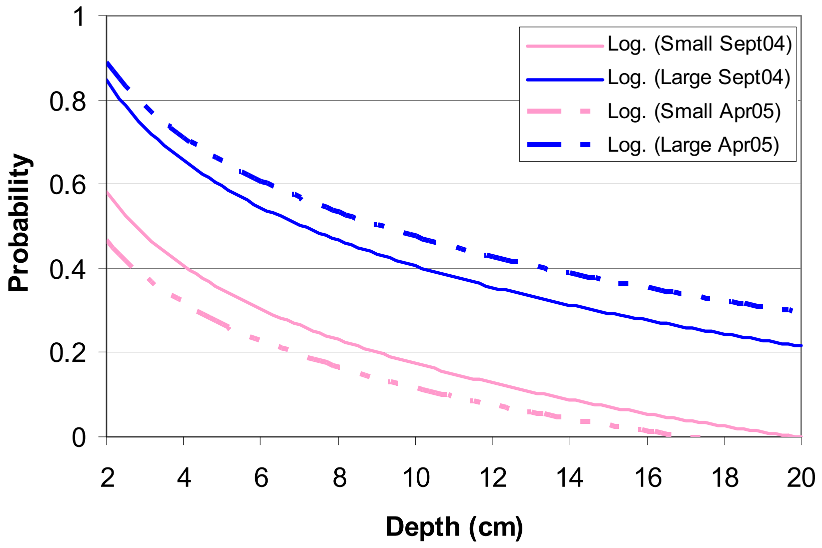
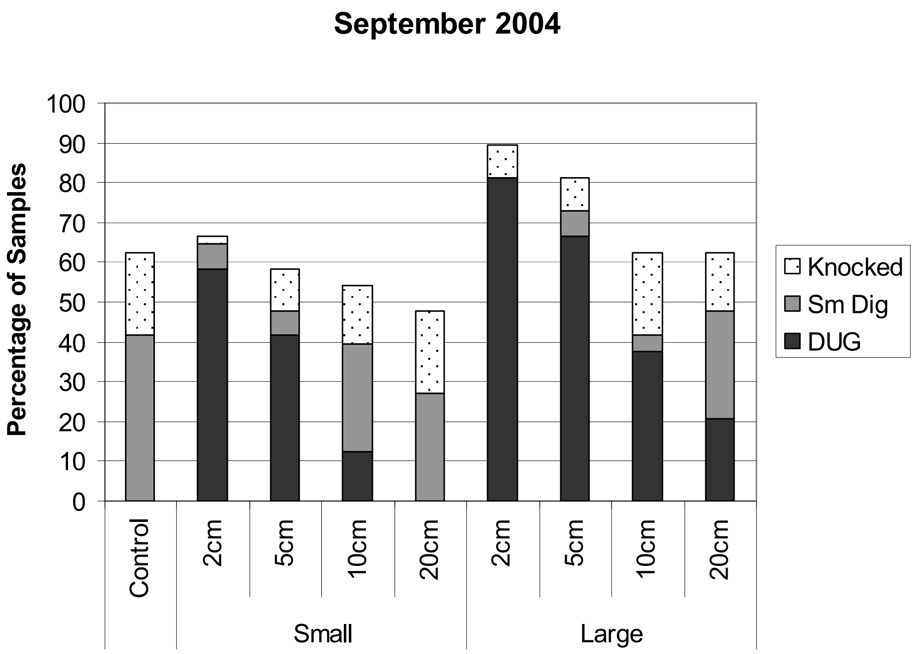


Figure 6.3: Logistic regression plot showing the probability of the large and small rice caches being DUG by bilbies and/or bettongs during the September 2004 and April 2005 experiments. Small Sept04: $r^2 = 0.23$, $p < 0.001$, Large Sept04: $r^2 = 0.21$, $p < 0.001$, Small Apr05: $r^2 = 0.22$, $p < 0.001$, Large Apr05: $r^2 = 0.20$, $p < 0.001$ ($n = 48$).

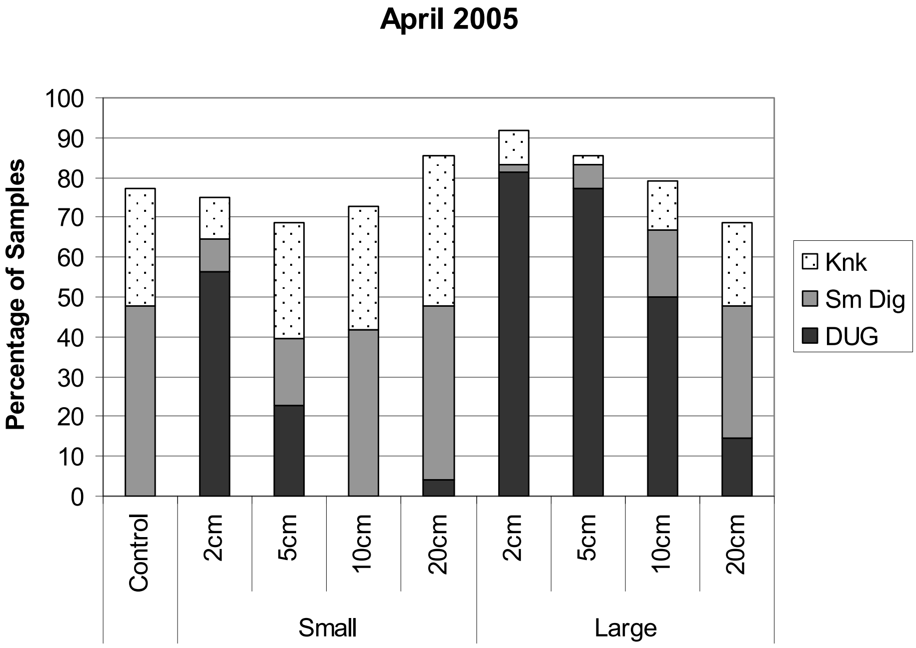
The percent of samples that were visited by bilbies and/or bettongs (either knocked, small digging or DUG) is shown in Figure 6.4. The overall level of visitation of all the treatments was higher in April 2005, especially for the smaller deeper caches. The small caches at 20 cm deep were visited more in April 2005 (85% of samples) than September 2004 (48% of samples). The percent of control samples that were visited was similar to the shallower small treatments and deeper large treatments, and slightly lower than for large caches buried 2 cm and 5 cm deep.

None of the DUG diggings were deeper than needed to obtain the rice cache. All diggings, including small diggings, were directly on the caches and there were no other diggings on the sites.

A few rice grains remained in either the digging or spoil of some of the DUG samples of both bilby and bettong diggings. At least 1 grain of rice remained at 20% of the DUG samples at small caches and at 38% of large caches in September 2004, and at 15% of small caches and 32% at large caches in April 2005.



(a)



(b)

Figure 6.4: The percentage of samples (over three nights) of each treatment where either the marker was knocked over (knk) or a small exploratory digging was made (Sm Dig) or the rice sample was dug up (DUG), during the (a) September 2004 and (b) April 2005 experiments. n=48 for both trials.

6.3.2 Foraging for native seeds

Bettong tracks were present at the most of caches of native seed species and the controls on the first night of the trial in July 2005, then again during the two nights before the final monitoring of the sites. Rain before and during this trial made it difficult to determine if or when bilbies visited the sites as the tracks of these smaller animals are less distinct than those of bettongs, but it is most likely that they visited and probably dug in both sites on at least the first night (personal observation).

All of the seed species were DUG, with a preference for *Acacia ligulata* and *Dodonaea viscosa* (Figure 6.5). The small exploratory diggings were mostly about 2 to 3 cm deep.

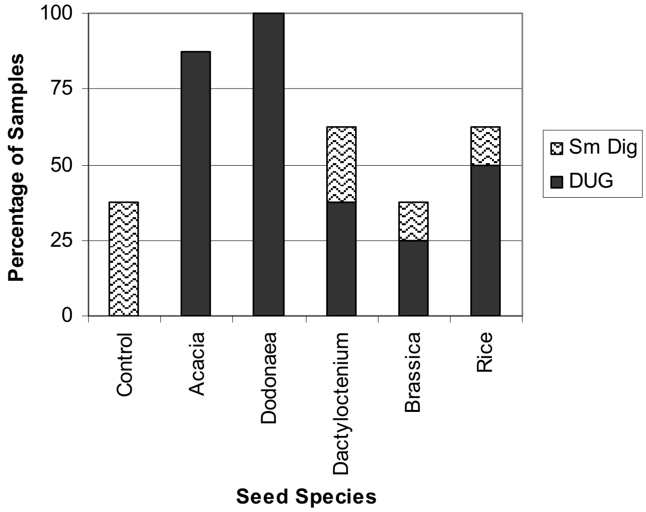


Figure 6.5: The percentage of samples of each seed species and the control at which a small exploratory digging was made (Sm Dig) or the sample was dug up (DUG). n=8.

6.3.3 Seed-harvester ant experiment

6.3.3.1 Location of seed caches

All of the eight *Pheidole sp.* ant nests excavated were similar in structure. Entrances were surrounded by conspicuous middens. The nest consisted of a main tunnel that went down almost vertically, either straight or in a slight spiral, to depths of 30 to 42 cm, depending on the hardness of the soil. This main tunnel then turned to run horizontally and was followed until it was lost (about 0.5 m in most cases). Very few side tunnels were found. Most of the tunnels contained only a few ants, and no eggs or larvae were found.

Ants removed between 41 and 100% (median 88%) of the 195 g rice that was fed to each of six nests in April 2005 and 26 and 31% of the rice fed to two nests in July 2005. Only a small portion of the rice taken into the nests was recovered during excavation (3 to 45% (median 19%) in April and 34 and 24%

in July) (Table 6.2). Although the nests were not observed during the 24 to 28 hours between feeding and excavation, there was no sign of ant trails going to other nests, or of ants carrying rice to nests other than the fed nest.

Table 6.2: The number of caches of blue rice found in each of the excavated harvester ant nest entrances (nests 1-6 in April 2005 and nests 7-8 in July 2005), and the depths and distances of these caches from the nest entrances, the size of the largest cache and the percentage of the rice taken by the ants that was recovered during excavation.

Ant Nest	No. of Rice Caches	Range of Rice Cache Depths (cm)	Range of Rice Cache Distance from Centre (cm)	Largest Cache of Rice (g)	Percentage of Rice Recovered (%)
1	4	1-18	0-45	19.2	13.5
2	5	1-14	0-28	4.8	2.8
3	8	5-28	0-60	11.3	24.5
4	6	2-30	2-39	9.7	27.4
5	6	5-16	1-18	14.7	9.9
6	10	2-40	0-100	18.1	45.3
7	2	3-10	0-2	10.0	24.0
8	6	3-42	0-44	10.0	34.1

The depth of caches containing rice ranged from 1 to 40 cm, with an average depth of 14.7 cm (s.e. = 1.7, n = 47). Most caches were found within 45 cm of the nest entrance, with one cache found 60 cm and another 100 cm away.

The size of the caches varied greatly, averaging 4.1 g (s.e. = 1.0, n = 47). Cache size increased with both increasing depth and increasing distance from the nest entrance in April, but not in July (Figure 6.6).

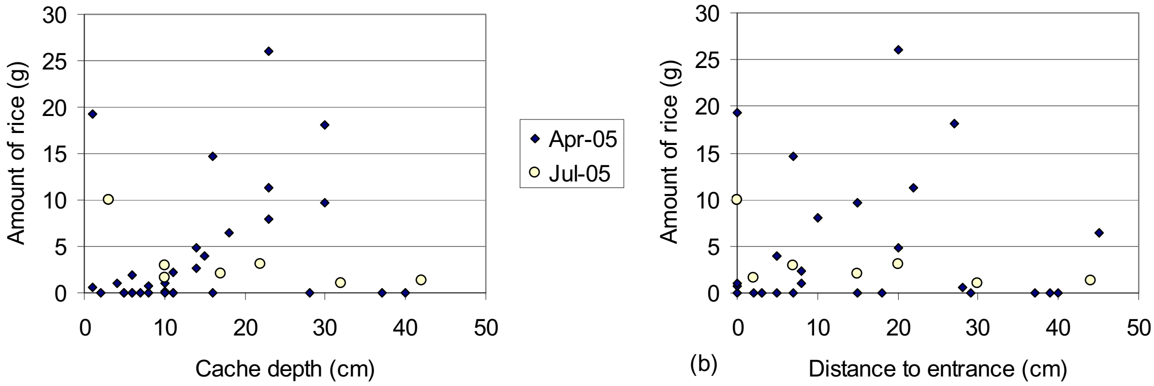


Figure 6.6: The size of rice caches compared to the (a) depth and (b) distance from the nest entrance found by excavation of the eight *Pheidole* sp. seed-harvester ant nests that had been 'fed' with rice in April and July 2005.

Twelve species of seeds were found cached within the nests (Table 6.3), though most of the individual caches contained only 1 to 3 seed species. Most of the caches were found within the main tunnel from the nest entrance and contained both blue rice and other seeds (40% of caches) or just blue rice (40% of caches). The total mass of seeds found in all the nests was less than 1% of the mass of the rice recovered, with considerably less seeds recovered from nests in July 2005 than April 2005.

The spoil heaps around the nest entrances contained a total of 8 species of seeds (Table 6.3), only a few of which were intact, and small pieces of plant material. Three spoil heaps also contained pieces of beetle shells and dead ants. Several grains of blue rice were deposited on the spoil heaps around the nest entrance of four of the eight nests, while 20 g of rice was deposited on the spoil heap of another.

Table 6.3: The species of seeds that were found on the spoil heaps and the number of seeds in the seed caches of the eight excavated *Pheidole* sp. ant nests (nests 1-6 excavated in April 2005 and nests 7-8 in July 2005). The shaded blocks show the seed species found on the spoil heap. The numbers of caches do not include caches that only contained blue rice.

Seed Species	*Pheidole* sp. ant nests							
	1	2	3	4	5	6	7	8
Acacia ligulata	1							
Brassica tournefortii	200					6	1	
Calotis hispidula	▨ 3		▨	▨	52			
Daisy sp.		▨ 50			▨ 51	1		▨
Dodonaea viscosa					2			
Enchylaena tomentosa							▨ 1	
Enneapogon sp.							▨	▨
Erodium cygnorum	▨ 10	▨ 3	▨	▨ 1	▨	▨ 13		1
Tetragonia sp.	▨ 50	▨ 3	▨	▨ 2	▨ 3	▨ 87	▨	14
Tribulus terrestris	3					1		
Salsola kali	▨	▨				▨ 27		
Sclerolaena sp.	25	1			▨ 12	▨ 26	▨ 8	▨ 3
Zygophyllum ammophilum					6	2		
Number of caches	3	3	0	2	2	8	1	2

6.3.3.2 Foraging at ant nests

Foraging diggings were observed at 15 (83%) of the 18 'fed' harvester ant nest entrances the morning after the ants had been fed rice. Tracks showed that some diggings were visited by both bilbies and bettongs. Faecal pellets of both species were also on the spoil of some diggings. However the shape and size of the diggings suggested that they were dug by bilbies (personal observation). Ants were active at most of the entrances at the time the diggings were recorded. There was no digging at any of the 22 control ant nest entrances.

