PRECISE ECOLOGY

A foundation for an integrated and quantifiable theory of animal, plant, population and community ecology.

by

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PREFACE

The publications in this thesis are directed towards the construction of a theoretical basis for the science of ecology. The general method is that of formalization, a technique which belongs to the field of formal symbolic logic. The *modus operandi* is to construct a new branch of pure mathematics using the concepts of modern logic. These require in outline first the establishment of a semantic basis, the universe of discourse. Secondly primitive terms undefined in the system are laid down; these are based on biology in the present work in contrast to the many branches of mathematics which stem from physics. The primitive terms are then used in formal definitions which range across population and community ecology, beginning with animal ecology and extending to plant ecology in the final paper in this collection.

This line of research was started early in 1977 after three years of preliminary work. Prior to this I had used standard well-known mathematical methods such as stochastic simulation modelling and difference and differential equations for problems in ecology, breaking new ground with a stochastic simulation model of *Tribolium* populations published in 'Physiological Zoology' in 1967. However my original training in pure mathematics and physics had given me a good knowledge of the basic role played by mathematics in theoretical physics and I was well able to contrast this with the lack of fundamental mathematically-based theory in ecology. By 1973 I was fully aware that the mathematics developed for physics was often not suitable in ecology and that a new kind of pure mathematics was essential for a satisfactory scientific theory. The methodology I adopted followed that given by J.H. Woodger in his 1937 book 'The Axiomatic Method in Biology'. In an article in the 'British Journal for the Philosophy of Science' in 1952 Woodger wrote "In considering the relation of mathematics to biology we must distinguish between the process of applying existing mathematics to biology and the less familiar process of letting the biological statements suggest new mathematical ones". Woodger's first process is that of mathematical modelling; his "less familiar process" is the one followed in this thesis; it is within the academic discipline of formalization in the non-physical sciences. In contrast to Woodger I aimed at producing results which would be of immediate use to field ecologists, in particular those of the Andrewartha School of animal ecology in the University of Adelaide. Thus initially and for some years the work was confined to animal ecology and in particular to population ecology of single animal species. Furthermore in order to obtain useful results I dropped the restriction to first-order logic which is customary in a formalization. My decision to use higher order logic and draw when necessary on techniques and symbolism from the whole of modern mathematics was aided by useful discussions with Mr Dene Barnett in the School of Humanities at Flinders University whose lectures on logic I attended in 1977 and 1978.

By December 1977 I had obtained the first useful although rather crude result. This was a formal symbolic definition of the (theoretically) total environment of an animal. The ecological ideas which I used to obtain this result came from four main sources:

(i) Andrewartha H G (1971). Introduction to the Study of Animal Populations, 2nd Edn. Chapman and Hall, London.
(ii) Maelzer D A (1965). A discussion of components of environment in ecology. Journal of Theoretical Biology 8, 141-162.
(iii) Andrewartha H G and Browning T O (1961). An analysis of the idea of "resources" in animal ecology. Journal of Theoretical Biology 1, 83-97.
(iv) Many discussions about animal ecology with Professors Andrewartha and Browning and Dr Maelzer.

The new result was conveyed immediately to Professor Andrewartha (and others) at a seminar I gave in the Entomology Department, University of Adelaide, in December 1977. Professor Andrewartha made excellent use of the result in a fundamental recasting of his book 'The Ecological Web' published in 1984 jointly with Professor Charles Birch and they added an Appendix written by myself which is included in this thesis. From my mathematical definition Andrewartha developed a highly stylized diagram which opened out the complex network yielded by the definition of the environment and projected it on to a plane. I have made extensive use of these 'envirograms' in my later work. I published a slightly improved version of this early result in 1980 in the 'Australian Journal of Ecology'.

A more sophisticated version together with some suggestions about niche, community and ecosystem appeared in 'Erkenntnis' in 1982 and an inference drawn from this work in the 'Journal of Theoretical Biology' in 1983.

At this stage of the work it became clear to me that a correct definition of environment was of critical importance to the entire developing system. I therefore decided that it was essential to do a very careful check of my mathematical definition in addition to the previous ongoing check of several score individual examples of objects in various animals' environments. I undertook a series of studies of the environment of each of twenty-five species of animals, ranging across the phyla from the sponges to the non-human primates. They were:

(a) Five lower invertebrates: sponge, coral, sea gooseberry, tapeworm, earthworm.
(b) Six arthropods: copepod, waterflea, mosquito, honeybee, blowfly, butterfly.

(c) Five higher invertebrates: freshwater snail, terrestrial snail, squid, octopus, brachiopod.
(d) Nine vertebrates: fish, frog, toad, fulmar, penguin, wallaby, dolphin, gorilla, chimpanzee.

I chose these species deliberately within the four groups on the basis that they were well-known either with many papers or a book easily available. Clearly the scientific journals would have been unable to cope with the massive output of my results so I published these as occasional papers from Griffith University. The system was that the papers were read only by the Editor who would call on staff members to assist when necessary. They were published immediately and advertised world-wide. I was assisted by a Research Assistant, Mr M G Stewart under a grant from the Australian Research Grants Scheme, during 1981 and 1982. Mr Stewart was an enthusiastic assistant and I included his name on all publications for which he had at least some input. I was also assisted by Honours student J C Moore for a brief period.

I read a paper on the structure of the environment at the Australasian Association for Logic Conference in 1983, using the three-spined stickleback as an example. An abstract appeared in the 'Journal of Symbolic Logic' in 1984 and is included in this collection.

The twenty-five animal study gave me confidence in my mathematical definition of environment since I could not find an object referred to in the literature as being an element of the animal's environment which could not be classified. I also gained knowledge of the topological structure of the (defined) environment. It became clear as the work proceeded that an improved formulation was necessary, first in order to cope with technical difficulties associated with my use of the conditional in first-order logic and secondly because the relatively high level of mathematical sophistication necessary to obtain a correct classification militated against the wide use of the method particularly by undergraduates.

For these reasons a new formulation suited to teaching undergraduate Zoology students was developed and used immediately for updating the studies of the sponge, tapeworm, octopus, toad and chimpanzee of the original set of animals. The resultant papers were published in 1987 and 1988 in the 'Australian Journal of Zoology'.

I proceeded immediately to develop my ideas on animal community and published a paper in 1988 in 'Coenoses' in which I gave a formal definition of community and showed the connection with the algebra of categories by writing the axioms of that algebra in terms of my formalization. The important axiom concerning the existence of an identity morphism was deduced from my 1983 paper. The definition uses the notion of the functionally connected modifier chains of the environment which connect animals in the community. It lends itself also to the classification of real-life communities and I give examples in the paper. An interesting mathematical object is a 'product', the term having the meaning assigned to it in the algebra of categories. This turned out to be a representation of the 'food-web' of animal ecology. It is possible to derive a representation of a food-web from that of the total environment or community but it is not possible to derive a representation of the total environment or community from a knowledge of the food-web.

I then turned to the notion of niche for which I required a formal definition of animal species. I used the ideas of H E H Paterson here and published a separate paper on this point. The two publications appeared in 'Rivista di Biologia' and 'Coenoses', both in 1989.

At this point I wrote a short monograph published in 1989 in which I set out the general philosophy of the approach and gave a summary of the results, also presenting a Venn diagram of the primitive terms of the system which shows how the concepts of environment, species, niche and community are linked at a basic level, i.e. a linkage of population and community ecology. The Editor of the monograph series in Griffith University consulted three referees before accepting my monograph for publication. One of these, W T Williams, wrote to me directly suggesting an extra paragraph in the Introduction listing all the symbols which I then added.

It was then time to extend the system to plant ecology and the initial extension was published in 'Coenoses' in 1992. Animal and plant ecology at the population and community level are now combined. The ideas on plant ecology stem largely from J L Harper's 1977 book 'Population Biology of Plants'.

Early in the work it became clear that it would be necessary to make special provision for humans. A single example will suffice. Consider as an object a specific cigarette in a specific human's environment. This object would be classified as a malentity under my definition since it is inimical to the subject human (but is not a predator). However a cigarette-smoking human does not regard a cigarette as a malentity but rather as a kind of resource and often a social asset. Basic ecological mathematics which does not take account of such strong human reactions and the associated cultural and sociological milieu is bad mathematics and unlikely to further the cause of science. Unfortunately my early ideas on human ecology (not yet published) were too late for Andrewartha and Birch (1984) and they used my definition of environment for humans also.

My work provides an integrated and precise basis for a large segment of ecological theory which until now has been only qualitative. The developing system is stochastic in two ways. First at a fundamental semantic level the two primitive terms G for plants and H for animals both contain probabilistic ideas. Either G or H is incorporated in all definitions. Secondly the definition of mate for animals and co-reproducer for plants contain a probabilistic sentence. The system is also totally interactive *via* the directed-interaction primitive. It is time-dependant; provision is made for the environment of an individual organism to change from instant to instant. All definitions are functional; it is the functional relations among animals or plants which provide both the structure of the environment and that of the community. By excluding the primitive term Hab from the environment definition I have made the concept of environment habitat-independent. This enables us, for example, to include the blight *Endothia parasitica* among the predators of the chestnut tree even in the case that the tree in which we are particularly interested is growing in an area far removed from the place where the observation was made.

Both my initial papers in animal and plant ecology contain the terms 'direct environment' and 'indirect environment' in contrast to Andrewartha and Birth (1984) who replaced these expressions by 'centrum' and 'web'. In mathematics 'modifiers of order 0, 1, 2,...' would seem more natural.

Throughout the work I have attempted to strike a sensible balance between the amount of symbolism and explanation in ordinary English where the latter can be done without losing too much precision.

In science classification itself is of fundamental importance. However the precise classification of objects in an animal's environment has advantages in addition to (or perhaps because of) the simplicity of the method. First it is easy to justify the classification of objects by using semi-formalized sentences. Secondly ecologists are able to see immediately where their specialized observations and experiments fit into the overall research on the species. They can compare progress from one organism to another, for instance it is clear from such analyses that more is known about the cane toad than the King penguin. Furthermore the environment analysis makes it possible to combine reports from various sources and different disciplines in a standard form which is then accessible to all.

The future potential of the work is difficult to assess but is certainly very big. Already it is the case that the research has thrown light on issues which have not been direct aims. One of these is the general and somewhat vague idea that in nature everything is connected to everything else. The modifier chains of the present system give precision to this vague idea. Furthermore they provide us with a *modus operandi*. Beginning with any living organism in our chosen community we can write down the modifiers one by one, repeating the process until the entire structure is evident. A second point is that hypotheses which are set up for testing in field ecology can now be stated with precision; only by using precise definitions can we state precise hypotheses.

Using the precise foundation presented in this thesis it should now be possible to develop biologically-based ecological mathematics. For instance suppose we have (in theory) two communities, contiguous in space, which are of low order, say two or three and connected by some predator. It should be possible to combine these within an overall habitat by writing down an equation which gives us a kind of logical sum of the two communities. The result will certainly be a community but the order of this community has to be determined. Depending on the circumstances the logical sum may be a 'tight' community of order three or a looser community of higher order. If it turns out that such logical sums are subject to fixed laws then it will be possible to construct a calculus of communities which will deal with small changes in a community over a short period of time. Thus we should be able to predict the precise effect of adding a new plant or animal to an existing real-life community. Such a development is likely in the distant future after much work to enable us to make precise predictions about real-life communities. The analogous situation in physics is that the mathematically-based theory enables us to do the arithmetic required to predict the future state of the system. At present it is the case that the precise prediction of the future state of an ecological system has been possible only in certain special cases. However given a sound mathematical basis for ecological theory prediction in ecology should be as feasible as in physics.

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The formal definition of the environment of an animal

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Abstract

The article describes the first step in the formalization of the theory of animal ecology developed by H.G. Andrewartha, L.C. Birch, T.O. Browning, D.A. Maelzer and their students. The classification of the environment given by H.G. Andrewartha in Introduction to the Study of Animal Populations *(1971) is formalized, with the exclusion of the component 'weather'. In addition, the notion due to D. A. Maelzer that certain objects 'only modified the value of some resource or other component of environment' is also formalized and extended. The class of malentities is enlarged to include the case of an animal eating a poisonous animal. This enlarged class includes some animals formally classified as 'aggressors'. Symbiosis is also discussed.*

Introduction

The classification of the components of the environment given by Andrewartha & Birch (1954) has been modified successively by Browning (1963), Maelzer (1965) and Andrewartha (1970). The original set of four components namely (i) weather, (ii) food, (iii) other animals and organisms causing disease and (iv) a place in which to live was eventually replaced, in the 1970 publication, by five components: resources; mates; predators, pathogens and aggressors; weather; malentities. The object of the present study is to formalize this latest classification. This is the first step in the formalization of the theory of animal ecology associated with the names of the above authors. The formalization is being undertaken for three main reasons:

(i) To facilitate the development of the theory. A formalization will aid in ensuring that all the assumptions are explicitly laid down; in particular it will give an accurate way of saying explicitly what assumptions are incorporated in a chain of deductions. The rules of deduction (which are formally laid down as part of a formalization) will enable us to arrive at the consequences of our assumptions in a systematic way: by formalizing, we are less likely to omit important consequences. The use of clearcut definitions (the subject of this article) is almost essential for the exact communication of the theory to others. The use of a natural language in this communication necessarily involves us in the paradoxes which arise in a natural language.
(ii) To provide a basis for comparison of this theory with other theories of animal ecology.
(iii) To clarify the theory itself. A formalized language for a scientific theory provides an aid to intuition, a corrective to faulty thinking and a systematic method of criticizing obscure ideas.

Clearly, there may be more than one logical (or mathematical) formalization of a scientific theory. An example is that infinite matrices, instead of Hilbert spaces, may be used as the theoretical aspect of quantum theory. In the present case, lengthy discussion took place among animal ecologists and myself during the course of the work: the symbolism given below is satisfactory in the sense that it has clarified and simplified the previous notion of the environment. So far we have not found a counter-example, that is, an example of a real-life situation in which a certain object should, according to the intuitive notions of the ecologists, be included in (excluded from) the environment of the animal but does not (does) accord with the formal defin-

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itions given. This is not to say that the present formalized description of the environment is immutable.

As the work proceeded it became clear that the component called 'weather', which had been included in all previous classifications, could not be adequately defined in terms similar to those used for the other four components. The device finally adopted is to work with the *direct* environment, as suggested by Maelzer (1965); this notion requires only four components, essentially similar to those of Andrewartha (1970), but without 'weather'. These are supplemented by the so-called 'Maelzer Modifiers' (another device suggested by Maelzer in the 1965 paper) which are defined in terms of the four main components.

A list of symbols used is given in the Appendix.

The general approach

The general approach is that adopted by Andrewartha & Birch (1954) in that, to begin with, we concentrate our attention on one, and only one, animal.

The animal in which we are interested is conceived to be surrounded by objects, some of which are animate. All of these objects are assumed to be measurable. We distinguish various classes of objects which are called R_1, R_2,...R_k M, P and C.

In order to formulate precise definitions a number of concepts, hitherto somewhat vaguely expressed, are replaced by more exact statements. In particular, statements about variations in temperature and intensity of light are replaced in the theoretical structure by statements about precisely measured objects consisting of known numbers of units of energy – heat-energy or light-energy. Throughout the study the animal is visualized as being surrounded by objects which admit of exact measurement, for example, 'hole' (in a tree-trunk) as a place to live for the great tit *Parus major* is replaced by the object 'tree with a suitable hole in the trunk'. Andrewartha & Browning (1961) classify a 'hole' as a resource, that is, they regard a hole as a concrete object. In an interesting discussion of this point Lewis & Lewis (1970) equate 'hole' to 'hole-lining' thus obtaining a nominalistic approach. However, for our purposes, 'object with suitable hole' although admittedly vague (since the suitability depends on a number of factors but especially on the particular animal) would seem to suffice and has been used in the example given in Table 1 below. Furthermore, exact measurements of time are incorporated throughout: when we consider, say, a particular apple as a resource for a caterpillar the object 'apple at time t_1', is assumed to differ from the object 'apple at time t_2' ($t_1 \neq t_2$). Units of energy are handled in much the same way as pieces of food. We recognize that some of the food is excreted and some of the energy is returned to the atmosphere; in this way we may think of an animal as absorbing and excreting units of heat- or light-energy. Another object at first sight strange is a unit of kinetic energy; we treat a unit of kinetic energy as a measurable object which, at a particular time, t, is brought into 'close physical proximity' with the animal.

The term 'close physical proximity' is a term incorporated in the definitions; it is not defined; it may well continue to be an undefined notion in future studies.

By 'ξxa_t' we mean that object x is brought into close physical proximity with animal a at time t, evoking (immediately) some physical, physiological or behavioural response in the animal.

$H_t(a)$ is a real positive number equal to some combination of:

(i) the expectation of life (at birth) of the animal a, or the probability that a (on entering its present stage of the life cycle) will proceed to the next stage,
(ii) the probability that a will reproduce.

It is understood that (i) and (ii) are to be calculated under the conditions prevailing at time t. The second term in (i) applies only to multi-stage animals. H is not defined precisely. We require however that an increase in either (i) or (ii) will result in an increase in H.

We say that H increases when the value of H, as measured when the object is present, is larger than the value of H measured when the whole class of like objects is absent. Thus we say that H is larger when the animal eats a particular food-object than H would be if no food-objects whatsoever were available to be eaten. Similarly H is smaller when the animal is attacked by a predator than it would be if the entire class of predators were absent. The same considerations apply to malentities and mates, for example,

TABLE 1 Examples from the animal ecological literature reclassified in light of the formalizations presented in this article

Source of Example	Object	Original classification	Classification according to formal definition
Browning (1963) p.45	Amount of heat-energy corresponding to temperature of 24°C.	Weather in the environment of the salmon *Oncorhyncus tschawytscha*.	(A) Change in physiology of salmon. (B) (a) Expectation of life, thus H(salmon), increased. (b) Total no. units heat-energy unchanged. (c) Heat-energy inanimate, thus no H involved. From (a), (b) and (c) this particular chunk of energy is a resource of the salmon.
Browning (1963) p.45	Amount of heat-energy corresponding to temperature of 25°C.	Weather in the environment of the salmon *O. tschawytscha*.	(A) Change in physiology of salmon. (B) (a) Expectation of life reduced, thus H(salmon) reduced. (b) Total no. units heat-energy unchanged. (c) Heat-energy inanimate, thus no H involved. From (a), (b) and (c) this particular chunk of heat-energy is a malentity for the salmon.
Browning (1963) p.51	Measured volume of water at a temperature of 27°C.	Weather in environment of egg of *Acheta commodus*.	(A) Change in physiology of egg. (B) (a) Probability of hatching, thus H(egg), increased. (b) Total no. units water decreased. (c) Water inanimate thus no H involved. From (a), (b) and (c) this particular 'chunk' of water is a resource for the egg.
Browning (1963) p.61	Tree with suitable hole in it.	Resource (nesting-site) for the great tit, *Parus major*.	(A) Change in behaviour of tit. (B) (a) Probability of reproducing increased, thus H(tit) increased. (b) Total number of trees with suitable holes unchanged. (c) Tree unaffected. From (a), (b) and (c) the tree is a resource for the tit.
Andrewartha (1970) p.78	Vole, *Microtus agrestis*, originally in cage.	Aggressor in the environment of the introduced (stranger) vole, *M. agrestis*.	(A) Change in physiology of introduced vole. (B) (a) Expectation of life, thus H(stranger), reduced. (b) Total number of voles decreased or unaffected. (c) H(original vole) unaffected. From (a), (b) and (c) the original vole is a malentity in the environment of the stranger.