The diggings were mostly at the entrance of the fed nests, though three diggings were a short distance away (5, 50, and 90 cm from a nest entrance). The average size of the diggings was 19 cm (s.e. 0.5) x 14.4 cm (s.e. 0.3) x 14.6 cm (s.e. 0.4) deep. The digging depths ranged from 5 cm to 25 cm (median 14 cm).

The amount of rice that the bilbies and/or bettongs obtained from the diggings could not be determined, although two to eight pieces of rice were found in 65% of the diggings and 76% of the spoil heaps.

6.4 DISCUSSION

6.4.1 Foraging for buried seeds

Both bilbies and bettongs were able to sense and dig for rice that was buried 20 cm deep, although they were more likely to dig for seed in shallower and larger caches. This is consistent with these animals using their sense of smell to locate the seeds, as the success of granivorous rodents that use olfaction to find seeds usually decreases as the depth of burial increases or as the seed cache size decreases (Lockard and Lockard 1971, Reichman and Oberstein 1977, Vander Wall 1998, Geluso 2005).

Soil moisture has been found to have a significant effect on the ability of granivorous rodents to locate buried seeds, as they are able to locate seeds more often in moist soil than dry (Johnson and Jorgensen 1981, Vander Wall 1995, Geluso 2005). The sand at the trial plots was visibly moist below the soil surface during the September 2004 trial, but dry during April 2005 (personal observation). The higher levels of exploratory activity, including knocking over markers and making small digs, and the lower probability of digging for small caches in April 2005 suggest that the animals may have been less able to locate smaller seed caches under these drier conditions.

Another difference between the September 2004 and April 2005 trials of this seed foraging experiment was the different interaction between cache size and depth. In September 2004, the probability that a certain size of cache would be dug was not dependent on the depth of cache, whereas in April 2005, the probability that a certain size of cache would be dug was dependent on cache depth. This difference between the two trials, along with the higher visitation of the small 20 cm deep samples in April 2005, suggests a difference in the intensity of foraging for the buried rice between the two trials. This could result from differences in soil moisture, in the bilbies and bettongs becoming familiar with rice as a food resource, or in the availability of alternative food resources.

The results of the small experiment with buried native seed species showed that as well as being able to detect and dig for rice, bettongs and possibly bilbies, will also dig for buried native seeds. Further experiments are needed to determine preferences for particular seed species and to what depth the bilbies and bettongs can detect these seeds.

As the tracks of both bilbies and bettongs were observed at many of the samples during the seed foraging experiment, further experiments in areas with only one species are needed to determine the relative contribution of each. Observations of diggings at buried supplementary food in pens at Arid

Recovery in which these species were kept separately indicated that both bilbies and bettongs will dig for food resources (unpublished data). Bettongs only dug rarely when they were first reintroduced to Arid Recovery in 1999 and held for a month in an eight ha release pen (K. Moseby, personal communication, 2008). Furthermore, bilby activity and/or numbers, but not bettong activity and/or numbers, as determined by track transects, was highly correlated with the rate of diggings, suggesting that the temporal variation in digging numbers was most strongly related to bilbies (Chapter 3).

Recent studies have demonstrated that human scent on seeds can increase their detection by granivorous rodents (Duncan *et al.* 2002, Wenny 2002). Although care was taken during this seed foraging experiment to keep human scent off the rice seeds, there still would have been olfactory (human scent on the soil) and visual (soil disturbance and paddle pop sticks) cues that would have indicated the location of the samples, but not necessarily the presence of seeds. Burrowing bettongs, in particular, are known to be curious about human disturbance (K. Moseby, personal communication, 2003). On several occasions during these trials, bettong tracks showed that the animals had explored all the sample locations. Therefore the results of this experiment might be influenced by the overall disturbance of the site, and the visual cues of the markers. Results could be confirmed by experiments using buried native seeds where markers are of natural materials and at a known distance from samples, and animals are prevented from accessing the site for a week before diggings are monitored to clear the sites of human scent (Duncan *et al.* 2002).

Rice was left in the digging or in the spoil heap of about 30% of the successful diggings in both trials of the seed foraging experiment and 80% of the diggings at rice-fed harvester ant nests. This suggests that foraging for buried seed may result in some buried seeds being moved to a shallower depth that might be more favourable for germination (Guo *et al.* 1998), as well as becoming more available to other seed predators like ants and rodents (Manzaneda *et al.* 2005). Similarly, Vander Wall (1993) observed that both deer mice and chipmunks left seeds at cache sites when digging. However since the relationship between predation, possible burial of seeds by ants and seed survival is very complex (Hughes and Westoby 1992, Manzaneda *et al.* 2005), it is not possible to predict whether the movement of buried seeds to the surface at bilby and/or bettong diggings would be ecologically important.

6.4.2 Foraging seed-harvester ant nests

Bilbies and/or bettong diggings at the *Pheidole* sp. ant nests to obtain the blue rice fed to the ants helps to confirm reports that bilbies obtain seeds from seed-harvester ant underground seed caches (Smyth and Philpott 1968, Johnson 1989, Gibson 2001, Southgate and Carthew 2006). The complete lack of digging at the unfed control nests suggests that the animals may only excavate these ant nests when large caches of seed are present, as feeding the colonies with rice greatly increased the amount of seed stored. The quantity of rice recovered from the excavated rice-fed nests was similar to the quantity of grass seeds found by Gross *et al.* (1991) in *Pheidole* sp. granaries in Northern Australia, and thus represents a realistic amount of seeds that could accumulate in ant caches during periods when seeds are abundant. As there is no readily available information on other granivores that forage on seeds from seed-harvester ant nests, the foraging at ant nests by bilbies and/or bettongs may be accessing a seed source that is not utilised by species other than the ants themselves.

The lack of structure other than a central tunnel with caches along the sides observed in the excavated ant nests is typical of *Pheidole* spp., which have narrow galleries and small chambers that are easily damaged by disturbance (Hughes 1990, Harrington and Driver 1995). Only small quantities of seeds were recovered from spoil heaps and the excavated *Pheidole* sp. nests. This might either show that overall seed availability was low at the time of the study, or that many seeds were missed during excavation either from incomplete excavation of seed caches, or that seeds were not seen because they were in caches without rice, or were too small to be recovered by sieving.

The depth of the caches of rice in the excavated *Pheidole* sp. nests ranged from 1 to 40 cm deep, similar to that observed by Harrington and Driver (1995) in western New South Wales (2 to 30 cm), but deeper than that observed by Hughes and Westoby (1992) near Sydney, New South Wales, (up to 9 cm deep) for nests of the same ant genus. As only about a fifth of the rice fed to the nests was recovered, and very few ants and no brood were found, it is likely that considerable parts of the ant nests were missed during excavation. Studies on other ant genera in North America have found that brood are often located in the deepest parts of the nests (Bristow *et al.* 1992, Mikheyev and Tschinkel 2004). The *Pheidole* sp. nests possibly also have seed caches in deeper areas of their nests that are rarely if ever foraged by bilbies and bettongs, and would thus protect both the ant colony and some of its stored seed from serious impacts by these fossorial animals. As ant caches are likely important sources of seeds for bilbies (Chapter4), further research on the architecture of the nests and impacts of bilby and bettong foraging on the nests is important for understanding the nature of the interactions of these taxa.

Another reason for the low recovery of rice from the ant nests may be that some of the rice was eaten by the ants. Hughes and Westoby (1992) fed *Pheidole* sp. nests plastic beads and seeds, and excavated the nests after two days, recovering 70% of the beads but only 30% of the seeds, suggesting that a large portion of the seeds taken by this *Pheidole* sp. was eaten soon after the seeds were collected.

Twelve naturally occurring species of seed were found in the excavated *Pheidole* sp. nests, similar to the number found in other seed-harvester ant nests (10 to 20 species) in western New South Wales

(Davison 1982). However, Gross *et al*. (1991) found that the nests of another *Pheidole* species in tropical Northern Australia often only contained one to three grass seed species, though the seed composition of the caches of seed-harvesting ants in the area varied between different ant species, between nests of the same species at different sites, and over time. In this present study the species of seed that were most abundant in the ant nests (*Brassica tournefortii, Calotis hispidula, Tetragonia* sp. and *Sclerolaena* sp.) were also abundant in the Mulga seed bank in April 2004 (Chapter 5), 15 months before the excavation of the ant nests, and thus may represent the most common seeds in this habitat.

If the bilbies (and possibly bettongs) were obtaining seeds from ant seed caches, it would be expected that the species of seeds in the seed caches would match the seeds seen in bilby and/or bettong diets. However, of the 13 seed species found in the nests and soil heaps of the ants, only five of these species were found in the diet (through faecal analysis) of the bilbies and bettongs during two separate studies, one year (Chapter 4) and four years (Bice and Moseby 2008) before the ant nests were excavated. This difference could indicate that the seed species in the ant caches may vary over time (Gross *et al.* 1991), that the bilbies and bettongs are very selective in the seeds they consume from ant caches, or that the bilbies and bettongs primarily forage from the seed caches of other ant species. Old foraging diggings were observed at several *Pheidole* sp. ant nests (personal observation), though the bilbies and bettongs may also be foraging from the nests of other seed-harvester ant species, as there is high species richness of ant fauna in this arid region (Read and Andersen 2000). As the nests of many seed-harvesting species are less conspicuous than the nests of the *Pheidole* species studied (Hughes 1990), diggings on these nests entrances would go unnoticed without more focused studies of these ants.

6.4.3 Conclusions

The ability of bilbies and/or bettongs to sense and dig for seeds buried up to 20 cm deep suggests that they would be able to use buried seed resources unavailable to other granivores at Arid Recovery. The trophic links between granivorous ants and bilbies and bettongs may be pivotal in seed bank dynamics at Arid Recovery as ants consume or bury surface seeds (Abramsky 1983, Hughes *et al.* 1994) and ant caches may both make very small seeds accessible to fossorial granivores like bilbies, and extend the period of availability of many seed species (Chapter 4). As ants may be the major granivore in arid areas (Predavec 1997), and bilbies possibly obtain many of their seeds from ant caches, more information on possible relationships between ants and bilbies at Arid Recovery would further clarify seed bank dynamics at the Reserve.

CHAPTER 7 Experimental evaluation of seed accumulation in foraging diggings of greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*)

7.1 INTRODUCTION

Greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) have been reintroduced to large, predator-free reserves within their former range, such as Arid Recovery in South Australia, as part of recovery efforts for both species and to assist in ecosystem restoration (Moseby and O'Donnell 2003, Finlayson and Moseby 2004). Since these are confined populations, it is important to monitor their environmental effects as part of their overall management.

Both bilbies and bettongs are omnivorous and make numerous foraging diggings (Johnson 1989). Martin (2003) proposed that these diggings were extremely important in the maintenance of soil structure, and dispersal of seeds and mycorrhizal fungi before the decline and local extinctions of these and other ground-foraging mammals following European settlement in Australia.. The reintroduction of these ground-foraging mammals to their former ranges could therefore assist in the rehabilitation of arid landscapes (Martin 2003, Byers *et al.* 2006, Noble *et al.* 2007b). Reintroduction projects such as Arid Recovery are providing important opportunities for research into these possible roles of bilby and bettong diggings in ecological restoration.

Foraging diggings are small-scale soil disturbances that can have both direct and indirect effects on the ecological processes of semi-arid and arid landscapes (Alkon 1999, Whitford and Kay 1999). Diggings form temporary soil pockets in which soil, water, organic matter and seeds accumulate, creating productive microhabitats which support higher plant densities, biomass and species richness than the surrounding soil matrix (Gutterman *et al.* 1990, Gutterman 1993, Boeken *et al.* 1995). Whitford and Kay (1999) reviewed research into the ecological importance of foraging diggings in semi-arid and arid regions from North America, South America, the Middle East and southern Africa, concluding that the effects of foraging diggings in all these regions have remarkable similarities across taxa and habitats. Research at Arid Recovery has confirmed that bilby and bettong diggings accumulate seeds and organic matter and facilitate seed germination (Sparkes 2001, James 2004, Chapter 3).

One component of an ecosystem that might potentially be affected by diggings is soil seed banks, since seeds both collect and become buried in diggings (Chapter 3 and 7). Soil seed banks are of vital importance as a source of regeneration and food supply (Janzen 1971, Chambers and MacMahon 1994), especially in arid regions where environmental conditions may be unfavourable to plant growth and survival for long periods of time. Surveys of the soil seed banks at Arid Recovery approximately four years after the reintroductions of both bilbies and bettongs found that in one of the major habitat types, sand dunes, seed densities in the top two cm of soil inside the Reserve were lower than those in an area where no bilbies or bettongs were present (Chapter 5). This lower soil seed bank density at Arid Recovery could be related to a combination of factors including granivory by the bilbies and bettongs, the redistribution of seeds in the seed banks by becoming buried in diggings, and natural variations between the study areas. The ecological consequences of this lower density of seeds in soil seed banks are unknown, though an understanding of the causes and potential future changes could assist in the management of the Reserve.

This chapter reports on an experiment using beads as seed mimics that was designed to determine to what extent the lower density of the shallow seed bank in dune habitat at Arid Recovery could be explained by the collection and burial of seeds in bilby and bettong foraging diggings. Seeds have been shown to accumulate in natural depressions (Reichman 1984), artificial depressions (Chambers 2000), bilby and bettong diggings at Arid Recovery (Sparkes 2001, James 2004, James and Eldridge 2007), and the foraging diggings of other species such as goannas (Whitford 1998) and porcupines (Boeken *et al.* 1995). However, little attempt has been made to quantify this accumulation, or to relate it to densities of seeds remaining in the soil matrix between diggings, or to the characteristics of the seeds.

Boeken *et al*. (1998) conducted a similar experiment in the Negev Desert of Israel using artificial diggings similar to those of Indian crested porcupine (*Hystrix indica*) to assess the impact of digging densities on plant diversity and productivity. They found that the number of seeds, plant density and productivity in the diggings decreased with increasing density of diggings, though this effect varied significantly between years, depending in part on the amount of rainfall.