Table 1—*cont*

Source of Example	Object	Original classification	Classification according to formal definition
Andrewartha (1970) p.83	Adult beetle, *Tribolium castaneum*.	Aggressor in the environment of the egg of *T. castaneum*.	(A) Change in physiology of egg. (B) (a) Expectation of life, thus H(egg), reduced. (b) Total number of adults unaffected. (c) Expectation of life, thus H(adult) increased. From (a), (b) and (c) the adult is a predator of the egg.
Andrewartha (1970) p.124	Measured amount of light-energy in unit volume surrounding the animal, corresponding to average daylight.	Weather in environment of the cockroach, *Periplaneta americana*.	(A) Change in behaviour of cockroach. (B) No change in expectation of life or probability of reproduction, thus H(cockroach) unchanged. However a food-type object in the vicinity of the cockroach ceases to be a resource in the presence of light: the object is a Maelzer Modifier of the first order.
Browning (1963) p.77	Man who builds fence which limits movement of sheep and prevents sheep-tick from climbing on sheep to feed.	Member of other species in the environment of sheep-tick.	(A) Change in behaviour of sheep-tick. (B) H(sheep-tick) not directly affected by man so object not in direct environment of sheep-tick. If, however, we could find a particular sheep which is in a position such that, were the fence removed, the tick would climb on it and feed, then the sheep's blood would be a resource of the tick and the fence a Maelzer Modifier of the first order. The man, who may or may not put the fence in that particular place, is a Maelzer Modifier of second order.
Andrewartha (1970) p.23	Burrow.	Resource in the environment of the rabbit *Oryctolagus cuniculus*.	(A) Change in behaviour of rabbit. (B) H(rabbit) not directly affected, however extremes of temperature and flooding in the vicinity of the rabbit which would otherwise be malentities in the rabbit's environment are no longer so. The burrow is a Maelzer Modifier of the first order in the environment of the rabbit.

Source of Example	Object	Original classification	Classification according to formal definition
-------	Male sheep-tick *Ixodes ricinus*.	Mate of female sheep-tick, *I. ricinus*.	(A) Change in behaviour of female tick. (B) (a) Probability of reproduction of female tick increased thus H(female tick) increased. (b) Total no. of male ticks will probably increase (in the future). (c) Probability of reproduction of male tick increased thus H(male tick) increased. From (a), (b) and (c) the male sheep-tick is a mate for the female sheep-tick. In this example we may interchange animal and object and achieve the same result.
Andrewartha (1970) p.22	Tall rice plant.	In discussion of water in rice-field as resource of mosquito *Anopheles culifacies*.	(A) Change in behaviour of mosquito. (B) H(mosquito) not directly affected but water no longer a resource for mosquito. The tall rice-plant is a Maelzer Modifier of the first order. (The short rice-plants are not in the environment of the mosquito.)
Browning (1963) p.56	Measured amount of kinetic energy corresponding to high stream flow.	Weather in environment of larva of mosquito *Anopheles minimus*.	(A) Change in behaviour of larva. (B) (a) Expectation of life reduced, thus H(larva) reduced. (b) Total number of units of kinetic energy available to larva unchanged. (c) Kinetic energy inanimate thus no H involved. From (a), (b) and (c) the object is a malentity for the larva.

when an animal copulates in the normal way the probability of having off-spring is immediately increased, thus H is increased if we compare this situation with one in which no animals of the same species and opposite sex were present. A situation which at first sight seems strange is one in which an amount of heat energy corresponding to a certain temperature is the object: if the temperature is favourable to the animal's chances of surviving or reproducing we say that H increases. In fact we are comparing this situation with one in which the whole class of heat-energy objects is absent.

The number H should not be confused with 'Darwinian Fitness'. H is a number which is a function of two other numbers, one a probability, the other a life expectation. The estimation of these two latter numbers does not enter into the matter: we know that in the case of one animal at least (man) reasonably reliable methods of estimation are known and in common use. The concept of 'fitness', on the other hand, is a difficult one. Mather & Jinks (1971) write: 'Thus fitness may be definable in principle as the capital element in our consideration of evolutionary and selective changes, but it is extremely difficult to measure and often far from easy to define in usable terms'.

In the sections below the various components of the environment are dealt with separately, a list of examples drawn from previous literature on the subject is given and, finally, the general procedure is discussed and those objects which form the complement of the set {objects in direct environment U Maelzer Modifiers} are specified.

Resources

By 'resources' we mean '. . . material necessities of life which are 'used' by the animal . . .' (Andrewartha 1970). A resource is an object which will increase the expectation of life of the animal (or its chance of proceeding to the next stage of the life cycle) or the probability of reproducing. In other words, we classify as a resource of the animal, a, an object which will increase H(a). We have to distinguish carefully, by making precise measurements, the exact range of quantities characteristic of any particular class of objects which will result in an increase in H(a): too much water will kill a man; if he has too little he will also die. The class of objects of the type x gms water (per day, say) where x is too high or too low for the requirements of the animal is not a class of resources. We insist that x gms water is a different object from y gms water for $x \neq y$. When x lies within a certain range we have a class of resources. The same considerations apply to units of heat-energy. A particular animal will 'use' objects which are (measurable) amounts of heat-energy corresponding to a particular range of ambient temperature. At too high or too low a temperature the animal will die; the quantity H(a) decreases; the classes of objects corresponding to very high or very low temperatures are not resources. The situation may seem confused because an animal may excrete water, or give off heat which may then be 'used' again (recycled). However, the main points are clear. The quantity H(a) should increase and the total amount of that kind of resource available (i.e. the number of objects in the class) is either decreased or unaffected; it cannot increase. If the resource is another animal b, say, which is eaten, then H(b) is reduced since b's expectation of life is decreased. These considerations lead to the following formal definition of a resource.

Let R_l be the class of resources of a particular kind for animal a and $r_l \varepsilon R_l$. By $\bar{\bar{R}}_l$ we mean the total number of elements in R_l. Then we write 'Res $r_l a_t$' for 'r_l is a resource of animal a at time t', and

$$\text{Res}\ r_l a_t =_{df} \xi\, r_l a_t \supset [\{H_t(a) > H_{t-\alpha}\ (a)\}$$
$$\& \{\bar{\bar{R}}_{l,t} \leq \bar{\bar{R}}_{l,t-\alpha}\} \& \{\text{An}(r_l) \supset_{r_l}$$
$$H_t(r_i) \leqslant H_{t-\alpha}\ (r_l)\}]$$

The number represented by 'α' is a positive quantity chosen to suit the particular situation. By 'An(r_l)' we mean that the resource r_l is an animal, so the last term reads 'if r_l is an animal then $H_t(r_l) \leqslant H_{t-\alpha}(r_l)$'.

Mates

This class seems so familiar that we hardly need to define it. We remark two important points. First, the relation is symmetrical; if animal a is a mate of animal b then so also is b of a. Second, we expect offspring to result; when an adult male *Tribolium* beetle commits a sexual assault on a pupa we do not talk about 'mates'. Since offspring probably result, then at some later date, depending on the species of animal and the general conditions, the total number of mates available will probably increase. Thus we are led to the following definition.

By M is meant the class of objects which could be mates of animal a; m ε M; we write 'Mat ma_t' for 'm is a mate of animal a at time t'. The class M contains $\bar{\bar{M}}$ objects.

$$\text{Mat } ma_t =_{df} \xi \; ma_t \supset [\{H_t(a) > H_{t-\alpha}(a)\} \;\&\; \{\text{Prob } (\bar{\bar{M}}_{t+,\beta} > \bar{\bar{M}}_t) > \text{Prob}(\bar{\bar{M}}_{t-\alpha+\beta} > \bar{\bar{M}}_{t-\alpha})\} \;\&\; \{H_t(m) > H_{t-\alpha}(m)\}]$$

The positive constant β included in the probability statement depends on the generation time of the animal.

Predators and Parasites

A predator (or parasite) is an animal which increases its life expectancy, or increases its chance of reproducing at the expense of the animal a. In other words, H(predator) is increased but H(a) is reduced. The total number of predators, (parasites) may increase.

We write 'Pred pa_t' to mean 'animal p is a predator or parasite of animal a at time t'. P is the class of all possible predators and parasites of animal a and $\bar{\bar{P}}$ the total number in that class. p ε P. Then,

$$\text{Pred } pa_t =_{df} \xi \; pa_t \supset [\{H_t(a) < H_{t-\alpha}(a)\} \;\&\; \{P_{t+\gamma} \geqslant \bar{\bar{P}}_t\} \;\&\; \{H_t(p) > H_{t-\delta}(p)\}]$$

The positive constant, γ, depends on the physiology or generation time of the particular predator (parasite): α and δ are chosen to suit the situation with regard to animal and predator.