This experiment asked the following questions: 1) Do seeds accumulate in bilby and bettong foraging diggings? 2) Does the density of diggings affect seed accumulation in diggings? 3) Does the accumulation of seeds in diggings affect the number of seeds remaining in the undisturbed soil matrix? 4) Could the accumulation of seeds in diggings explain the lower soil seed bank density found in Dune habitat inside the Reserve?

Beads were used to mimic seeds to control against the effects of seed predation. Three types of beads were used to emulate different mobility's of seeds.

7.2 METHODS

7.2.1 Site description

This study was conducted in Arid Recovery (30°29'S, 136°53'E), located approximately 20 km north of Roxby Downs in central South Australia. This 60 km^2 reserve is surrounded by a 1.8 m high predator-proof fence. All feral cats (*Felis catus*), foxes (*Vulpes vulpes*) and rabbits (*Oryctolagus cuniculus*) have been removed from the Reserve, and four locally extinct species reintroduced. These are greater bilbies (*Macrotis lagotis*), burrowing bettongs (*Bettongia lesueur*), greater stick-nest rats (*Leporillus conditor*) and western barred bandicoots (*Perameles bougainville*). For a more detailed description of the study site and the reintroduced species see Chapter 2.

Arid Recovery is located in the arid zone where the summers are hot (mean daily maxima exceeding 35°C in January and February) and winters are mild (mean minimum of 4.3°C in July) (Read 2002). The long-term average annual rainfall for this region is 166 mm, though this is variable and unpredictable.

The three main habitat types within the Reserve are longitudinal sand dunes dominated by sandhill wattle (*Acacia ligulata*) and sticky hopbush (*Dodonaea viscosa*), clay inter-dunal swales dominated by the chenopods bladder saltbush (*Atriplex vesicaria*) and low bluebush (*Maireana astrotricha*) and patches of mulga (*Acacia aneura*) woodlands.

This experiment was conducted in fairly level open areas along the crests of sand dunes in two separate management areas at Arid Recovery: the Inside area (14 km^2) where bettongs and bilbies were reintroduced in 1999 and 2000 respectively, and the Control area (6 km^2) where there were no reintroduced species. This experiment was conducted in both management areas in order to see if bilbies and bettongs decreased the number of seeds buried in diggings by foraging on seeds trapped in diggings.

Dune areas were used for this experiment as this habitat was the only one of the three main habitat areas in the study area where the shallow seed bank densities Inside were significantly lower compared with the Control (Chapter 5), and thus of interest to this experiment. In addition, dunes had large, flat and vegetation-free areas suitable for the experimental plots, and the soft sand was readily dug. The dune soil is fine red sand (approximate grain size range 0.1 to 0.5 mm) with very little clay.

7.2.2 Experimental plots

This experiment tested seed accumulation in diggings at four different densities: none, low (1 digging m^{-2}), medium (3 diggings m^{-2}) and high (6 diggings m^{-2}) (Figure 7.1). These represent the range of densities of bilby and bettong diggings that were found in Arid Recovery at the time of this experiment (Chapter 3).

Three replicate sets of experimental plots of the four digging densities were established in both the Inside and Control areas, with the different density plots placed in a random order within each set. Each plot within a set was 5 to 10 m apart with 50 to 100 m between each set.

Each experimental plot was 2 m x 2 m, with the inner 1 m^2 of each plot considered the test area, leaving a 0.5 m buffer to minimise edge effects. The artificial diggings were randomly spaced in the plots to give the required density of diggings both in the central test area and the edge areas (Figure 7.1). These diggings were approximately 8 x 9 x 10 cm deep, round bottomed, and slightly angled away from the vertical to simulate an 'average' bilby and/or bettong digging (Chapter 3). The locations of these artificial diggings in the central test area were recorded as the distances to the centre of the digging from the two nearest pegs at the corners of the plots.

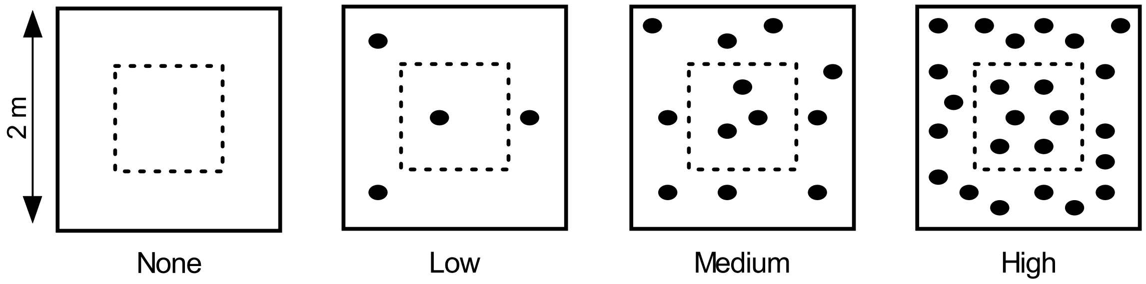


Figure 7.1: Diagram of one set of the four digging densities of the experimental plots that were used for this experiment, showing the inner 1 m^2 test area (dotted line) and the four digging densities – none, low (1 digging m^{-2}), medium (3 diggings m^{-2}) and high (6 diggings m^{-2}). The black dots represent diggings which were randomly spaced over the experimental plots.

Three types of beads were used to mimic seeds: plastic beads to mimic wind-blown seeds, and two sizes of glass beads to represent less mobile seeds (Table 7.1, Figure 7.2). The plastic beads were applied to all plots before the artificial diggings were made in order to simulate antecedent seed rain. Glass A and glass B beads were applied after the diggings had been made in order to simulate a burst of post-digging seed rain. All beads were applied as evenly as possible using a shaker. Only enough glass beads were available for one plot of each digging density in each of the Inside and Control areas.

Table 7.1: The characteristics of the three types of beads that were used to mimic seeds in this experiment and the amount of each applied to the plots. The plastic beads were applied to all of the experimental plots while the glass A and B beads were applied to only one set of the experimental digging density plots in each of the Inside and Control areas of the Reserve.

Type of Bead	Composition	Shape	Diameter (mm)	Mass (mg/bead)	Amount per plot	When applied
Plastic	White plastic	Roughly spherical	3	25	40 g (1640 beads)	Before digging
Glass A	Clear glass	Spherical	2.5	25	27 g (1100 beads)	After digging
Glass B	Purple glass	Short cylinder with centre hole	1.5	12.5	9 g (750 beads)	After digging

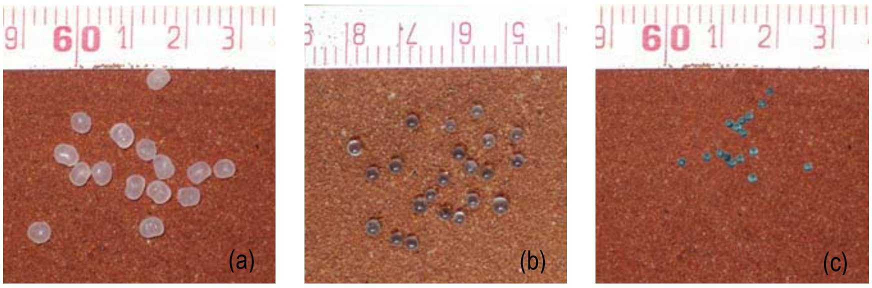


Figure 7.2: Examples of the three types of beads used to mimic seeds in this experiment: (a) plastic, (b) glass A, and (c) glass B beads.

7.2.3 Sampling of the beads

The plots were established in September 2004, and were sampled 18 weeks later in January 2005. Twenty-nine mm of rain fell a few hours after the experimental plots were finished. The weather during the 18 weeks between establishing the plots and sampling was unusually windy (B. Hill, personal communication, 2005), with a further 80 mm of rain, about half the yearly average for Arid Recovery.

At the time of sampling, most of the diggings and all of the spoil heaps were no longer visible on the experimental plots, with only a few slight depressions remaining. A scattering of plastic, glass A and glass B beads was still visible on the surface, although very few plastic beads could be seen on the plots in the Inside area of the Reserve.

Each experimental plot was sampled by excavating all of the diggings in the 1 m^2 inner test area and 5 randomly placed samples of the undisturbed soil matrix between the diggings. Diggings were located by triangulation using the recorded distances from two corner pegs. Both the diggings and control samples were excavated using a length of bore casing (15 cm diameter), which was placed over the estimated centre of the diggings and hammered into the ground. The soil was then removed in layers (surface, 0-2, 2-4, 4-6, 6-8, 8-10, 10-15 and 15-20 cm), and sieved through a 1 mm sieve to collect the beads and naturally occurring seeds, which were then sorted and counted. The correct location of the diggings was confirmed by the presence of litter in the excavated sand and beads.

The horizontal dispersal of the beads outside the experimental plot was assessed by excavating a strip 1 m wide and 6 cm deep around the perimeter of one high density digging plot in the Control area.

7.2.4 Data Analysis

The number of beads/seeds that had accumulated in the diggings was compared to the undisturbed soil matrix and between the digging densities using the non-parametric Kruskal-Wallis H test (SPSS 2007).

Estimates of the percentage of beads applied that still remained on the plots was calculated for each digging density by estimating the number of beads remaining on the plots using the average number of beads on the undisturbed soil matrix and the average of the total number of beads that had accumulated in the diggings at each digging density.

7.3 RESULTS

7.3.1 General observations

Observations of the experimental plots two days after establishment found that the rainfall had washed sand and beads into most of the diggings, leaving them between approximately 70 to 90% of their original depths. Examples of the plots after they were established, after the initial rainfall and at the time of sampling are shown in Figure 7.3.

On Inside plots, bettong tracks and tail drag marks showed that the animals had explored the diggings in many of the plots. Plots with bettong tracks, especially those with high densities of diggings, generally had fewer plastic beads visible both on the soil matrix and in the diggings than plots without tracks (Figure 7.3). A group of 22 beads had been moved about 2 m upslope from one of the plots, and deposited in a pile on the sand.

At the time of sampling in late January 2005, most of the diggings had filled in with only a few slight depressions remaining, and all of the spoil heaps had disappeared. A scattering of plastic, glass A and glass B beads was still visible on the sand in the Control area, but very few plastic beads and mainly glass beads with could be seen on the Inside plots.

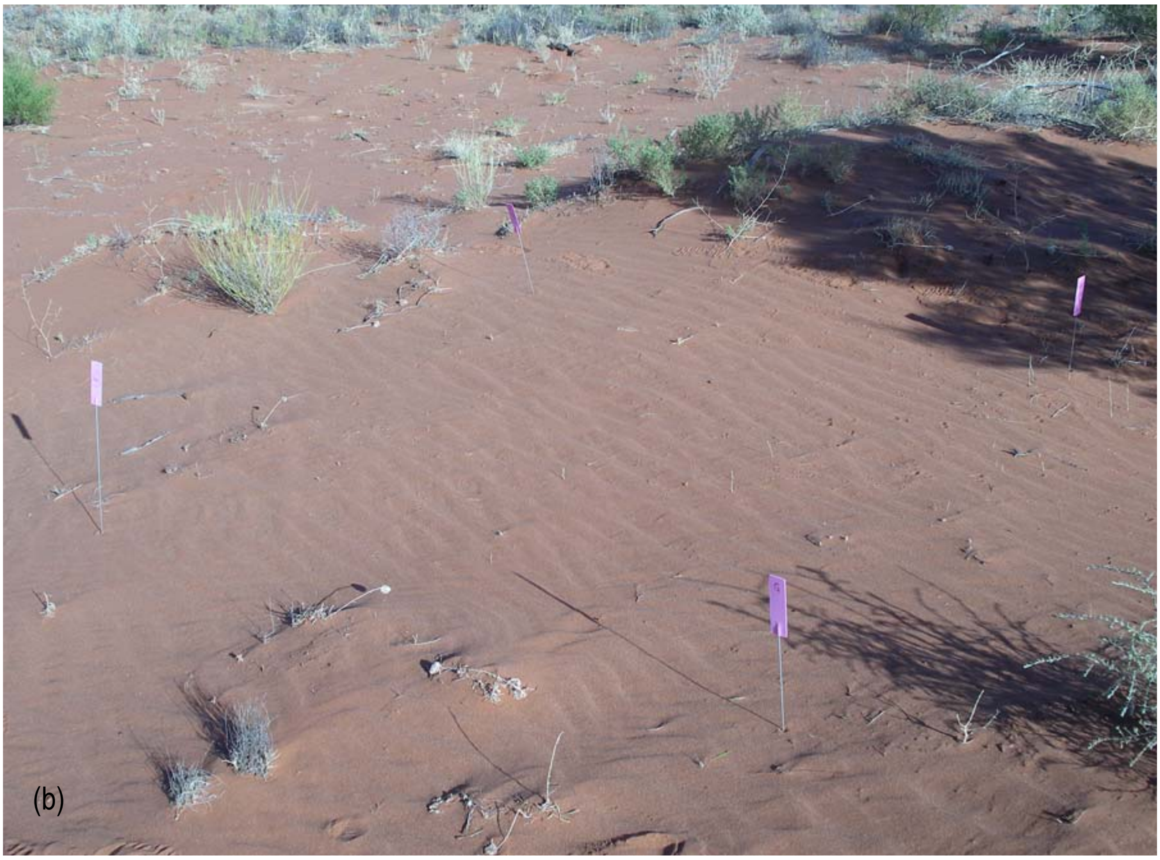


Figure 7.3: Photographs of the experimental plots: (a) a high density plot immediately after site the site was established, (b) a plot after 18 weeks at the sampling time, and two of the experimental plots two days after they were established following 27 mm rain, and (c and d) two of the experimental plots following 27 mm rain just after they were established: (c) a high density site in the Inside area showing bettong tracks exploring diggings, and (d) a high density site in the Control area with plastic beads visible on the sand surface.


(c)
(d)

7.3.2 Bead and seed accumulation in diggings

7.3.2.1 Plastic beads

In the Control area, the average number of plastic beads trapped in each digging decreased significantly as the digging density increased (H = 15.5, d.f. = 2, p <0.001) (Figure 7.4). The total number of plastic beads recovered from the diggings of each plot was highest for the medium digging density, which was on average 71% of the number of beads that were applied to the inner 1 m^2 test area of the experimental plots.

Very few plastic beads were recovered from the diggings in the Inside area with the bilbies and bettongs (Figure 7.4).