Also included in this class in Andrewartha (1970) were animals classified as 'aggressors'. However an object causing 'shock disease' or 'social stress' in the animal in which we are interested should rather be classified as a malentity (see below). An object affecting some major component of our animal's environment (such as another animal snatching or providing its food) is a Maelzer Modifier of the first order (see below).

Malentities

This term was introduced by Andrewartha (1970) to describe those objects, both animate and inanimate, which are inimical to the animal, a, without themselves being affected by the encounter. Thus H(a) is reduced, but if the malentity is an animal, b say, H(b) will not be affected. The idea of a malentity incorporates the notion of an accidental occurrence. It is a development of the conception of a 'hazard' given by Browning (1963). The human being who steps on an ant is a malentity in the environment of the ant. The same sort of consideration applies, however, to the event that an animal eats (by accident) a poisonous animal. In this case both H(a) and H(b) are reduced, thus in strict accordance with Andrewartha we would not classify the poisonous animal as a malentity. If however we allow H(b) to be either reduced or unaffected we cover a wider class of objects, formerly difficult to classify. Objects are included which were formerly classified as 'aggressors' causing 'social stress', that is, disturbance of biochemical balance resulting in reduced expectation of life in situations of overcrowding. The definition of 'Mal ca_t', that is 'c is a malentity for animal a at time t' follows.

Let C be the class of all possible malentities for animal, a. $\bar{\bar{C}}$ is the number of objects in C. c ε C. Then

$$\text{Mal } ca_t =_{df} \xi \; ca_t \supset [\{H_t(a) < H_{t-\alpha}(a)\} \;\&\; \{\bar{\bar{C}}_{t+\alpha} \leqslant \bar{\bar{C}}_t\} \;\&\; \{\text{An}(c) \supset_c H_t(c) \leqslant H_{t+\delta}(c)\}]$$

The positive constant δ is chosen to suit the particular malentity.

The Maelzer Modifiers

Certain objects in the vicinity of animal a 'only modified the value of some resource or other component of environment' (Maelzer 1965). In the terminology of the present study a main component of the direct environment which has been changed in some way, so that its final effect on the animal is changed, is classified as a different object. So a Maelzer Modifier is an object which replaces a component of the environment of the animal by a different component, or by an object which was not a component. We also allow a particular Maelzer Modifier to replace an object which was not a component by one which is; for example, a certain measured quantity of calcium may have no effect on an animal; in the presence of (a measured quantity of) vitamin D it does have an effect; the vitamin D is a Maelzer Modifier; the object which at time t was not a component of the environment becomes a different object (which is now a resource) at time $t + \varepsilon$. We do not have to combine the vitamin D with the calcium in order to create a new (compound) object 'vitamin D + calcium' (we may do this, of course, if it seems convenient), our insistence that the 'calcium objects' are different at time t and time $t + \varepsilon$ is sufficient; we cannot allow vitamin D to be both applied to the animal and not applied to the animal simultaneously.

As another example, consider a pair of animals of opposite sex copulating normally. Now introduce a sterility drug (or contraceptive). The drug is a Maelzer Modifier since animal b is no longer a mate of animal, a, in the formal sense of the definition given above.

By '$MMda_{t'}$' we mean 'object d is a Maelzer Modifier in the environment of animal a at time t'. By '$Comp\ xa_t$' we mean that object x is a main component of the environment of animal a at time t, that is, x is a resource, mate, predator or malentity. 'ηxy_t' means 'object x is brought into close physical proximity with object y at time t, evoking some physical (including spatial), physiological or behavioural change in y'. Then a Maelzer Modifier of the first order is defined by

$$MMd^{(1)}\ a_t =_{df} (\exists x)\ [\{(\eta d^{(1)}\ x_t \supset Comp\ xa_t)\ \&\ (\sim \eta d^{(1)}\ x_t \supset \sim Comp\ xa_t)\} \vee \{(\eta d^{(1)}\ x_t \supset \sim Comp\ xa_t)\ \&\ (\sim \eta d^{(1)}\ x_t \supset Comp\ xa_t)\}]$$

We define a Maelzer Modifier of the (n+1)th order, $d^{(n+1)}$, in terms of a Maelzer Modifier of the nth order (n = 1,2,3,...) thus:

$$MMd^{(+1)}\ a_t =_{df} (\exists d^{(n)})\ [\{(\eta d^{(n+1)}\ d^{(n)}{}_t \supset MMd^{(n)}\ a_t)\ \&\ (\sim \eta d^{(n+1)}\ d^{(n)}{}_t \supset \sim MMd^{(n)}\ a_t)\} \vee \{(\eta d^{(n+1)}\ d^{(n)}{}_t \supset \sim MMd^{(n)}\ a_t)\ \&\ (\sim n d^{(n+1)}\ d^{(n)}{}_t \supset MMd^{(n)}\ a_t)\}]$$

So in order to classify an object as a Maelzer Modifier of the first order $d^{(1)}$, we must be able to find an object x (i.e. $\exists x$) which, at the appropriate times, is either:

(i) not a component of the environment: by introducing $d^{(1)}$ it will become one,
or (ii) a component: by removing $d^{(1)}$ this will no longer be true,
or (iii) a component: by introducing $d^{(1)}$ this will no longer be true,
or (iv) not a component: by removing $d^{(1)}$ it will become one.

To classify an object as a Maelzer Modifier of the second order, $d^{(2)}$, we must be able to find a Maelzer Modifier of the first order (i.e. $d^{(1)}$) which, at the appropriate times, is either

(i) not a Maelzer Modifier of first order: by introducing $d^{(2)}$ it will become one,
or (ii) a Maelzer Modifier of first order: by removing $d^{(2)}$ this will no longer be true,
or (iii) a Maelzer Modifier of first order: by introducing $d^{(2)}$ this will no longer be true,
or (iv) not a Maelzer Modifier of first order: by removing $d^{(2)}$ it will become one.

For convenience we usually drop the superscript and write $MMda_t$.

The device allows us to have a connected chain of Maelzer Modifiers, as in the example in Table 1.

We also incorporate in the class of Maelzer Modifiers of the first order those animals which, by interfering with the resources or mates of the animal of interest, cause a reduction in H. Shelter (from predators or malentities) formerly classified as a resource is usually a first-order Maelzer Modifier.

Examples

The objects listed in Table 1 are individuals, that is, when we write '*Ixodes ricinus*, the sheep-tick' we mean one particular sheep-tick, and so on. In order to classify an object in the vicinity of the animal we proceed systematically by asking the following questions:

(A) is a change evoked in the physical state, physiology or behaviour of the animal.

(B) (a) Is H(animal) increased (decreased, unchanged)?
  (b) Is the total number of like objects available to the animal increased (decreased, unchanged)?
  (c) If the object is an animal is H(object) increased (decreased, unchanged)?

Discussion

It is instructive to consider those objects in the vicinity of the animal which do not fall within the direct environment of the animal. First, we have those objects which are such that H(animal) is not directly affected. Some of these may be Maelzer Modifiers. Secondly, there are those objects which are such that H(animal) is increased and thirdly those objects such that H is decreased. Consider these separately.

(i) H(animal) increased, the class of elements increased, but H(object) reduced or inapplicable. I cannot think of an example of this. If the class of objects is unchanged but H(object) is increased that is a symbiotic relationship between the two animals. This is something like the relation of being a mate, but no offspring result. However, when we examine the relation of symbiosis more closely we usually find that there exists an intermediate object which is a resource for one of the animals. Thus if a beetle is 'sheltered' by ants, this is because the beetle provides food for the ants: in turn the beetle is protected from predators by the ants. So the beetle provides a resource in the environment of the ant and the ant is a Maelzer Modifier of the first order in the environment of the beetle. In the case of a lichen the fungus obtains organic food from the alga and the alga obtains water and dissolved salts from the fungus, thus each organism provides a resource in the environment of the other. (Strictly speaking we would not classify either as an animal). The provider of a resource, if it excretes that resource, has transformed some object so that it becomes a resource and so is also a first-order Maelzer Modifier.

(ii) H(animal) decreased. We have the case that the total number of relevant objects is increased but H(object) decreased or unaffected: I cannot think of an example here. Also there is the case that the total number of objects is decreased but H(object) increased, for which also I cannot give an example.

In general, the formal classification accords well with the previous (Andrewartha 1970) classification. The major change is that the component 'weather' has disappeared.

There seems to be no doubt that this formal classification, if satisfactory to ecologists, will form a basis for further mathematical development of the theory. Certain mathematical statements follow immediately from the definitions, for example that the relation of being a mate is symmetrical and that a Maelzer Modifier of a Maelzer Modifier is a Maelzer Modifier.

An object may lie in more than one chain of Maelzer Modifiers. In fact these chains form the kind of network among animals which we observe when we look at an ecosystem. Also the same object may be both a main component of the environment and a Maelzer Modifier, for example, if a caterpillar feeds within an apple, the apple is both a resource (food) and, by providing shelter from some malentity, a first-order Maelzer Modifier.

It may sometimes be useful to consider time itself to be a resource (Kitching 1977). This accords with the formal definition only if we accept that some unit of time constitutes an object: we would have to consider that some length of time, say l hours, is brought into close physical proximity with animal a at time t and some response is immediately evoked. As a result of this the probability of reproduction is increased sufficiently so as to counteract the concomitant reduction in the expectation of life of a, with the final effect of increasing H(a). Similarly a certain length of time might sometimes be considered a malentity. These examples seem somewhat artificial, as much as anything because we cannot conceive the situation that the object is removed from the vicinity of the animal. We may starve an animal or remove all its possible mates, predators or malentities, but we cannot remove a 'time-object' by reversing the direction of the time-flow. Another possible class of objects is that of the time X heat-energy compounds, measured in units of day-degrees. We have the same difficulty here with the direction of the time-flow. We cannot remove from the vicinity of the animal an object consisting of a measured amount of day-degrees.

The four main components fall naturally into two classes; (a) resources and mates; H(a) increasing, and (b) predators and malentities; H(a) decreasing. Further development of the mathematical theory will certainly take advantage of these similarities. For the moment, it should be noticed that it may sometimes, in a specific example, be quite difficult to classify precisely, for example, just as the sheep, acting as a first-order Maelzer Modifier, provides blood as a resource for the sheep-tick, so we may consider a mate to act similarly in providing sperm as a resource. The confusion as to 'aggressors' arose because predators and malentities are really rather similar.

In this study the real positive number H includes neither the ability of an animal to disperse in order to find mates or food, or escape predators, nor any mention of the expectation of life of future generations. It may be advisable to include one or both of these. For the moment I do not know of an example of an object which clearly should be classified as a main component of the environment but which is such that neither of the two present constituents of H are affected.

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References

Andrewartha H.G. (1970) *Introduction to the Study of Animal Populations*. 2nd edn. Chapman and Hall.

Andrewartha H.G. & Birch L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press.

Andrewartha H.G. & Browning T.O. (1961) An analysis of the idea of 'resources' in animal ecology. *J. theoret. Biol.* **1**, 83–97.

Browning T.O. (1963) *Animal Populations*. Hutchinson.

Kitching R.L. (1977) Time, resources and population dynamics in insects. *Aust. J. Ecol.* **2**, 31–42.

Lewis D. & Lewis S. (1970) Holes. *Aust. J. Phil.* **48**, 206–12.

Maelzer D.A. (1965) A discussion of components of environment in ecology. *J. theoret. Biol.* **8**, 141–62.

Mather K. & Jinks J.L. (1971) *Biometrical Genetics*. 2nd edn. Chapman and Hall.

Appendix

Symbols used

$=_{df}$	Is defined as (is, by definition).
$\sim$	Negation.
$\supset$	Implication. Read '$A\supset\beta$' as 'if A then B'.
$\supset_a$	Implication with reference to all a.
$\cup$	Union. $A\cup B$ is the class (set) of elements belonging to either A or B (or both).
ε	Element of
&	Conjunction. Read 'A&B' as 'A and B'.
v	Disjunction. Read 'AvB' as 'A or B (or both).
$\exists$	The existential operator. Read '$\exists x$' as 'there is at least one x'.
$>$	Greater than.
$\geq$	Greater than or equal to
R_i, M, P, C.	The classes of resources, mates, predators, malentities.
r_i, m, p, c.	Individuals; a resource, a mate, a predator or a malentity.
$\alpha, \beta, \gamma, \delta, \varepsilon$	Positive constants.
MM	Maelzer Modifier.
ξ	Read '$\xi x a_t$' as 'object x is brought into close physical proximity with animal a at time t, evoking a physical, physiological or behavioural change in a'.
η	Read '$\eta x y_t$' as 'object x is brought into close physical proximity with object y at time t, evoking a physical, physiological or behavioural change in y'.
H, H(a), H_t(a).	A positive number.

B. S. NIVEN

FORMALIZATION OF THE BASIC CONCEPTS OF ANIMAL ECOLOGY

SUMMARY. Formal definitions of the following concepts of animal ecology are given: environment, niche, locality, local population, natural population, community, ecosystem. Five primitive (undefined) notions are used including "animal", "offspring" and "habitat", the latter in the sense of Charles Elton. The defining equations for the environment of one animal are first given, then niche (in the Elton sense) is formally defined in terms of the environment. The fifth primitve notion "habitat" is then introduced in order to define the remaining concepts.

INTRODUCTION

This article contains formal definitions of certain concepts basic to the theory of animal ecology. Initially, as a basis for the formalization, I have used the ideas of the population ecologists H. G. Andrewartha, L. C. Birch, T. O. Browning and D. A. Maelzer. Central to their theory is the classification of the environment of one typical animal. The original classification, given by Andrewartha and Birch [2] was developed by Browning [4], Maelzer [10] and Andrewartha [1]. The classification in the latter publication had five components. They were (i) resources; (ii) mates; (iii) predators, pathogens, aggressors; (iv) weather; (v) malentities. An example of (i) is an item of food. Examples of (v) are an animal which accidentally treads on the animal of interest and crushes it, or vagaries of the physical surroundings which accidently kill or damage the animal (e.g. a falling rock).

The theory, as given by Andrewartha [1] is then extended to encompass the interaction of the animal with the five components and further extended to populations of animals. Included are such concepts as the "niche" of an animal, i.e., its relations to food and enemies, and the interlocking of niches in an ecological complex. A formalization of the environment of the animal was given by Niven [12]. A short account of an improved version of the formalized environment is given in the Appendix to Andrewartha and Birch [3]; a more detailed account is included in this paper. Also in this paper are definitions of "niche", "community", "eco-

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system", "local population", "locality" and "natural population", together with explanations of their use by ecologists.

An animal is assumed to be surrounded by objects, both animate and inanimate, not all of which are in its environment although they may well be in the locality or in the habitat. Measurable quantities of energy are assumed to be objects. Animals are conceived as absorbing and exuding energy-objects in much the same manner as they eat and excrete food. In general, a formalization is undertaken for three main reasons:

(i) To facilitate the development of the theory. A formalization will aid in ensuring that all the assumptions are explicitly laid down; in particular it will give an accurate way of saying explicitly what assumptions are incorporated in a chain of deductions. The rules of deduction (which are formally laid down as part of a formalization) will enable us to arrive at the consequences of our assumptions in a systematic way; by formalizing we are less likely to omit important consequences. The use of clearcut definitions (the subject of this article) is almost essential for the exact communication of the theory to others. The use of a natural language in this communication necessarily involves us in the paradoxes which arise in a natural language.

(ii) To provide a basis for comparison of this theory with other theories of ecology.

(iii) To clarify the theory itself. A formalized language for a scientific theory provides an aid to intuition, a corrective to faulty thinking and a systematic method of criticizing obscure ideas.

In particular, in ecological discussion the terms "environment" and "habitat" are often confused, even by ecologists. As I show below the concept of an animal's habitat is not contained in the formal definition of the animal's environment – the two terms are quite separate. Furthermore, controversy has arisen between advocates of "population ecology" and "ecosystem ecology". In this paper I show that the terms "population" and "ecosystem" are closely related; the same four primitive terms are used in the two definitions; an extra primitive term is required to define "ecosystem". There has also been controversy as to which is the more fruitful approach for a field ecologist, a systematic study of the environment of certain chosen animals (as advocated by Andrewartha and Birch), or alternatively, a study of the entire ecosystem *ab initio*. However, it may be inferred from the results given in this paper that the study of the environment of certain chosen animals is a natural initial move by an ecologist who wishes to study an ecosystem; the infrastructure of the ecosystem is a complex network which may be built up from a knowledge of the precise environments of the relevant set of animals within the chosen habitat; we may start with any suitable animal and proceed step by step to the total community and hence to the ecosystem.

Philosophers of science have by and large ignored conceptual problems in ecological theory. This article is written with the intent of introducing some of the problems of ecology to philosophers of science.

THE PRIMITIVE (UNDEFINED) SYMBOLS

There are five of these:

An
Off
H
ξ
Hab

'An(x)' is used to mean that x is an animal. We may regard living organisms as being plants, animals or protists. Apart from a few rare occasions it is quite clear in the field or laboratory to which of these three categories the organism of interest belongs. In the theory described here the organism of main interest is in all cases assumed to be an animal. It may have living organisms which are not animals in its environment.

By 'x Off_t y' I mean "x is an offspring of y at time t (for the first time).

'$H_t(x)$' is a positive real number which is a non-decreasing function of:

(i) the expectation of life of x at birth or on entering its present stage of the life cycle, and

(ii) the probability that x will have an offspring.

It is assumed that it is possible to estimate (i) and (ii). This has been done for humans. Life expectation and fecundity have also been estimated for some other animals: see for example Caughley [5] for mammals and Mertz *et al.* [11] and Park *et al.* [14] for the *Tribolium* beetle.

By '$\xi_t xy$' I mean that object x is brought into close physical proximity with object y at time t, evoking immediately in y some physical, physiological or behavioural response or a change of position in space, and that no other object reduces or enhances this effect of x on y, i.e. that x affects y directly. The sub-index "t" is replaced by "τ" when the action takes place during an interval of time τ. Judgement as to whether or not a (significant) response occurs is made by the ecologist, thus certain actions of the animal of interest would normally be ignored. For example, if the animal gazes at some object, this is a response of the animal to the presence of the object and doubtless some sort of physiological or biochemical process is evoked; however, normally an action of this type would be regarded by the ecologist as trivial and ignored. Also the "closeness" of x and y will depend on the situation. Among mammals contact is normally necessary for procreation. This is not necessary among fishes. Nor indeed is it necessary when a farmer uses artificial insemination to improve his livestock.