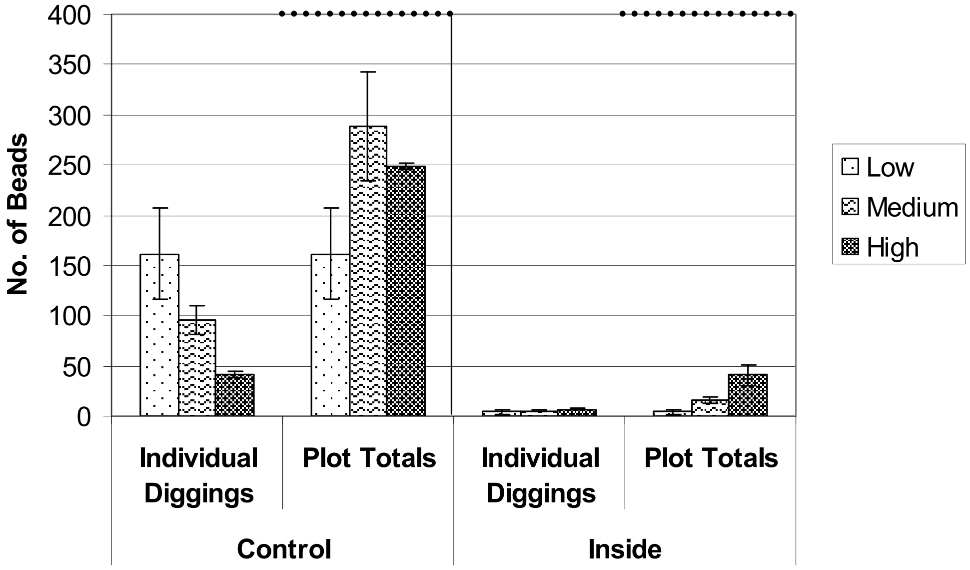


Figure 7.4: The mean (±s.e.) number of plastic beads recovered from the individual diggings for each digging density, and the mean (±s.e.) total number of beads recovered from the diggings within the test areas of the experimental plots. Digging densities: Low: 1 dig m^{-2}, Med: 3 dig m^{-2}, High: 6 dig m^{-2}. The dotted line shows the number of plastic beads that were applied to the inner test areas of each of the plots (400 plastic beads). Four times this number of beads was applied to the total area of the experimental plots, some of which could have moved into the inner test area. Individual diggings: Low: n = 3, Med: n = 9, High: n = 18; Plot totals: n = 3 for each density.

7.3.2.2 Glass beads

The number of beads recovered from in the diggings was similar between the two experimental areas for both glass A and glass B beads (Figure 7.5). Only trends could be determined between the different digging densities as there was only one replicate plot for each digging density for each type of glass bead. As there was little difference in the number of beads per digging between the digging densities, the total number of beads recovered from the diggings of each plot increased with increasing digging density for both glass A and B beads (Figure 7.5). A higher proportion of the applied glass B beads (maximum 94%) were recovered from diggings than for the glass A beads (maximum 72%).

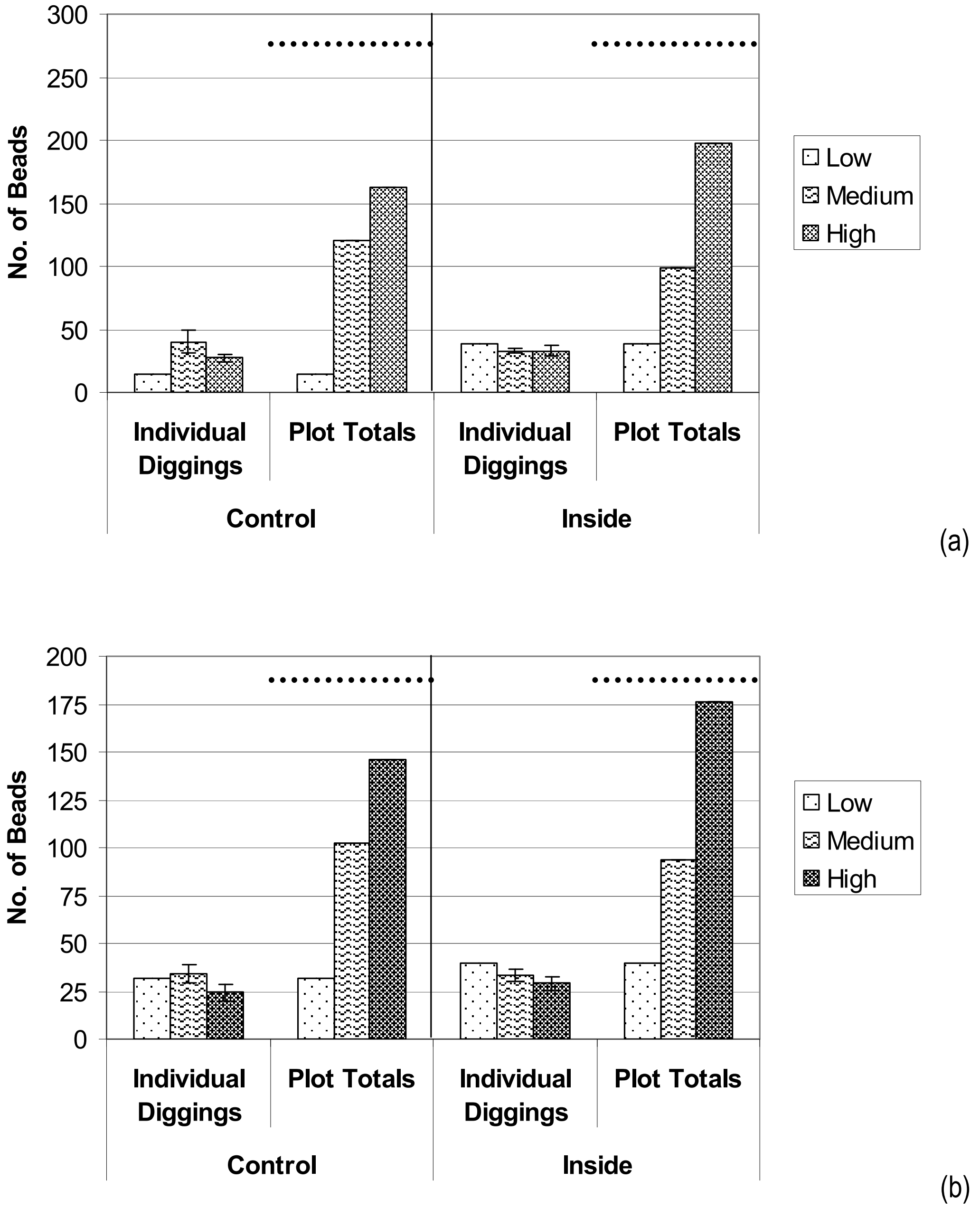


Figure 7.5: The mean (±s.e.) number of (a) glass A and (b) glass B beads recovered from the individual diggings for each digging density, and the mean (±s.e.) total number of beads recovered from the diggings within the test areas of the experimental plots. Digging densities: Low: 1 dig m^{-2}, Med: 3 dig m^{-2}, High: 6 dig m^{-2}. The dotted line shows the number of beads that were applied to those central test areas of each of the plots (glass A – 275, glass B - 185 beads). Four times this number of beads was applied to the total area of the experimental plots, some of which could have moved into the inner test area. Individual diggings: Low: n = 1, Med: n = 3, High: n = 6; Plot totals: n = 1 for each density.

7.3.2.3 Naturally occurring seeds

The number of seeds in the diggings was not significantly different between the different digging densities in either the Control (H = 1.9, d.f. = 2, p = 0.38) or Inside (H = 3.4, d.f. = 2, p = 0.19) areas, though there was a trend in both areas towards fewer seeds with increasing digging density (Figure 7.6). The overall pattern of seed capture was very similar to that shown for plastic beads (Figure 7.4), especially for the Control area.

Overall 25 species of seeds were found in the diggings and surrounding soil matrix (Appendix 7.1). The majority of the seeds were the wind-dispersed seeds of *Polycalymma stuartii* (87.7% and 24.4% of the seeds from the Control and Inside areas respectively), possibly as this annual daisy species was seeding at the time of the beginning of the experiment. *Brassica tournefortii,* a small-seeded annual weed that was also seeding at the beginning of the experiment, was the second most abundant seed (1% and 58% of the seeds from the Control and Inside areas respectively).

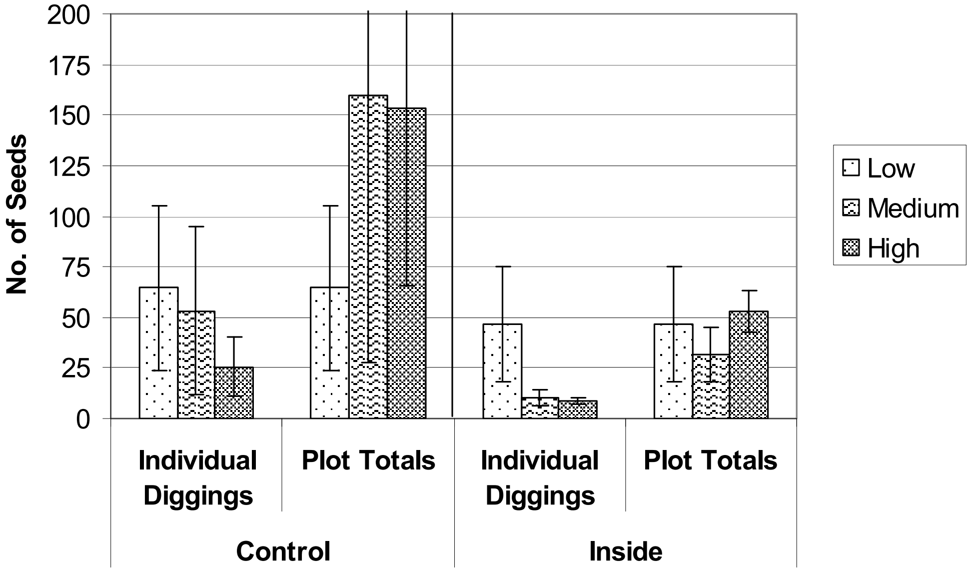


Figure 7.6: The mean (±s.e.) number of naturally occurring seeds recovered from the individual diggings for each digging density, and the mean (±s.e.) total number of beads recovered from the diggings within the test areas of the experimental plots. Digging densities: Low: 1 dig m^{-2}, Med: 3 dig m^{-2}, High: 6 dig m^{-2}. Individual diggings: Low n = 3, Med n = 9, High n = 18; Plot totals: n = 3 for each density.

7.3.2.4 Vertical distribution in diggings

The three types of beads recovered had similar vertical distributions in the diggings (Figure 7.7), with little difference between digging densities or experimental areas. However, the depth distribution of the naturally occurring seeds was different from that of the beads, with proportionally more seeds in the 0 to 4 cm depths, and proportionally fewer seeds at 10 to 15 cm depth (the depth of the diggings).

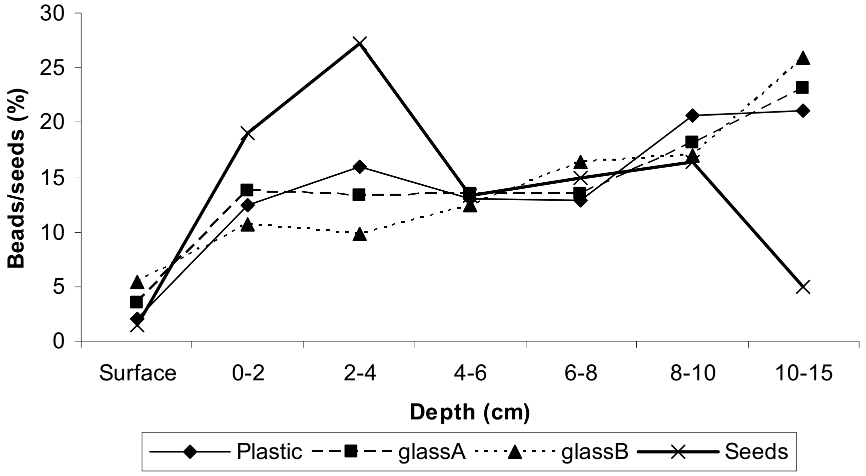


Figure 7.7: The average percentage of the three types of beads and the naturally occurring seeds recovered from the diggings that were buried at each depth. For each type of beads and the seeds, the data plotted is calculated from the pooled data from both areas and all density of diggings, as the plots were graphically similar for both areas and digging densities.

7.3.3 Undisturbed soil matrix

Substantially lower numbers of all three types of beads were recovered from the soil matrix between diggings than were applied, especially for plastic beads (Table 7.2). Significantly fewer beads were recovered from the undisturbed soil matrix than the diggings (plastic: H = 105.5, d.f. = 1, p <0.001; glass A: H = 35.8, d.f. = 1, p <0.001; glass B: H = 36.4, d.f. = 1, p <0.001) showing that all three types of beads had moved from the matrix and accumulated in the diggings. Numbers of naturally occurring seeds were also significantly lower in the matrix than in diggings (H = 57.3, d.f. = 1, p <0.001).

Very few plastic beads were recovered from the undisturbed soil matrix of the experimental plots in the Control area, and none were recovered in the Inside area (Table 7.2). The number of plastic beads that were recovered from the soil matrix of the Control area increased with increasing digging density (H = 8.2, d.f. = 3, p = 0.04). All these beads were on the soil surface or buried less than 2 cm deep.

Both the glass A and glass B beads showed a trend of decreasing numbers recovered from the soil matrix with increasing digging density in both areas (Table 7.2). The density of Glass A beads on the matrix was generally higher than Glass B beads. Most of these beads remained on the soil surface or buried less than 4 cm deep, although two glass B beads were recovered from 6 to 8 cm deep.

There were low numbers of naturally occurring seeds in the soil matrix, with no significant differences between the digging densities (Inside area: H = 4.7, d.f. = 2, p = 0.09; Control area: H = 4.9, d.f. = 3, p = 0.92) (Table 7.2). These seeds were found down to 20 cm deep, although 16% were found on the soil surface and another 49% buried less than 4 cm deep. As no attempt was made to remove naturally-occurring seeds from the soil seed bank in the experimental plots before the experiment, many of these seeds, especially the deeper ones, may have been present before the beginning of the experiment.

Table 7.2: The mean (±s.e.) number of beads in 0.018 m^2 of the undisturbed soil matrix of the experimental plots. The number of bead that were applied to the area sampled: plastic - 7, glass A – 2.6, glass B – 3.3. n/a refers to experimental plots where the soil matrix was not sampled due to time constraints. n (plastic and seeds) = 3, n (glass) = 1.