'x Hab y' means that x is a habitat of animal y. Elton [6] uses the word "habitat" to mean a place chosen by the ecologist. Roughly speaking, it is a place in which the ecologist confidently expects to find the animals of interest. Other ecologists, notably Odum [13] use the word "habitat" in a different sense, however, it is essentially in Elton's sense that I use it here. In this theory, however, I introduce also the dimension of time. So by "habitat" I mean a four-dimensional entity, of which any three-dimensional time-slice is a habitat in Elton's sense. A system of Cartesian co-ordinates is set up by first imagining a plane orthogonal to the line joining some point in the Elton habitat to the centre of the planet, then erecting a vertical axis, orthogonal to the plane. We then start the ecologist's clock to measure time. The ecologist's clock will show a series of real numbers which are a record of times suited to the situation. For example, suppose we are studying a wallaby living in a eucalypt forest. It may well be satisfactory to record the activities of the animal at 6-hourly, daily or even monthly intervals of real time. The ecologist's clock, instead of recording 7 a.m. on Tuesday 14th July for example, simply records some number, say 6.52. It is now possible to think of the location of the animal in a four-dimensional interval in terms of quadruplets of numbers, rather than think of an animal moving through a habitat over a period of time. For instance, instead of thinking of the wallaby in motion through the forest over a period of several years we represent the position of various parts of the animal (say the centre of its left eye, the tip of its tail, and so on) by sets of ordered quadruplets $\langle a,b,c,d\rangle$ in which the first two numbers give the position in the horizontal plane, the third the height and the fourth the (ecologist's) time. Thus a plot of the third and fourth elements on a two-dimensional graph for fixed a,b might look like the diagram of Figure 1.

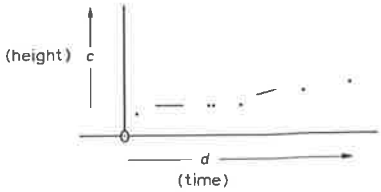

Fig. 1

The points occur at discrete intervals as the world-lines of the animal cut across the point (a,b) in the horizontal plane. A line sloping upwards occurs when the animal leaps. On average, the points will have an upward drift because the animal grows.

The symbols 'An', 'Off', 'H' and 'ξ' are used below to define the environment of an animal. 'Hab' is used in the definition of "locality" and hence "local population" and "natural population" and also in the definitions of "community" and "ecosystem".

THE ENVIRONMENT OF AN ANIMAL

The environment of animal a at time t is defined as the union of the centrum of a at t and the web of a at t:

$$E_t a =_{\mathrm{Df}} (C_t\, a \cup W_t a)$$

where $C_t a$, the centrum of a at time t is a set containing $(k + 3)$ elements, as follows:

$$C_t\, a =_{\mathrm{Df}} \{R_{1t}, \ldots, R_{\tau t}, M_t, P_t, C_t\}.$$

R_{it} is the class of all potential resources of a of a particular kind, (the i-th kind), M_t the class of all potential mates, P_t of predators and C_t of malentities, all at time t.

Write

'$r_i \mathrm{Res}_t a$', for "r_i is a resource of a at time t"

'm Mat$_t a$' for "m is a mate of a at time t",
'p Pred$_t a$' *for* "p is a predator of a at time t",
'c Mal$_t a$' for "c is a malentity of a at time t".

Then

$$r_i \mathrm{Res}_t a =_{\mathrm{Df}} \xi_t r_i a \supset [\{H_t(a) > H_{t-\alpha}(a)\} \; \& \; \{\mathrm{An}(r_i) \supset_{r_i} H_t(r_i) \leq H_{t-\gamma}(r_i)\}],$$
$$m \; \mathrm{Mat}_t a =_{\mathrm{Df}} \xi_t ma \supset \mathrm{Prob}\{(\exists x)(x \; \mathrm{Off}_{t+\beta} a \; \& \; x \; \mathrm{Off}_{t+\beta} m)\} > \mathbf{0},$$
$$p \; \mathrm{Pred}_t a =_{\mathrm{Df}} \xi_t pa \supset [\{H_t(a) < H_{t-\alpha}(a)\} \; \& \; \{H_t(p) > H_{t-\gamma}(p)\}],$$
$$c \; \mathrm{Mal}_t a =_{\mathrm{Df}} \xi_t ca \supset [\{H_{t-\alpha}(a)\} \; \& \; \{\mathrm{An}(c) \supset_c H_t(c) \leq H_{t-\gamma}(c)\}].$$

(α,β and γ are positive constants chosen to suit the particular situation; β is related to the gestation time of the animal).

By these definitions the animal a may not be a resource or predator or malentity of itself. It may, however, be a mate of itself; this is the case in parthenogenesis. The classes are now defined in terms of these elements. Thus R_{i_t} is the class of all R_i at time t and so on.

Examples of objects which are resources are:

(i) an item of food. $H_t(a)$ is increased because expectation of life is increased. If the resource itself is an animal then H_t(resource) is decreased because this animal will be damaged or will die as a result of the action (being eaten).

(ii) a quantity of energy. For example units of thermal energy are considered to be measurable objects. A quantity of thermal energy corresponding to a favourable temperature of the surrounding air results in an increase in H, when compared with a situation in which this object is absent. Since in this case the resource is not an animal the second term in the conjunct does not apply.

The definition of mate is similar to ordinary usage. Note that an animal which has been sterilized cannot be a mate.

"Predator" applies also to those organisms usually described as parasites or pathogens. H_t(animal) is decreased, since the animal becomes ill or is damaged or killed. H_t(predator) is increased since either its expectation of life or its probability of reproduction is increased as a result of the act of predation.

A malentity is an object adversely affecting the animal by accident such as a poisonous animal which is eaten. In this case H_t(malentity) is decreased, since the poisonous animal dies. More usually, in the case that the malentity is an animal, H_t(malentity) is unaffected, as in the case of some larger beast stepping on the animal.

$W_t a$, the web of a at time t, is the set of modifiers (also called Maelzer modifiers after D. A. Maelzer), and is defined in terms of the centrum.

The modifiers are objects in $E_t a$ which are linked to a only via some other object or objects. A first-order modifier w is "nearer" a than modifiers of higher order in the sense that only one object intervenes between w and a.

For convenience, rename objects in the centrum of the animal a "modifiers of order zero". Then write 'w Mod_t^n a' for "w is a modifier of order n in the environment of a at time t". So $w\ \mathrm{Mod}_t^0\ a$ iff $w \in C_t\, a$. And

$$\begin{aligned}
& w\,\mathrm{Mod}_t^{n+1} a =_{\mathrm{Df}} (\exists x)\,[\{[(\xi_t wx \ \vee\ \xi_t wy) \supset x\,\mathrm{Mod}_t^n a]\ \&\ [(\sim\xi_t wx \ \vee\ \sim\xi_t wy) \\
& \supset\ \sim x\mathrm{Mod}_t^n a]\} \\
& \vee\ \{[(\sim\xi_t wx \ \vee\ \sim\xi_t wy) \supset x\,\mathrm{Mod}_t^n a]\ \&\ [(\xi_t wx \ \vee\ \xi_t wy) \supset\ \sim x\,\mathrm{Mod}_t^n a]\}], \\
& n = 0,1,2, \text{---};\ y \text{ is either } a \text{ or a modifier of order} \leq (\mathrm{n} - 1).
\end{aligned}$$

So, in order to classify an object w as a first-order modifier we must be able to find an object x which is, or is not, an element of the centrum, depending on the presence or absence of w (or vice-versa). Similarly, a second-order modifier modifies a first-order modifier and so on. By the definitions every animal is a modifier in its own environment. This is a limiting case; in general we expect two similar animals to be modifiers in each other's environments.

Some examples of modifiers are:

(i) A measured amount of light-energy in unit volume surrounding a particular cockroach, of species *Periplaneta americana*. The cockroach will not eat an item of food in the presence of the light. If the light is removed the item of food will become a resource and the animal will proceed to eat it.

(ii) The burrow of a particular rabbit of species *Oryctolagus cuniculus*. The burrow protects the animal from foxes and other animals which would otherwise be predators in the environment of the rabbit, and from extremes of temperature or from flooding, i.e. from possible malentities in the environment of the rabbit.

(iii) A farmer who builds a fence between a particular sheep-tick and a sheep which might otherwise provide its food is a second-order modifier in the environment of the tick. The fence is a first-order modifier in the environment of the tick, since its presence prevents the sheep from entering the environment as a resource. The fence is regarded as an object which is moveable by the farmer, thus the farmer is an object modifying a first-order modifier.

An object may be in both the centrum and the web of an animal. An example is an apple in the environment of a particular caterpillar which uses the apple both as food and as protection against its enemies and vagaries of the weather.

NICHE

According to Elton [6] the niche of an animal means "its place in the biotic environment, *its relations to food and enemies.*"

Write N Nch a to mean N is a niche of animal a. N is defined to be a class of ordered triplets as follows:

(i) The first member of each triplet is an animal;
(ii) One of the triplets has a as first member;
(iii) The second member of each triplet is either empty or an ordered set of objects each of which is in the centrum of the first member;
(iv) The objects in the i-th place of the second members either all belong to the same phylum or, if inanimate, to the same well-defined class of material objects, and are all resources, or all mates, or all predators, or all malentities.
(v) The third member of each triplet is either empty or an ordered set of objects in the web of the first member.
(vi) The objects in the i-th place of the third members usually all belong to the same phylum or, if inanimate, to the same well-defined class of material objects, and they are all modifiers of the same order.
(vii) At least one of the second or third members is not empty.

Elton gives an example of a niche of the African tick-bird. These animals pick the ticks off other animals for food. He lists three animals in this niche. The corresponding ordered triplets are:

⟨African tick-bird, tick, ungulate⟩
⟨Starling, tick, ungulate⟩
⟨Scarlet land-crab, tick, aquatic lizard⟩

In the example, there is only one object as second member and one as third member. The second member is a resource of the first member. The third member is a first-order modifier in the environment of the first member.

COMMUNITY AND ECOSYSTEM

A community consists of "co-existing interdependent populations" of animals (Price [15]). Animals are interlinked via their environments, e.g., a predator of one animal may be a resource of another animal, or an object in the centrum of one animal may be in the web of another. A community is a set of animals which is found within a particular habitat. Remembering that every animal is in its own environment, since it must necessarily be a modifier of itself, we may build up a community by first choosing a suitable animal, a, within habitat Y, i.e., Y Hab a. We choose also a time interval τ, equal to the duration of Y and select those objects u_0 which are in the environment of a during τ. We then add to a every animal b_0 located in Y which has at least one object in its environment which is a u_0. We continue by adding every animal b_1 located in Y which has at least one object in its environment which is also in the environment of at least one b_0. We continue this scheme until no new animals are added. The process must terminate since the total number of animals in Y is bounded. The final set of animals, K, located in Y, is the community of a within habitat Y. Every animal in K has at least one object in its environment during τ which belongs also to the environment of some other animal in K.

This may be written more formally as follows. First, write 'x loc Y' for "x is located in Y", i.e., at least one of the co-ordinates of the points giving the position in four-dimensional space-time of the object x falls in the appropriate interval of Y. Notice that 'x loc Y' is not equivalent to 'Y Hab x'. Write '$x \in E_\tau\, a$' for "x is in the environment of a for at least some part of the interval τ". Define the set K_0 as follows:

$$K_0 = \{b_0\colon \mathrm{An}(b_0)\ \&\ (b_0 \text{ loc } Y)\ \&\ (\exists u_0)\ [(u_0 \in E_\tau\, a)\ \&\ (u_0 \in E_\tau b_0)]\}.$$

Now define the sets K_1, K_2, K_3 … recursively.

$$K_i = \{b_i\colon \mathrm{An}(b_i) \mathbin{\&} (b_i \mathrm{\ loc\ } Y) \mathbin{\&} (\exists u_i)\,[(u_i \in E_\tau\, b_{i\text{-}1}) \mathbin{\&} (b_{i\text{-}1} \in K_{i\text{-}1}) \mathbin{\&} (u_i \in E_\tau b_i)]\},$$
$$i = 1, 2, 3, \ldots.$$

The process is continued until that stage j such that

$$\bigcup_{i=0}^{j} K_i = \bigcup_{i=0}^{j+1} K_i = K.$$

Then K is the community of animal a within habitat Y.

The definition given above requires the inclusion within a community of animals connected only by very high order modifiers. In practice it may be useful to restrict the definition of environment to the union of the centrum and modifiers of low order only. In the following example from Kitching [9] only the centrum and first-order modifiers are used.

The habitat Y in this example was a water-filled tree-hole in a beech tree in Wytham Woods, Berkshire, England, over a period of some months. Six different species of animals were present: two mosquitoes, two midges, a hoverfly and a small beetle, all in their larval form. The larvae were all saprophages, i.e., they ate rotten compost-like materials present in the water. In addition to the detritus, some of them were observed to eat algae, fungi and bacteria. They may also occasionally feed on the decomposing flesh of dead earthworms and other animals accidently drowned in the habitat.

To construct the community we may start with any one larva, say one particular beetle larva. Call this a. We now focus attention on a particular particle of detritus in Y. Call this u_0. Then u_0 is a resource in the centrum of a. Since the two midges, both mosquitoes and the hover-fly are also detritus-eaters, as well as all other beetles, all these animals have u_0 in their centra as a resource until a time t when u_0 is eaten. The eater, if it is not a, is then acting as an aggressor, i.e., a first-order modifier in the environment of a. So these animals appear in each others environments as first-order modifiers and all belong to the set K_0. The set K_1 contains the same animals as K_0. So in this case we have $K = K_0 \cup K_1 = K_0$.

Price [15] uses the word "ecosystem" to mean "the community and its physical environment". If we are willing to include certain living organisms, e.g., pathogens in the environment, we may define an ecosystem as the union of the community of the animal a and all objects located in the habitat of a which belong to the environment of at least one member of the community. Formally, suppose K is the community of animal a within habitat Y which is of duration τ. Then the ecosystem is defined by:

$$E\,(a,\,K,\,Y) \;=_{\mathrm{Df}}\; \{v : (v \in E_{\tau}\; b)\;\&\;(b \in K)\;\&\;(v \text{ loc } Y)\}.$$

In this formulation an ecosystem consists of a set of objects, both animate and inanimate. It is not obligatory that all objects in every time-slice of the habitat Y are included. Notice that in order to define an ecosystem we require to choose an animal a, an interval of time τ and a habitat Y of duration τ. The primitive terms 'ξ', 'An', 'H' and 'Off' are also contained in the definition of ecosystem.

LOCALITY, LOCAL POPULATION, NATURAL POPULATION

Consider the set of objects X such that each element $x \in X$ is in close physical proximity with animal a at some time during an interval of time τ, invoking a response, i.e.,

$$X = \{x : \xi_{\tau}\; x\; a\}.$$

Suppose Y Hab a. Assume Y has duration greater than τ. Let Z' be the minimum (four-dimensional) interval of Y which includes the positions of all $x \in X$. Now construct the rectangular parallelepiped $Z(a,\tau)$ which is bounded by the minima and maxima of the first three co-ordinates of all points in Z'. Then $Z(a,\tau)$ is the locality of animal a for the time-interval τ.

$Z(a,\tau)$ is not a set of objects. It is an interval in ordinary three-dimensional space. The concept is used in ecology when discussing ecological action, e.g., when animals disperse they move from one locality to another. As an example consider the construction of the locality of a mosquito. Focus attention on some one particular female of species *Anopheles culifacies* and choose a particular time-interval, τ, of duration exactly ten minutes. During this period the animal will be flying about. Suppose that at the beginning of the interval it is feeding on a human being. It then flies to a neighbouring small bush, alights on a twig and remains there for the rest of the interval. Take as a minimum vertical co-ordinate of Z (mosquito, τ) the position of the lowest root fibre of the bush and as the maximum vertical co-ordinate the position of the top of the person's head. The minimum and maximum co-ordinates horizontally will be determined by the movements of the person during τ and by the position of the bush.

The local population of animals of the same species as a is a set $L_{a,Z}$. Included in this set are the mates and the mates of mates of a within the locality $Z(a,\tau)$.

More formally, let S_τ be the set of all objects in the locality $Z(a,\tau)$. $s \in S_\tau$ iff at least part of s occupies at least one position during τ such that one of its three spatial co-ordinates falls within the rectangular parallelepiped which is $Z(a,\tau)$. Let M_1 be the set of mates of a and M_2 the mates of mates of a all of which are also elements of S_τ. So, for a time t in the interval τ

$$(m_1 \in M_1) \text{ iff } (m_1 \text{ Mat}_t\ a) \ \&\ (m_1 \in S_t);$$
$$(m_2 \in M_2) \text{ iff } (\exists m_1)\ [(m_1 \text{ Mat}_t\ a) \ \&\ (m_2 \text{ Mat}_t m_1)] \ \&\ (m_2 \in S_\tau)$$

Then

$$L_{a,Z} =_{\text{Df}} M_1 \cup M_2.$$

Thus in order to construct a local population first choose a suitable animal, e.g., the female mosquito of the example above. Include all her potential mates in the locality and all their potential mates also in the locality. If it is desired to refer to a larger population the locality may be extended by increasing the time-interval τ.

A natural population, for the same interval τ, is the union of all local populations over some specified set of localities e.g.

$$\bigcup_{Z < \text{Poland}} L_{a,Z}$$

CONCLUDING REMARKS

The formalization of the concepts dealt with above have been developed in close co-operation with a number of field ecologists. At the present time of writing (1980) we have not found an example of a real-life situation in which a certain object should, according to the intuitive notions of the ecologists, be included in (excluded from) the environment of the animal but does not (does) accord with the formal definitions. This is not to say that the present formalized description of the environment is immutable.

The idea of "connectance" [8], which expresses the probability that any pair of species will interact, is presently being used in ecology. It is estimated by the ratio of the number of known links between species to the number of topologically possible links. Connectance does not include the detail of the different pathways which may link two animals in a community, even when they are of different species, e.g., if the habitat in the example of Section 5 (the water-filled tree-hole) is enlarged to include many such tree-holes in a forest then beetle larvae and mosquito larvae may well be linked via their predators, as well as by a resource. It may well prove useful to take account of all such pathways when measuring linkage between species in a community.

If we consider an ecosystem to be a set of animals and the pathways connecting them, then an ecosystem immediately begins to look something like a mathematical category. However, we have to take into account that pathways between distinct pairs of animals are not always non-intersecting, since two animals may be linked by one or more chains of modifiers in addition to sharing an element of both centra.

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REFERENCE

[1] Andrewartha, H. G.: 1971, *Introduction to the Study of Animal Populations*, 2nd edition, Chapman and Hall, London.
[2] Andrewartha, H. G. and L. C. Birch: 1954, *The Distribution and Abundance of Animals*, University of Chicago Press.
[3] Andrewartha, H. G. and L. C. Birch: 1982, *The Ecological Web: and the Distribution and Abundance of Animals* (with An Appendix by B. S. Niven), University of Chicago Press.
[4] Browning, T. O.: 1963, *Animal Populations*, Hutchinson, London.