Digging Densities	Plastic		Glass A		Glass B		Seeds	
	Control	Inside	Control	Inside	Control	Inside	Control	Inside
None	0.07 (±0.07)	0	n/a	n/a	n/a	n/a	1.73 (±0.64)	n/a
Low (1/m^2)	0	0	2.60 (±0.24)	2.80 (±1.2)	1.60 (±0.24)	1.00 (±0.55)	1.27 (±0.28)	1.8 (±0.58)
Medium (3/m^2)	0.47 (±0.27)	0	2.00 (±0.55)	3.00 (±1.3)	1.40 (±0.93)	1.80 (±0.97)	2.33 (±0.92)	3.6 (±0.93)
High (6/m^2)	0.53 (±0.24)	0	1.00 (±0.63)	1.60 (±0.24)	0.20 (±0.20)	0.60 (±0.40)	1.27 (±0.43)	1.2 (±0.97)

7.3.4 Overall recovery of beads from plots

The overall percentage of the applied beads that remained on the plots was generally highest in the medium digging density and lowest in the low density of diggings (Table 7.3). A very low percentage of plastic beads were recovered from any of the plots in the Inside area.

Table 7.3: Estimates of the percentage of beads that were applied that remained on the plots of each digging density in the two sections of the Reserve. n (plastic) = 3, n (glass) = 1. Dig density: Low: 1 dig m^{-2}, Med: 3 dig m^{-2}, High: 6 dig m^{-2}.

Dig Density	Plastic		Glass A		Glass B	
	Control	Inside	Control	Inside	Control	Inside
Low	39.4	2.7	58	70.4	59.8	51.9
Med	72.5	3.7	83	94.5	97.5	105.3
High	63	9.9	77.7	101.4	84.6	112.9

More plastic beads than glass beads were found to have dispersed into the 1 m wide strip outside the experimental plot. For plastic beads, 4.9% of the beads applied were up to 50 cm away from the edge of the plot, and 2.4% were 50 to 100 cm away. A further 4% were found several metres away in a downwind direction. For glass beads, 1.5% of glass A beads, and 1.7% of glass B beads were recovered from less than 50 cm from the edge of the plot, and none 50 cm to 100 cm away.

7.4 DISCUSSION

The three types of beads, used to mimic seeds in this experiment, accumulated and were buried in the artificial diggings, which were similar in size and shape to the diggings of greater bilbies (*Macrotis lagotis*), and burrowing bettongs (*Bettongia lesueur*). Naturally occurring seeds, especially wind-blown seeds of the daisy *Polycalymma stuartii*, were also recovered from the diggings in significantly higher numbers than they were found on the soil matrix between the diggings. This confirms previous studies at Arid Recovery that also found that seeds accumulate in bilby and bettong diggings (Sparkes 2001, James 2004, Chapter 3).

The plastic and glass beads in this experiment showed different patterns of retention on the experimental plots and of accumulation in the diggings. Gutterman *et al.* (1990) and Boeken and Shachak (1994) found that diggings had a sorting effect for seeds by dispersal mode of that seed, with higher numbers of runoff and wind-dispersed seeds, and of larger seeds accumulating in diggings. Chambers *et al*. (1991) demonstrated that seed morphology, in particular the surface area of a seed, would affect its horizontal movement across the soil surface. Therefore, as the plastic beads were relatively light and had a large surface area, they would have been expected to be more mobile than the smaller, denser glass beads, and therefore accumulate more in the diggings. As predicted, fewer plastic than glass beads remained on the surface of the plots and remained on the plots overall. However, only an equal or smaller proportion of the plastic beads applied than the glass beads were captured in the diggings.

The use of the three types of beads in this experiment also demonstrated that the way the density of diggings affected the accumulation of seeds in diggings depended on seed morphology. The number of plastic beads trapped in each digging decreased with increasing digging density, suggesting that at high densities, diggings interfered with each other in the capture of the limited number of these relatively mobile beads, similar to that shown by Boeken *et al*. (1998) for seeds. As digging density increased, the available area from which a digging drew its seeds decreased until the areas ‘accessed’ by adjacent diggings overlapped, and the number of beads captured per digging decreased.

Digging density, however, may have much less effect on the accumulation of less mobile seeds, as the digging density did not affect the numbers of both glass bead types that were trapped in each of the diggings. This suggests that for these less mobile beads there was no interference between the diggings, possibly because the area of matrix acting as a source for each digging was small enough to have little or no overlap with the collection area of adjacent diggings.

The effect of digging density on the accumulation of the naturally occurring seeds was similar to that of the plastic beads, with seed numbers per digging decreasing with increasing digging density. As the majority of the seeds captured in the digging were the relatively large, wind-blown seeds of *P. stuartii*, it is likely that they dominated this pattern.

The pattern of numbers of beads that remained on the soil surface of the different digging density plots was different for the plastic and glass beads. The numbers of plastic beads on the soil surface increased with increasing digging density, probably as they were buried by the spoil from the diggings as the beads were applied before the diggings were made. The number of glass beads, which were applied after the diggings, showed a trend of decreasing numbers remaining on the matrix with higher digging densities. Boeken *et al.* (1998) found that the density of seedlings growing on the soil matrix during a similar experiment on the capture of seeds by different digging densities in the Negev Desert of Israel also decreased with digging density although these trends were not significant, and only apparent during the driest of the three years of the experiment.

The main aim of this experiment was to explore whether the lower density of the shallow dune seed bank in the Inside area at Arid Recovery (Chapter 5) could be explained by the collection and burial of seeds in bilby and bettong foraging diggings. The lack of a significant decrease of bead numbers remaining in the soil matrix suggests that in the short term, accumulation of seeds in diggings may have little effect on the soil seed bank density. However, the high percentage of the beads applied to the plots that accumulated in the diggings suggests that in the longer term, seed accumulation in diggings could be a factor that would affect the seed density of the soil seed banks. The overall impact would depend on many factors including the intensity, distribution, and timing of seed rain (Chambers and MacMahon 1994), the morphology of the seeds (Chambers *et al.* 1991) and the density of diggings at the time of seed rain (Boeken *et al*. 1998).

Accumulation of seeds in diggings does not remove them from the soil seed banks, but merely redistributes them. The depth profiles of all three bead types in the diggings were similar to each other but were different from that of naturally occurring seeds, which had a higher proportion buried more shallowly (Figure 7.7). The diggings were partially filled and beads washed into them by rain shortly after the experiment was commenced, resulting in the similar depth profiles of all bead types. In addition, the depth of burial of a large portion of the beads was more similar to the original depth of the diggings than to the depth of the digging after the rain. By contrast, most of the seeds recovered from the diggings would have come from transient seed populations over a longer period of time. Excavation of the seeds that had accumulated in bilby and bettong diggings found a similar depth profile to that of the naturally occurring seeds during this experiment (unpublished data). This shows that rather than decreasing the number of seeds in the shallow soil seed bank, seeds accumulating in diggings may just increase the patchiness of their spatial distribution. However, since these patches may be missed during sampling to determine seed bank density, seed capture by diggings might result in seed bank densities being underestimated.

Plastic and glass beads were used to mimic seeds in order to study the abiotic effects of wind and rain on the capture of seeds by foraging diggings without the influence of seed predation. Similar beads have been successfully used to replace seeds in other studies because of their ease of recovery and resistance to predation (e.g. Andresen 2002, Hampe 2004, Mohler *et al.* 2006). However, the disappearance of the majority of the plastic beads from both within the diggings and the soil matrix, in the Inside area of the Reserve suggests that ‘predation’ of these beads occurred, probably by the bettongs and/or bilbies, as the presence of these species was the main faunal difference between the Inside and Control areas of the Reserve.

Observations and historical records suggest that bettongs rather than bilbies are more likely to have removed the plastic beads. Bettongs are particularly curious of foreign objects (personal observation). Historical records have also noted that burrowing bettongs cached seeds such as wheat (Abbott 2008), desert quandong (*Santalum acuminatum*) and turpentine bush (*Eremophila sturtii*) (Noble *et al.* 2007a). Another species of bettongs, woylies (*Bettongia pencillata*), has also been shown to cache seeds of quandong (*Santalum spicatum*) (Murphy *et al.* 2005). Although bettongs have not been observed to cache seeds at Arid Recovery, it is possible that bettongs may only cache seeds when they are in abundant supply, similar to caching of fruit by musky rat kangaroos (*Hypsiprymnodon moschatus*) (Dennis 2003).

Bettongs and/or bilbies may have also removed plastic beads from within the diggings as well as the soil surface, as although beads were washed into the diggings during the rain just after the establishment of the sites, very few were recovered from the diggings (personal observation). This suggests that bettongs and/or bilbies may use old diggings as concentrated sources of seeds, known as the treasure effect (Gutterman 1987, Claridge and Barry 2000). Granivorous rodents, and bilbies and bettongs, have been shown to preferentially forage large clumps of seeds over smaller clumps, either on the soil surface or buried (Reichman and Oberstein 1977, Reichman 1979, Cabin *et al.* 2000, Chapter 6). Thus this treasure effect might effectively increase the number of seeds eaten, as seeds eaten from diggings might have otherwise not been eaten when more scattered on the soil matrix between diggings.

The relatively low numbers of naturally occurring seeds recovered from diggings in both Inside and Control areas in this experiment suggests that spinifex hopping-mice (*Notomys alexis*), which were present in large numbers in both study areas (Arid Recovery 2006) might also forage on seeds captured in diggings, as well as possibly bilbies and bettongs. Hopping-mice consumed a wide variety of seeds during seed dish experiments in both Inside and Control areas, making it impossible to estimate seed consumption by bilbies and bettongs (Appendix 1), but confirming that hopping-mice forage on surface seeds (Murray and Dickman 1997). The alternative possibility for the low numbers of seeds buried in diggings during this experiment, that seed rain was low during this period, is somewhat unlikely as the beginning of this experiment in September 2004 was during a burst of winter flowering not seen in the region for 10 years following 82 mm of rain in May and June 2004 (Arid Recovery 2005)

The results of this experiment suggest that capture of seeds by diggings might be a factor in reducing the measured density of shallow seeds in the seed banks in dunes in the area with bilbies and bettongs. Additional research over longer periods of time, and focused on different seed morphologies and patterns of seed rain is needed to further evaluate the importance of diggings on the distribution of seeds in the seed banks.

APPENDIX 7.1

The seed species and average number of naturally occurring seeds of each species that were recovered from the diggings and the surrounding soil matrix in the experimental plots. Values are number seeds (± s.e.) per digging or equivalent area of matrix, and are for all digging densities combined, as digging density had no significant effect on the number of seeds in diggings or on the soil matrix.

	Control Area		Inside Area	
	Digging (n = 30)	Matrix (n = 60)	Digging (n = 30)	Matrix (n = 15)
Acacia aneura	0	0	0.03 (±0.03)	0
Atriplex vesicaria	0.07 (±0.07)	0	0	0
Aristida contorta	0.10 (±0.06)	0.13 (±0.08)	0	0
Boerhavia sp.	0.10 (±0.06)	0.05 (±0.04)	0	0
Brassica tournefortii	0.40 (±0.18)	0.05 (±0.03)	7.7 (±2.8)	0.60 (±0.35)
Calotis hispidula	0.03 (±0.03)	0	0	0
Crotalaria eremaea	0.93 (±0.30)	0.20 (±0.07)	0.07 (±0.05)	0.07 (±0.07)
Cucumis myriocarpus	0	0	0.03 (±0.03)	0
Dodonaea viscosa	0.30 (±0.12)	0.32 (±0.12)	0.47 (±0.13)	0.33 (±0.23)
Enchylaena tomentosa	0	0.03 (±0.03)	0.07 (±0.05)	0
Euphorbia drummondii	1.53 (±0.75)	0.1 (±0.06)	0.17 (±0.10)	0
Paractaenum novae-hollandiae	0.73 (±0.22)	0.28 (±0.11)	0.30 (±0.18)	0.27 (±0.12)
Phyllanthus lacunarius	0.03 (±0.03)	0	0.23 (±0.09)	0.33 (±0.23)
Polycalymma stuartii	32.9 (±15.26)	0.2 (±0.08)	3.1 (±1.12)	0.07 (±0.07)
Sclerolaena sp.	0.03 (±0.03)	0	0	0
Sida ammophila	0.33 (±0.15)	0.13 (±0.06)	0.57 (±0.20)	0.13 (±0.13)
Trachymene glaucifolia	0.07 (±0.05)	0.05 (±0.03)	0	0
Tribulus terrestris	0.03 (±0.03)	0.03 (±0.02)	0	0
Triraphis mollis	0	0.02 (±0.02)	0	0
Zygophyllum ammophilum	0	0	0.03 (±0.03)	0.07 (±0.07)
Unknown A	0.13 (±0.08)	0.07 (±0.03)	0.27 (±0.10)	0.27 (±0.15)
Unknown B	0	0	0	0.07 (±0.07)
Unknown C	0.03 (±0.03)	0	0	0
Unknown D	0	0	0.07 (±0.05)	0
Unknown E	0	0	0.07 (±0.05)	0
TOTAL number of species	17	14	15	10
Average number of seeds	37.80 (±15.5)	1.65 (±0.31)	13.13 (±3.5)	2.2 (±0.53)

CHAPTER 8 General discussion

Arid Recovery has successfully reintroduced greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) as a step towards achieving its goal of facilitating the restoration of arid zone ecosystems in Australia (Arid Recovery 2006). This thesis has evaluated some of the changes these faunal reintroductions, and the removal of feral predators and rabbits, have made to ecosystem functioning and to the restoration of these ecosystems, and recommends future directions for management and research.

8.1 ECOLOGICAL ROLES OF BILBIES AND BETTONGS

The results of this study showed that bilbies and bettongs have three major roles in ecosystem functioning: as consumers, as ecosystem engineers, and as dispersers of seeds and fungi.

8.1.1 Consumers

Both the bilbies and bettongs were both omnivorous, as both species consumed both above-ground and underground food resources including root-dwelling larvae, fungi, roots and seeds (Bice and Moseby 2008, Chapter 4). The seeds, at least in part, were likely obtained from the underground seed caches of seed-harvester ants (Johnson 1989, Gibson 2001, Southgate and Carthew 2006, Bice and Moseby 2008, Chapter 4 and 6). By accessing buried foods, bilbies use food sources not generally available to other species (Murray and Dickman 1994), except possibly goannas (*Varanus gouldii*) (Whitford 1998). In addition, bilbies are the only extant mammal in Australia, other than man, known to make extensive use of the seeds from monocot species (Southgate and Carthew 2006, Chapter 4).

Both bilbies and bettongs demonstrated dietary flexibility, with large differences in the species of seeds consumed between this study (Chapter 4) and a dietary study three years previously, shortly after the animals were reintroduced to Arid Recovery (Bice and Moseby 2008). Lower density of seeds of many grasses in the seed banks in Inside areas with bilbies and bettongs (Chapter 5), and greatly reduced consumption of grass seeds by bilbies during this study compared with three years previously (Chapter 4) both suggest that increased consumption of these seeds by bilbies has indeed changed their availability. Possible contributing factors to these dietary changes include (a) increased competition for seeds by the three to seven-fold increase in bilby and bettong numbers, (b) differences in seed production resulting from different rainfall patterns between studies, (c) possible changes in seed production resulting from herbivory by bilbies and bettongs and the loss of herbivory by rabbits, and (d) the effects of diggings on productivity. More detailed evaluation of the reasons for these changes in diet was not possible because of lack of data on the phenology and productivity of dietary plant species during both studies, and on the effects of herbivory by bilbies, bettongs, and rabbits on specific plant species.

8.1.2 Ecosystem engineers

This study demonstrated that bilbies and bettongs have important roles as ecosystem engineers as suggested by Martin (2003) and James and Eldridge (2007). The bilby and bettong diggings covered on average 2 to 3% of the total surface of the Inside study area (Chapter 3). These numbers of diggings and the volumes of soil excavated from these diggings were similar to or larger than reported for other Australian (Claridge *et al.* 1993, Johnson 1994a, Garkaklis *et al.* 2003) or overseas semi-fossorial species (Alkon 1999, Bragg *et al.* 2005). This showed that the scale of the diggings was large enough to potentially have environmental effects (Chapter 3).

The ecological role of diggings would be dependent on the extent to which they are able to facilitate the development of vegetation patches either within or near diggings that are able to further capture resources (Alkon 1999, Shachak *et al.* 2008). Although this study provided further evidence on some aspects of the possible ecosystem engineering effects of the diggings, namely entrapment of seeds and litter, and enhancement of germination (Sparkes 2001, Chapters 3 and 7, James and Eldridge 2007), further research is still required to define the role of these diggings in actual changes to vegetation composition and structure in this arid environment.

8.1.3 Dispersers

Bilbies and bettongs may also be important as dispersers of viable seeds in their faecal pellets (Chapter 4), especially as the germination of these seeds might be enhanced by ingestion (Traveset 1998). These mechanisms could potentially be an important means for bilbies and bettongs to increase the distribution and production of dietary species (Noble *et al.* 2007a).

Bilbies may be important dispersers of mycorrhizal fungi as over a third of the faecal pellets contained fungal spores (Chapter 4). Many mycorrhizal fungi produce their sporocarps underground and so rely on animals for the dispersal of their spores, either as a consequence of their digging activity exposing the spores to the surface for dispersal or through ingesting the spores and subsequent dispersing them through their pellets (Reddell *et al.* 1997).

8.2 ROLES IN RESTORATION

One way to evaluate the functional roles of bilbies and bettongs on their ecosystems, and the potential for ecosystem restoration, is to consider the way these roles affect landscape function and productivity (Ludwig *et al.* 2000, King and Hobbs 2006). Plants form water- and nutrient-enriched biomass patches that increase landscape diversity and productivity (Shachak *et al.* 2008). Overall landscape function and productivity in arid regions is limited by the amounts of inputs, especially water (Noy-Meir 1973, Stafford Smith and McAllister 2008). The overall productivity of an ecosystem is therefore determined by the way flows of organic, soil, and water resources are maintained within the ecosystems (Holm *et al.* 2003), which in turn depend on patches of vegetation and other surface structures such as logs, and rocks to control these flows (Ludwig *et al.* 2004).

Conceptually, landscapes can be placed along a continuum (Figure 8.1) from fully functional landscapes which are highly patchy, and from which no organic, soil or water resources are lost, to fully dysfunctional landscapes which do not trap any of the available resources (Ludwig *et al.* 2002). The three main ecosystem roles of bilbies and bettongs, as consumers, as ecosystem engineers, and as dispersers of seeds and fungi, tend to change the functional level of the landscape as indicated by the arrows in Figure 8.1. The position of the three main habitats at Arid Recovery along this functional continuum is yet to be determined, though it is likely to be different between habitats, and to be variable within each habitat, and to change with changes in vegetation structure.

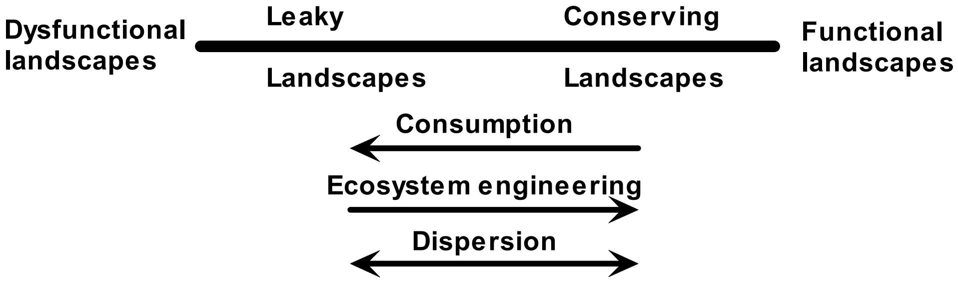


Figure 8.1: A conceptual diagram showing the relationship of three main ecological roles of bilbies and bettongs: consumption, ecosystem engineering and dispersion, to the maintenance of landscape functionality. Landscape functionality is shown as a continuum between dysfunctional landscapes where lack of structure to the overall landscape means resource flows are lost from the landscape to 'well structured' landscapes which retain most resource flows. (adapted from Ludwig *et al.* 2000).

Consumption tends to reduce the functionality of landscapes, as it removes resources from the primary producers that form the landscape structures. However, in many cases, such as low levels of grazing by cattle, this effect could be very small (Lunt *et al.* 2007), and possibly offset by increased vegetation growth in response to herbivory (Belsky 1986). In cases where consumption damages vegetation, such as browsing on bark and seedlings by rabbits and bettongs (Ryan *et al.* 2003, Noble *et al.* 2007a, Bice and Moseby 2008), or reduces the recruitment of plant species, as might occur with prolonged granivory on seeds of *Paractaenum* sp. by bilbies (Maron and Gardner 2000, Chapters 4 and 5), loss of vegetation and their associated vegetation patches could result in increased loss of resources.

Ecosystem engineering effects of the diggings of bilbies and bettongs have the potential to increase the functionality of these landscapes (Martin 2003) through the development of new vegetation patches and the facilitation of the growth of other patches (Eldridge and Mensinga 2007, Shachak *et al.* 2008). The actual expression of these potential effects of diggings would depend on many factors including specific location of the digging; density, and longevity of diggings (Boeken *et al.* 1998, Chapter 3 and 7); soil types (Tongway *et al.* 2003); presence or absence of biological crusts (Eldridge and Mensinga 2007); and timing and intensity of rainfall events (Boeken *et al.* 1998).

Conversely, any increased soil movement from loosening the soil by diggings (Yair and Shachak 1982) has the potential to decrease the establishment of vegetation patches, and increase soil loss from some habitats, especially the Dunes (Chapter 5). This could be of particular concern in areas where existing erosion may have been initiated by overgrazing prior to the establishment of the Reserve. The four-fold greater number of diggings by bilbies and bettongs than by rabbits, and the five to eight times increase in amount of soil excavated with the reintroduction of bilbies and bettongs (James and Eldridge 2007) might increase this erosion whenever wind and rainfall patterns favoured erosion over the establishment of new vegetation patches (Ludwig *et al.* 2005, Hesse and Simpson 2006). Such soil movement tends to stabilise vegetation patterns by shifting fertility and soil resources from interspaces to shrub patches (Asner *et al.* 2004), making restoration of finer-scale vegetation patches more difficult.

The dispersal of seeds, and fungi by bilbies and bettongs through their pellets (Chapter 4) and diggings (Chapter 3 and 7) could result in increases in landscape functionality by establishing new vegetation patches, and invigorating existing ones if the seeds were dispersed to suitable safe sites for successful growth of plants (Maron and Gardner 2000), and the fungi reached suitable plants for mycorrhizal colonisation (O'Connor *et al.* 2001b, Gehring *et al.* 2002).

Although Arid Recovery is well inside the geographical limits of the historical distribution of both bilbies and bettongs, average annual rainfall at Arid Recovery is considerably lower than that for other surviving or reintroduced populations (Southgate 1990a, Short and Turner 1993), and may possibly be inadequate to maintain persistent bilby and/or bettong populations. Sub-fossil records show that both species once occurred in the region (Arid Recovery 2005). However, the metabolic strategies of bilbies and their relatively low fat stores suggest that this species might be vulnerable to drought and may not have persisted in such arid areas (Gibson and Hume 2002). Long-term survival of bettongs at Arid Recovery poses different problems. Although the bettong’s ability to store fat in its tail (Short and Turner 1999), and to consume roots and bark makes it much more able to withstand drought (Bice and Moseby 2008), damage to perennial vegetation from its browsing could decrease landscape functionality.

The ecosystem engineering effects of bilby and bettong diggings at Arid Recovery might be dependent on adequate rainfall as this would affect the likelihood that the resources trapped by diggings could influence plant growth and productivity (Alkon 1999). Most previous research that has demonstrated effects of diggings by semi-fossorial species on plant productivity has been in higher rainfall areas than Arid Recovery (e.g. Whitford 1998), or in more arid regions where rocky areas have been shown to be important in enhancing surface flows to the diggings (e.g. Boeken *et al.* 1998). However, seeds and litter buried in diggings during drier periods would still influence local fertility and possibly plant production when rain returned. As Australian soils are generally of very low fertility (Stafford Smith and Morton 1990), small changes in nutrient pools related to diggings may possibly have large effects on productivity (James and Eldridge 2007). Therefore although ecosystem changes related to diggings might be slow and temporally variable in arid environments, diggings would still be expected to have important ecological effects.

An additional risk to the maintenance of landscape functionality at Arid Recovery is the lack of dingos (*Canis lupus dingo*), the top predators in Australian landscapes, and mesopredators like cats and foxes, inside the Reserve. This increases the possibility that populations of herbivores and granivores like bilbies, bettongs and spinifex hopping-mice (*Notomys alexis*) will increase to levels where they decrease vegetation biomass (Glen *et al.* 2007) and hence functional structure. Arid Recovery is presently developing an alternative approach to regulating bilby and bettong populations using one-way gates (Arid Recovery 2007) that would allow both bilbies and bettongs to establish new populations outside the Reserve when numbers Inside increase to levels at which the animals would naturally migrate to find new food supplies (Southgate *et al.* 2007).

Future climate predictions for the region suggest that longer dry periods may be more frequent (Hughes 2003), increasing concerns for the long-term viability of bilbies at Arid Recovery. Therefore, any positive effects of diggings, however slow, on increasing the efficiency of rainfall use (Ludwig and Tongway 1995), and soil fertility (James and Eldridge 2007) might be very important for increasing the resilience of these ecosystems and the survival of bilbies within them.

8.3 RELATIONSHIP OF CONSUMPTION TO ECOSYSTEM ENGINEERING

The overall concept that the net effects of reintroduced species result from both their effects as consumers and all other ecological roles they may have such as ecosystem engineers or dispersers of seeds is applicable to the analysis of effects of all taxa. The trophic roles of Indian crested porcupines (*Hystrix indica*), and pocket gophers (*Geomyidae*) have both been judged to have less overall effect on the plant communities than the ecosystem engineering effects of their digging (Wilby *et al.* 2001, Reichman and Seabloom 2002). Similarly, as exclusion of seed-harvester ants showed no effect on the plant community, the ecosystem engineering effects of their nest mounds was considered to be a more important environmental effect of this taxon (Wilby *et al.* 2001). The loss of soil disturbances by exclusion of kangaroo rats (*Dipodomys spp.*) from shrub habitat in the Chihuahuan Desert was more important than the changes in granivory in the return of this habitat to arid grassland (Brown and Heske 1990). Similarly, exclusion of herbivorous degus (*Octodon degus*) in a semiarid Chilean site resulted in an increase in shrubs and perennial grasses, through both loss of browsing on the shrubs, and loss of soil disturbances (Gutierrez *et al.* 1997).

However, for bilbies and bettongs, the low productivity of arid areas like Arid Recovery (Stafford Smith and Morton 1990) combined with the relatively high-energy demands of these species means that their impact as consumers could be high relative to productivity of the area. The low rainfall could also limit the effectiveness of their diggings in increasing productivity in the vegetation. Thus for these species in an arid area, the effect of ecosystem engineering could be greater than the effects of their consumption only during periods of higher rainfall. However, this analysis is possibly over-simplified and omits many factors for which predictions of overall effects are difficult. These include possible effects of redistribution of both seeds and fungi by endozoochory (Chapter 4), capture of seeds and litter in diggings (Chapter 3 and 7), and the effect of consumption of buried seeds by bilbies and bettongs as these seeds might not be accessed by other taxa except ants (Chapter 6). The net effects of the reintroductions of bilbies and bettongs to Arid Recovery will be determined over time within the Reserve, supporting the importance of such conservation projects in increasing overall understanding of arid ecology.

8.4 KEYSTONE SPECIES OR KEY ECOSYSTEM ENGINEER?

Although bilbies and bettongs are important species in these ecosystems as consumers, ecosystem engineers and potentially as dispersers, there is still insufficient information about the magnitude of their contributions to determine whether they are keystone species in these arid systems (Mills *et al.* 1993, Power *et al.* 1996, Davic 2003). Although this study has shown that, as ecosystem engineers, bilbies and bettongs have definite ecological impacts on food availability (Chapter 4), and capture of seeds and litter by diggings (Chapter 3), further research is still required to determine the importance of these diggings in arid areas. The three to five years between the reintroduction of these species to Arid Recovery and the present study may be insufficient for the overall impact of these species on aspects of the ecosystem such as vegetation communities or vegetation structure to be measurable, and/or the parameters (e.g. seed banks, Chapter 5) measured during this present study were not suitable to detect the ecological impacts that are occurring. However other studies in arid areas have found measurable responses in seed bank densities or vegetation to occur after only two to three years after the removal of granivores and/or herbivores (Guo *et al.* 1995, Gutierrez *et al.* 1997)

In addition, as the reintroduction of bilbies and bettongs essentially replaced rabbits in these ecosystems, the similarities in the roles of all three species may have reduced the environmental effects of reintroducing bilbies and bettongs. Although rabbits, especially at times of peak populations, might have had a catastrophic effect on vegetation and increased soil erosion in these areas (North *et al.* 1994), their diggings would still have trapped resources and maintained some or all of the ecosystem functions related to diggings. However, as bilbies and bettongs made more and deeper diggings than rabbits, their effect as ecosystem engineers might be greater than that of rabbits (Sparkes 2001, James and Eldridge 2007).

Other fossorial and semi-fossorial ecosystem engineers have been acknowledged as keystone species. Alkon (1999) considers Indian crested porcupines (*Hystrix indica*) keystone species in the Negev highlands because of the extent and the demonstrated ecological effects of their foraging diggings. Both kangaroo rats (*Dipodmys* spp.) and pocket gophers (Geomyidae) have been suggested to be keystone species because of the distinctive plant communities on and around their mounds (Reichman and Seabloom 2002, Jackson *et al.* 2003). Although the bilby and bettong diggings at Arid Recovery have been shown to be similar or greater in numbers and/or volumes of soil displaced than the diggings of any of the above species (Whitford and Kay 1999, Chapter 3), the similarity in ecological effects of the bilby and bettong diggings has yet to be demonstrated. It is possible that bilbies and bettongs will be shown to be keystone species at Arid Recovery when more data are available on the ecosystem engineering effects of their diggings on vegetation productivity and/or structure.

8.5 MANAGEMENT RECOMMENDATIONS

The return of bilbies and bettongs to Arid Recovery could be beneficial for the long-term preservation of these species, and the ecosystem engineering effects of diggings could have beneficial effects on landscape function over the longer term, which could be especially important in such arid areas. However, the results presented in this thesis and the more recent observation of damage from bettong foraging (Arid Recovery 2007) suggest that achieving the two management goals of ecological restoration of arid ecosystems and re-establishment of endemic species within a fenced reserve might require close monitoring of and, if necessary, control of the numbers of both bilbies and bettongs. Over-utilisation of resources may lead to deterioration or even destruction of an ecosystem, as an area may still be over-stocked even after losses to malnutrition or starvation (Petrides 1975), thus continuing depletion and preventing recovery. Supplementary feeding should therefore not be an option in times of extreme food scarcity, as it would result in continued degradation of vegetation and soils by the remaining animals. In cases of severe drought, animals could be moved to smaller enclosures where they could be fed until conditions improved for them to return to the rest of the reserve. Although such a step would mean that the populations would no longer be considered self-sustaining, it would maintain these populations through droughts. Reintroductions of native predators like the western quoll (*Dasyurus geoffroii*) and functional packs of dingoes (Glen *et al.* 2007) into populations of bilbies and bettongs wherever habitat areas were sufficiently large to support the reintroduced predators might also help minimise environmental damage from reintroduced bilbies and bettongs.

8.5.1 Future reintroduction projects

Future reintroduction projects might decide to reintroduce either bilbies or bettongs, which raises the question of what contribution each species would make to landscape functioning. Although clear evidence of the differences between the two species is limited in this study, general observations and experiences suggest the following differences.

Bilbies probably have a greater impact than bettongs on soil restoration and vegetation productivity through their diggings, as they dig more widely and more regularly (Chapter 3). For this reason ecosystem restoration could be improved if bilbies were reintroduced before the reintroduction of other CWR mammals such as bettongs. However, bilbies require continual access to both key plant foods, including grasses or bulbs, and a reliable supply of invertebrates like termites to support reproductive populations (Gibson *et al.* 2002, Southgate and Carthew 2006), and thus might not survive prolonged droughts (Gibson and Hume 2000).

Bettongs also made diggings, although these were possibly shallower, more localised and more sporadic than bilby diggings (Chapter 3). Bettongs therefore might have less impact than bilbies as ecosystem engineers. However, bettongs potentially would have more impact on vegetation, especially shrubs and trees, as consumers than bilbies (Arid Recovery 2007, Noble *et al.* 2007a). In addition, they have a greater resilience to drought than bilbies related to their ability to store fat in their tail (Short and Turner 1999) and their capacity to use lower quality fibrous foods like roots and bark (Bice and Moseby 2008).

New reintroduction projects should include either a Control area without reintroduced animals such as the one at Arid Recovery, or a number of smaller enclosures that are sited to enclose representative areas of specific food plants such as grasses and *Enchylaena tomentosa*. The larger Control area has the advantage of being more representative of the whole study area, though studies using such an area must be carefully designed to avoid problems relating to a priori differences between the Control and study areas (Chapter 5). Smaller enclosures would permit simple, cross-fence estimates of the intensity of foraging (Brown and Heske 1990), and productivity of target plant species, and thus be a useful management tool, but would be unsuitable for larger scale comparisons (Schindler 1998, Oksanen 2001).

8.5.2 Monitoring reintroduced populations

Arid Recovery has an extensive biological monitoring program, which is designed to evaluate processes of ecological restoration at the Reserve, and to support ecological research (Arid Recovery 2006, Chapter 2). Such long-term monitoring is invaluable for understanding ecological systems (Lamont 1995). However, current monitoring is not sufficiently focused on specific species and at a fine enough scale both temporally and spatially to record changes relative to rainfall and changes in animal populations that are important to shorter-term research projects such as this thesis. The following suggestions would improve the usefulness of current monitoring.

A system of formally recording the phenology of major plant species including times of germination, flowering and seeding in relationship to rainfall events would be valuable to both management and researchers. Other events such as outbreaks of insects (e.g. grasshoppers), and signs of herbivory or other damage to specific plant species should also be recorded. These observations could be both opportunistic, and at monthly intervals after major rainfall events. A network of rain gauges containing small amounts of oil to prevent evaporation, which were read monthly, could also assist assessment of possible effects of variation in rainfall between areas.

The current annual vegetation monitoring at Arid Recovery uses techniques designed to record long-term trends in vegetation at the Reserve (Arid Recovery, unpublished data). However, the limited number of sites used, the ephemeral nature of much of the vegetation, and the high degree of heterogeneity in the vegetation between monitoring sites (Chapter 5) together mean that the data from these surveys are inadequate to quantitatively determine trends for specific species between years or between areas with any degree of confidence (personal observation). More frequent estimates of cover or abundance of selected species along with records of the phenology of these species would greatly increase the usefulness of the current annual vegetation monitoring, as it is an impossible task to adequately monitor all species. Ideally such monitoring should be sited in areas of abundance for each species, and possibly in areas where the species was present at lower abundance. Suggested plant species and groups of species of special concern because of their importance in the diets of bilbies and bettongs include the grasses, especially *Paractaenum* sp., *Dactyloctenium radulans* and *Sporobolus actinocladus*; shrubs, including *Acacia* spp., *Dodonaea viscosa* and *Enchylaena tomentosa*; and the forbs *Zygophyllum ammophilum* and *Brassica tournefortii* (Chapters 4 and 5). *Brassica tournefortii* is included as it is an invasive weed (Chauhan *et al.* 2006) that increases in disturbed areas (Sandell 2002).

An ongoing collection of fresh faecal pellets of bilbies, bettongs, and the other reintroduced and indigenous mammals or lizards would be useful for monitoring changes in diet both in responses of all these species to drier periods, and in inter-species competition for food. The comparison of diets of bilbies and bettongs just after their reintroduction to the Reserve with the results of the current study showed the value of such comparisons in monitoring changes in availability of dietary items as measured by the relative consumption of these items (Chapter 4). Even if time and resources do not permit immediate analysis of the samples, collection and storage of samples could provide an invaluable resource for future researchers (Lundie-Jenkins *et al.* 1993).

Monitoring of changes in population size of bilbies using track transects and spotlighting counts, the main methods currently used at Arid Recovery (Arid Recovery 2007) could be influenced by changes in animal activity as well as numbers (Edwards *et al.* 2000, Morris 2003, Robley *et al.* 2004). The possible relationships between rate of digging and bilby numbers, as determined by track transects, therefore warrant further investigation, as diggings can be monitored in all three habitats, and would give useful information on relative use of the different habitats (Chapter 3). Monitoring rates of new diggings could supplement track transect and spotlighting data on animal populations and activity. This might be especially useful at times when animal numbers and track counts were low. Also if possible, track transects should be counted on consecutive days, instead of just a single day to increase the reliability of the counts.

Monitoring of the changes in the spatial patterning of the landscape and evaluation of the way these patterns are able to control resource flows should be an important part of monitoring at Arid Recovery, because of the possible effects of the reintroduced animals on this structure, as discussed in section 8.2. The initial evaluation of landscape structure at Arid Recovery (Hill and Reece 2004) using Landscape Function Analysis (Tongway and Hindley 2004) covered insufficient sites to assess the differences between the management areas, but did demonstrate the high level of heterogeneity between the sites sampled. Future studies need to include more sites, and possibly stratify the sites to, for example, vegetation patches containing specific species important for vegetation structure in each habitat (Shachak *et al.* 2008).

8.5.3 Further research

The re-establishment of bilbies and bettongs in arid landscapes is possible if feral predators are controlled. Their digging and disturbing the soil in search of food is likely to be important for the recovery of arid ecosystems. Additional research is needed to understand the importance of these fossorial mammals in Australian arid systems, as the breadth of this thesis has meant that the current research has laid the groundwork for further research in several areas.

The following are suggestions for larger research projects to build on the results of this thesis, and to further increase the understanding of the effects of bilbies and bettongs on ecosystem functioning, and the possible implications of wider reintroductions of these species throughout arid Australia with adequate control of feral predators. Although focused, shorter term studies could provide useful information, long-term studies such as Arid Recovery itself, and ideally replication of the Reserve in other arid locations, are required to confirm the importance and robustness of the trends suggested in this thesis (Lamont 1995, Carpenter *et al.* 1998, Schindler 1998, Johnson 2002). A more complete understanding of the importance of diggings in landscape functioning would be assisted by further research of the effects of diggings by other species in other ecosystems (Belovsky *et al.* 2004).

8.5.3.1 Effects of bilbies and bettongs on primary productivity

Martin (2003) suggested that the influence of the ecosystem engineering activities by CWR mammal such as bilbies and bettongs on soil health and fertility, and on primary production would greatly assist the restoration of arid ecosystems. Definite evidence supporting this hypothesis would give a strong impetus to efforts to reintroduce bilbies and bettongs to other areas of arid Australia, and assist the understanding of the functional roles of bilbies and bettongs, and the management of arid ecosystems.

Results from this thesis and from published research suggest several possible mechanisms for possible increases in productivity related to the reintroduction of bilbies and bettongs. These include (a) increases in numbers and biomass production of plants in safe sites provided by diggings and associated increases in water and nutrient availability to these plants growing within diggings, and possibly also to nearby plants (Alkon 1999, Chapter 3), (b) improved plant growth resulting from redistribution of fungi and other microorganisms (Reddell *et al.* 1997, Chapter 4), and (c) increases in abundance of plant species that are found in bilby and bettong diets through dispersal of viable seeds in faecal pellets (Chapter 4). Research focused on these areas, and possibly on selected dietary species (e.g. *Enchylaena tomentosa*, *Paractaenum* sp, *Dactyloctenium radulans*) could evaluate the relative importance of these mechanisms. The facultative effects of vegetation patches on production of associated plants, and the possible contributions of diggings to these effects should be considered in the design of such studies as these facultative effects are very important in determining productivity in arid ecosystems (Ludwig and Tongway 1995, Facelli and Brock 2000).

8.5.3.2 The ecology of native grasses at Arid Recovery

Grasses are important to Arid Recovery both in maintaining landscape function (Anderson and Hodgkinson 1997) and as a food source for bilbies and other species (Chapter 4). Endozoochory by bilbies may increase the abundance and distribution of dietary species, including grasses (Chapter 4). Increased understanding of the relationship of diggings and granivory/herbivory by bilbies, bettongs, rabbits, and ants to the distribution and productivity of grasses at Arid Recovery is thus important in evaluating the roles of both animals and grasses in these ecosystems. Grass species of special interest include *Paractaenum* sp., *Sporobolus actinocladus, Aristida* sp., and *Dactyloctenium radulans*. Enclosures located in areas of grass abundance to give cross-fence measures of productivity and granivory would be of special value in such studies (Brown and Heske 1990).

8.5.3.3 Relationships between bilbies and macroinvertebrates

Ants and termites are important for maintaining and restoring soil functions (Lobry de Bruyn and Conacher 1990), as well as food sources for bilbies, and possibly also bettongs, through their underground seed caches (Chapter 6). Specific information which would support and extend the results from this thesis include: information on the temporal, and interspecies variations in the composition and location of ant caches, especially those containing the seeds of the grasses, *Dactyloctenium radulans* and *Sporobolus actinocladus;* the response of the nests of seed-harvester ants to predation by bilbies and bettongs (Chapter 6); and temporal variations in the numbers of ants.

Termites are an important food source for bilbies and many other taxa since they remain available when other foods are scarce (Southgate and Carthew 2006). The effect of the increased consumption of termites by bilbies is therefore of special interest. All termite species at Arid Recovery are subterranean, making monitoring more difficult. Preliminary surveys of termite numbers were done at Arid Recovery in 2004 using a digging technique (Arid Recovery 2005), and also using a selection of different baits (Appendix 2). Annual surveys of specialist termite-eating geckos, *Diplodactylus conspicillatus* and *Rhynchoedura ornata*, at Arid Recovery since 1998 have found no differences in abundance between Inside the Reserve and Outside (K, Moseby, personal communication 2008) suggesting that either there is no difference in termite abundances between areas, or that the abundance of these geckos is not a suitable surrogate for measures of termite abundance (Read 1998). Further termite surveys would require adequate replication of sites, and careful site selection, possibly using cross-fence comparisons to minimise inter-area differences. Understanding the characteristics of the interactions between bilbies and these macroinvertebrates would greatly assist evaluation of the roles of bilbies and bettongs in these ecosystems.

8.6 CONCLUSION

The successful reintroduction of bilbies and bettongs at Arid Recovery has created an excellent opportunity for demonstrating the long term effects of bilbies and bettongs on arid ecosystems, including the possible restorative effects of diggings on soils and vegetation structure (Martin 2003). The short-term effects of bilbies and bettongs are most noticeable in the extent of their foraging diggings, although the demonstration of the restorative effects of these diggings will require much longer studies.

This study should be considered a first step towards understanding the roles of bilbies and bettongs in these ecosystems. As the ecosystems studied are unique, and the climatic conditions and animal populations during this study cannot be replicated, this project can only offer insights for this particular time and place. The interpretation of evidence presented was limited by a large number of potentially confounding factors that were either not measured, or not measurable. This resulted partly because the scope of the study was broad for the time and resources available. Ecological patterns such as the ones investigated are multi causal, and thus require long-term studies over a range of conditions, and locations to understand the mechanisms involved and their relative importance.

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Appendix 1: Seed preference trials

8.7 AIM

To compare the level of seed predation in the three management areas of Arid Recovery to determine the effect of (a) the removal of rabbits, cats and foxes, and (b) the reintroduction of greater bilbies and burrowing bettongs on the level of seed predation and the seed species consumed.

8.8 METHODS

8.8.1 Cafeteria trial

In order to determine what seed species were predated in Arid Recovery, a cafeteria trial was at two sites within each of the three management areas (Inside, Control and Outside). The sites were on flat, vegetation free areas on the sand dunes, and were separated by at least 2 km. This trial was conducted at the Inside and Control sites in September 2004 over three consecutive nights, and repeated in July 2005 at these sites as well as at two Outside sites over two consecutive nights.

In September 2004, ten native seed species (*Acacia ligulata, Boerhavia sp., Brassica tournefortii, Dactyloctenium radulans, Dodonaea viscosa, Enchylaena tomentosa* berries, *Euphorbia drummondii, Paractaenum* sp., *Sclerolaena* sp., and *Sida ammophila*) and two commercial seed species (Canary mix and brown rice) were trialed. The native seeds were collected from within the Reserve, either from the soil seed bank or directly off the plants. The native species that were trialed in July 2005 were *Acacia aneura, Acacia ligulata, Alectryon oleifolius, Atriplex vesicaria, Brassica tournefortii, Crotalaria eremaea, Dactyloctenium radulans, Dodonaea viscosa*, and *Enneapogon avenaceous*, and were obtained from commercial sources.

For these cafeteria trials, ten seeds of each species were presented separately on plastic petri dishes placed in random order in a transect with 1 m between each tray. Each site consisted of two such transects placed parallel and 1 m apart, giving two replicates at each site. The plastic petri dishes each had a hole drilled in the centre, and a large nail put through hole to hold the dish in place. The dishes were pushed into the sand so their sides were level with the ground surface and a small about of sand was placed in the bottom of the trays.

8.8.2 Direct observation of bettongs

Observations of bettongs feeding at the observation hide at Arid Recovery in July 2005 were used to determine which seed species bettongs feed on. Ten seeds of each of the species that were used for the seed preference trials in July 2005 were placed on the sand in front of the observation hide, and the locations marked with paddle pop sticks. Bettongs and spinifex hopping-mice (*Notomys alexis*) feeding at the hide were observed for approximately an hour after sunset (when the bettongs are most active), and the seeds consumed were noted. The samples were then checked to confirm how many seeds had been eaten. About six bettongs and two hopping-mice were present during the observation period.

8.8.3 Buried seed trial

A small experiment was conducted in July 2005 to test whether bilbies and bettongs would dig for native seeds as well as rice. The seed species tested were *Acacia ligulata, Brassica tournefortii, Dactyloctenium radulans, Dodonaea viscosa*, and rice.

This experiment used a similar site layout as that of the previous seed foraging experiment, but at different sites. Two sites were located on different dunes about 500 m apart with 2 replicates of the 5 seed species and a control sample at each site. For each sample, a 5 cm deep hole was dug (approx 15 cm diameter), the appropriate treatment (10 seeds or small pinch of the small seeds of *Brassica tournefortii* and *Dactyloctenium radulans*) was placed in the hole, and then the hole filled in. The control samples were dug and filled in without adding any seeds.

Sites were monitored the day after they were prepared, and 3 days later after replacement of the samples consumed on the first night. Rain prevented monitoring on the second night of the trial.

8.9 RESULTS

8.9.1 Cafeteria trial

For the cafeteria trials in September 2004, no bilby or bettong tracks were seen at one of the Inside sites, while bettong tracks were observed at the other Inside site over all three days. Hopping mice tracks were observed at all the sites in both areas. No signs of birds were seen in either area, while ants were observed dragging *Enchylaena tomentosa* berries from both sites in the Control area.

In July 2005, bettongs visited both Inside sites on both nights, while bilbies visited only both sites on the second night. Lots of mice tracks were seen at all sites in the Inside and Control. For the Outside sites, there were possible rabbit tracks at both sites on both nights, and the sand was too wet to see mice tracks. No signs of birds were seen, though at the Outside sites, ants were observed dragging *Acacia aneura* seeds (both seeds with and without elaiosomes).

The results of the cafeteria trials are shown in table 1. Substantially more seeds were taken in July 2005 than September 2004. Hopping mice tracks and left over seed husks suggested that most of the seeds taken from both the Inside and Control sites were by hopping mice, especially in September

2004. It was impossible to tell if bilbies and bettongs visiting the Inside sites had visited before or after the hopping mice had eaten the seeds.

More seeds were taken from the Inside and Control sites than the Outside sites, possibly as there was little rodent activity at the Outside sites.

8.9.2 Direct observation of bettongs

About six bettongs and two hopping-mice were present during the observation period. Table 1 shows the seed species that were observed to be consumed by either the bettongs or hopping-mice. Although not consumed the *Atriplex vesicaria* seeds were investigated by both the bettongs and hopping-mice.

8.9.3 Buried seed trial

The tracks of bettongs showed that they visited both of the experiment sites, while bilby tracks were only observed at one site on the first night. The percentage of the samples that were dug up is shown in Table 1. All of the seed species trialled were dug up at least once except *Crotalaria eremaea*.

Table 1: The percentage of seeds that were eaten during cafeteria trials in September 2004 and July 2005. * shows that seed husks and/or rodent tracks suggested that some or most of these seeds were taken by rodents. The direct observation indicates whether bettongs and/or hoppers were observed feeding on seed placed out in front of the observation hide. The buried seed trial shows the percentage of samples of the buried seed (buried to 5cm) that were dug by bilbies and/or bettongs.

Seed Species Tested		Cafeteria Trial (% of seeds eaten)					Direct Observation July 2005 (n=1)		Buried Seed Trial (n=8)
		Sept 2004 (n=120)		July 2005 (n=80)					
		In	Cont	In	Cont	Out	Bettong	Hopper	
Acacia aneura	Shrub	-	-	97.5*	100*	11	Yes	Yes	-
Acacia ligulata	*Shrub*	16.7	0	100*	100*	37	Yes	Yes	87
Alectryon oleifolius	*Shrub*	-	-	100*	100*	20*	Yes	Yes	-
Atriplex vesicaria	*Shrub*	-	-	26.3*	28.8*	0	No	No	-
Dodonaea viscosa	*Shrub*	34.2	15*	100*	100*	12	Yes	Yes	100
Enchylaena tomentosa	*Shrub*	10.8	15	-	-	-	-	-	-
Gunniopsis quadrifida	*Shrub*	-	-	100*	65*	1.3	No	No	-
Sida ammophila	*Shrub*	28.3	12.5	-	-	-	-	-	-
Boerhavia dominii	*Forb*	17.5*	8.3*	-	-	-	-	-	-
Brassica tournefortii	*Forb*	23.3	18.3	63.8*	77.5*	0	No	No	-
Crotalaria eremaea	*Forb*	-	-	41.3*	3.8*	0	No	No	0
Euphorbia drummondii	*Forb*	31.7	53.3*	-	-	-	-	-	-
Sclerolaena sp.	*Forb*	21.7	8.3	-	-	-	-	-	-
Dactyloctenium radulans	*Grass*	27.5*	23.3*	most	most*	1/6	Yes	?	37
Enneapogon avenaceous	*Grass*	-	-	51.3*	45*	9	Yes	?	-
Paractaenum novae-hollandiae	*Grass*	41.7	23.3	-	-	-	-	-	-
Bird Seed	*Test*	31.7	0	100*	100*	20*	Yes	Yes	-
Rice	*Test*	65.8	26.7	100	100*	12	Yes	Yes	50

DISCUSSION

The main differences in seed predation between the management areas were between Outside the Reserve and both the Inside and Control areas. This was probably mostly due to the difference in population of the spinifex hopping-mice, as it was difficult to tell if bilbies and bettongs had eaten any of the seeds. It was also difficult to tell how many of the seeds had been taken by ants.

Substantially more seeds were predated from the July 2005 cafeteria trial than that in September 2004. It is possible that this was due to a difference in differences in availability of other food sources. In September 2004, *Enchylaena tomentosa* berries and other species were seeding, while fewer seeds may have been readily available in July 2005. This difference between the sampling times could also have been due to differences in predation levels as Arid Recovery's annual trapping data for February each year suggests that hopping-mice numbers may have been higher in 2005 than 2004 (Chapter 2).

Surface seed predation inside the Reserve was extremely high, with up to 100% of seeds taken overnight. This high level of predation may, in part, be related to the curiosity factor of the sites, as hopping mice tracks were much more numerous on the test plots than in nearby areas.

The direct observation and buried seed trial found that bettongs do feed on a wide variety of seeds, and will dig for buried native seeds. Although bilbies do occur around the observation hide, they have rarely been observed, while bettongs are regular visitors. However, as bettongs visiting the hide are accustomed to supplementary feeding, their feeding behaviour may not be representative of the total population.

This study achieved its goal of comparing overall level of surface granivory by all taxa, although the uncertainty over which taxa actually foraged the seeds makes interpretation of these results difficult. There is also doubt over whether seed dish trials accurately represent the level of granivory under field conditions (Perez *et al.* 2006). Further trials on using buried seeds at two depths, 2 cm and 10 cm, might help clarify what seeds bilbies and bettongs will dig for and separate granivory by these species from that by ants, which forage only on surface seeds, and hopping-mice. It is unclear from this study, and from the literature if, and to what depth hopping-mice will dig for seeds, but it is unlikely to be more than 2 cm.

Appendix 2: Termite bait trial

8.10 INTRODUCTION

Termites are an important food source for bilbies (Southgate and Carthew 2006), and many other arid zone animals including numbats (*Myrmecobius fasciatus*), which have recently been reintroduced to Arid Recovery (Arid Recovery 2007).

The termites at Arid Recovery are all subterranean species. There are two general methods for surveying for the presence of subterranean termites: digging shallow trenches (e.g. Abensperg-Traun and De Boer 1990) or by the use of baits (e.g. Whitford 1999, Dawes-Gromadzki 2003, Dawes-Gromadzki and Spain 2003). A survey for termites using a digging transect method was conducted in 2004 to access the suitability of the Reserve for the reintroduction of numbats (Arid Recovery 2005).

This survey was conducted to evaluate the effectiveness of different types of baits for surveying for subterranean termites at Arid Recovery.

8.11 METHOD

The overall design of this experiment was similar to that of Dawes-Gromadzki (2003).

8.11.1 Site selection

The baiting trial was conducted at 10 sites within the Inside enclosure at Arid Recovery (with bilbies and bettongs). Each of these sites was situated approximately 20 m from one of the digging quadrats within similar habitat type. The 10 sites included 4 dune, 4 swale and 2 mulga sites. The bait trial sites were established between the 13 and 16 January 2004.

8.11.2 Trial design

Three different baits (pine stakes, toilet paper, litter), were trialled with different moisture statuses (wet, dry) and placements (soil surface, buried) (12 different baits overall). At each of the 10 sites, one of each of the 12 bait types were placed in a 4 x 3 m grid with 5 m between each of the baits. The 12 bait types were randomly allocated to the 12 points of the grid. This random allocation was done to give the termites an equal opportunity to find each bait type (Taylor *et al.* 1998).

For all surface baits, any leaf litter or small rocks were brushed aside to ensure that the baits were in direct contact with the soil surface. All surface baits were covered with shade cloth (green, 90%) held in place with wire pegs to slow disintegration.

The pine stake baits were 25 cm lengths of 40 cm x 30 cm untreated pine (*Pinus radiata*). They were placed horizontally on the surface or were buried vertically to a depth of 25-30 cm.

The surface toilet roll baits (unbleached, unscented, recycled) were placed upright on the soil surface with a flagging tag through the middle to hold them in place. The buried toilet rolls were placed in plastic sandwich bags (Multix Quick Zip resealable, 18 cm x 17 cm) with holes punched in them with a hole punch and were buried upright under at least 5 cm of soil. The bags were used make periodic inspections of the rolls possible, while still permitting easy access for termites.

The litter baits consisted of approximately 50 g of dead *Eragrostis setifolia* and dead *Salsola kali* (approximately 25 g of each) placed in large plastic sandwich bags (Glad resealable, 25 cm x 22 cm) with holes punched in them with a hole punch. The surface baits were placed on their sides on the soil surface while the buried ones were buried at least 10 cm under the soil surface.

The wet toilet paper rolls, leaf litter and pine stake baits were soaked in rain water for 1 min, 10 min, and 12 h respectively before installation.

8.11.3 Monitoring

Baits were monitored by examining the baits for termites or signs of termite attack. The degree of attack of the baits was scored according to the percentage of the bait consumed by the termites (0 = no attack, 1 = 1-24% of bait consumed, 2 = 25-49% of bait consumed, 3 = 50-74% of bait consumed, 4 = 75-99% of bait consumed, 5 = 100% of bait consumed). The number of termites, location of attack on bait, and pattern of this attack was also noted and samples of the termites taken for identification. After examination, the baits were replaced in their original position without adding moisture to the originally moist baits.

Sites were established 13-16 January 2004. Baits were monitored on 6-8 April 2004, 16 July 2004, and 28 September 2004.

8.12 RESULTS AND COMMENTS

Table 1 shows the number of baits that had been attacked by termites between monitoring periods. Although the numbers are accumulative, as the same bait was returned to its position after each monitoring period, this is not seen in some of the data as some baits were dug up, possibly by bettongs, and a few just disappeared.

Level of attack varied greatly, with only one bag of litter completely consumed by the end of the study, and 1 litter bag and 4 toilet rolls 75-100% consumed. Termite attack on the pine wood was less than

25% of each bait that was attacked. Some baits had termite carton under them or, in the case of one toilet roll, in them without the bait having been attacked.

Live termites, mostly just one or two termites, were found with only about a third of the samples that had termite carton and/or signs of termite attack. Termites appeared to come and go from samples as some samples had been visited by termites on the first and third monitoring periods, but not the second one.

Table 5: Number of baits attacked by termites at each monitoring time (all levels of attack combined). Numbers for bait type, moisture and position are for all habitats combined.

	Monitoring Times		
	April 2004	July2004	Sept 2004
Bait type (n=40)			
Litter	17	10	8
Toilet paper	6	12	14
Wood	3	5	8
Moisture (n=60)			
Dry	11	9	15
Wet	15	18	15
Position (n=60)			
Surface	15	16	13
Buried	11	11	17
Habitat (dune, swale n=40; mulga n=20)			
Dune	13	14	25
Mulga	7	10	5
Swale	6	3	4

Leaf litter buried while wet appeared to be the most effective bait during this study, with toilet paper a close second. Wetting baits did not make a great difference to the level of attack, except perhaps to increase the number of both surface and buried litter baits attacked. Baits in Dune were attacked more than those in the Mulga, while very few baits were attacked in Swale.

Several baits had been dug up and chewed, probably by bettongs, a factor which should be taken into account when planning trials of baits. There was no sign of bilbies coming to the baits to feed on termites feeding on the baits, but the monitoring may have been too infrequent to detect such predation by bilbies, if it occurred.

As for all trials at Arid Recovery, predation on the different types of bait was very variable, and a lot of replications would be necessary to achieve statistically meaningful results. As the total number of baits that had been attacked stayed fairly constant from 26 in April 2004 to 27 in July and 30 in September, little was gained by leaving the baits for longer than the original three months, especially as they had to be disturbed to monitor them. It is also possible that the low levels of new activity between April 2004 and September 2004 reflected lower termite activity during the winter.