[5] Caughley, G.: 1966, 'Mortality patterns in mammals', *Ecology* **47**, 906–918.
[6] Elton, Charles: 1966a, *The Pattern of Animal Communities*, Methuen, London.
[7] Elton, Charles: 1966b, *Animal Ecology*, Science Paperbacks and Methuen, London.
[8] Gardner, M. R. and W. R. Ashby: 1970, 'Connectance of large dynamic (cybernetic) systems: critical values for stability', *Nature* **228**, 784.
[9] Kitching, R. L.: 1971, 'An ecological study of water-filled tree-holes and their position in the woodland ecosystem', *J. Anim. Ecol.* **40**, 281–302.
[10] Maelzer, D. A.: 1965, 'A discussion of components of environment in ecology', *J. Theor. Biol.* **8**, 141–162.
[11] Mertz, David B., Thomas Park and W. J. Youden: 1965, 'Mortality patterns in eight strains of flour beetles', *Biometrics* **21**, 99–114.
[12] Niven, B. S.: 1980, 'The formal definition of the environment of an animal', *Australian Journal of Ecology* **5**, 37–46.
[13] Odum, Eugene P.: 1971, *Fundamentals of Ecology*, Saunders, London.
[14] Park, Thomas, D. B. Mertz and K. Petrusewicz: 1961, 'Genetic strains of *Tribolium*: their primary characteristics', *Physiol. Zool.* **34**, 62–87.
[15] Price, Peter W.: 1975, *Insect Ecology*, Wiley Interscience, London.

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LETTER TO THE EDITOR

Two Different Animals May Not Have the Same Environment

The symbolic definition of the environment of an animal given by Niven (1982) has been used by Andrewartha & Birch (1983) as a basis for their analysis of environment. In this note it is shown to be precisely true that if, at time t, a_t and b_t are different animals then their environments necessarily differ and the converse is also true. Formally, $E_t a \neq E_t b$ iff $a_t \neq b_t$, where $E_t s$ is the environment of the animal s at time t, according to the definition of Niven (1982). Also $E_t a = E_t b$ iff $a_t = b_t$.

In the symbolic definition the environment of the animal s is a set of objects. There are two subsets, called the "centrum" and the "web". The centrum is the set of objects which affect the animal directly; it is further divided into four subsets, called "resources", "mates", "predators" and "malentities". The web is the set of modifiers; it is convenient to refer to elements of the centrum as "modifiers of order zero"—these are modified by objects named "modifiers of first order", which in turn are modified by "second-order modifiers" and so on.

Now consider the case that a_t and b_t are different animals. From the definition of the web it follows immediately that a_t is a modifier of all orders greater than zero in its own environment. Furthermore, it is factually true that b_t is not a modifier of all orders greater than zero in the environment of a_t; to see that this statement is true consider two snails of the species *Lymnaea peregra* grazing next to each other (see Niven & Stewart, 1982). The first snail, s_1 say, is a first-order modifier of food resources in the environment of the second, s_2. But s_2 does not occupy this place in its own environment. Thus if $a_t \neq b_t$ we have that $E_t a \neq E_t b$. It follows logically that if $E_t a = E_t b$ then $a_t = b_t$.

Now consider the case that a_t and b_t are the same animal. Then it is factually true that $E_t a = E_t b$. It follows logically therefore that if the environment of a_t is not the same as the environment of b_t then a_t is not the same animal as b_t, i.e. if $a_t = b_t$ then $E_t a = E_t b$ and if $E_t a \neq E_t b$ then $a_t \neq b_t$.

From the four statements above we have, formally,

$$E_t a \neq E_t b \text{ iff } a_t \neq b_t \tag{1}$$

and

$$E_t a = E_t b \text{ iff } a_t = b_t. \tag{2}$$

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Statements (1) and (2) should be thought of as limits to an ordered set of sentences which amount to the (necessarily vague) notion that in a sequence of pairs of animals such that the members of the pairs become more and more like one another, then their environments become more alike.

Andrewartha & Birch (1983), in discussing this phenomenon (after giving many examples) conclude "... when two distinct species depend on the same niche but nevertheless continue to live together in the same habitat... either (1) their ecologies and adaptations can properly be said to be the same with respect to this particular niche. That is, the closer the contest the better the chance that the two species can live together... or (2) the animals have succeeded in partitioning the niche in a way that scientific inquiry has not yet revealed".

It should be noted that "habitat", the place where an animal lives, is used as a primitive term by Niven (1982); it is contained in the definition of the ecosystem, but not in the definition of the environment. The concept of 'niche' does not contain 'habitat' as a primitive; the niche is a class of ordered triplets and depends only on the definition of centrum and web. An explanatory note on the niche is given by Niven (to be published).

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REFERENCES

ANDREWARTHA, H. G. & BIRCH, L. C. (1983). *The Ecological Web and the Distribution and Abundance of Animals.* Chicago: Chicago University Press.

NIVEN, B. S. (1982). *Erkenntnis* **17,** 307.

NIVEN, B. S. & STEWART, M. G. (1982). *The Precise Environment of Some Well-Known Animals No.* VIII *The Wandering Snail Lymnaea peregra.* AES Working Paper No. 4/82. Brisbane, Australia: Griffith University.

Appendix: The Formal Definition of the Environment of an Animal

B. S. Niven

The object of this appendix is to give precise, formal definitions of the notions of "centrum" and "web," which are then used to define the "environment" of an animal. Precision is achieved by using the ordinary symbols of modern logic, supplemented by certain other symbols introduced for the express purpose of formalizing the concept of the environment of an animal.

The variable a designates an arbitrary animal, and $E_t a$ the environment of a at time t.

The animal is conceived to be surrounded by objects (things), some of which are animate. Objects are assumed to change in time—thus, for example, a particular apple at time t may differ from the same apple at time $(t + \delta t)$ where the change in time, δt, is of magnitude relevant to the ecological situation under study.

By $\xi_t xy$ I mean that object x is brought into close physical proximity with object y at time t, evoking immediately in y some physical, physiological, or behavioral response or a change of position in space, and that no other object reduces or enhances this effect of x on y—that is, that x affects y directly.

For an arbitrary a, $H_t(a)$ is a positive real number that is some function of:

(i) the expectation of life of a at birth or on entering its present stage of the life cycle and

(ii) the probability that a will have an offspring.

An(x) is used to mean "x is an animal."

By x Off_t y·I mean "x is an offspring of y at time t."

By Prob {X} I mean "the probability that the event X occurs."

I distinguish certain classes of objects surrounding a at time t, which I call $R_{1t}, R_{2t} \ldots R_{Kt}, M_t, P_t$, and C_t. R_{it} is the class of all potential resources of a of a particular kind (the ith kind), M_t the class of all potential mates, P_t of predators, and C_t of malentities, all at time t. The elements belonging to these classes are defined below.

The environment of a at time t is to be defined as the union of the centrum of a at t and the web of a at t:

$$E_t a =_{\mathrm{Df}} (c_t a \cup w_t a),$$

where $c_t a$, the centrum of a at time t, is a set containing $(K + 3)$ elements, as follows:

$$C_t a =_{\mathrm{Df}} \{R_{1t}, \ldots, R_{Kt}, M_t, P_t, C_t\}.$$

Write

$r_i\ \mathrm{Res}_t a$, for "r_i is a resource of a at time t,"

$m\ \mathrm{Mat}_t a$ for "m is a mate of a at time t,"

$p\ \mathrm{Pred}_t a$ for "p is a predator of a at time t,"

$c\ \mathrm{Mal}_t a$ for "c is a malentity of a at time t." Then

$$r_i\ \mathrm{Res}_t a =_{\mathrm{Df}} \xi_t r_i a \supset [\{H_t(a) > H_{t-\alpha}(a)\}\ \&\ \{\mathrm{An}(r_i) \supset_{r_i} H_t(r_i) \leq H_{t-\gamma}(r_i)\}],$$

$$m\ \mathrm{Mat}_t a =_{\mathrm{Df}} \xi_t m a \supset \mathrm{Prob}\{(\exists x)(x\ \mathrm{Off}_{t+\beta} a\ \&\ x\ \mathrm{Off}_{t+\beta} m)\} > 0,$$

$$p\ \mathrm{Pred}_t a =_{\mathrm{Df}} \xi_t p a \supset [\{H_t(a) < H_{t-\alpha}(a)\}\ \&\ \{H_t(p) > H_{t-\gamma}(p)\}],$$

$$c\ \mathrm{Mal}_t a =_{\mathrm{Df}} \xi_t c a \supset [\{H_t(a) < H_{t-\alpha}(a)\}\ \&\ \{\mathrm{An}(c) \supset_c H_t(c) \leq H_{t-\gamma}(c)\}].$$

(α, β, and γ are positive constants chosen to suit the particular situation; β is related to the gestation time of the animal.) By these definitions the animal a may not be a resource or predator or malentity of itself. It may, however, be a mate of itself; this is the case of parthenogenesis.

$w_t a$, the web of a at time t, is the set of modifiers (also called Maelzer modifiers after D. A. Maelzer) and is defined in terms of the centrum.

The modifiers are objects in $E_t a$ that are linked to a only through some other object or objects. A first-order modifier w is "nearer" a than modifiers of higher order in the sense that only one object intervenes between w and a.

Write $x\ \mathrm{Cent}_t a$ for "object x is in the centrum of animal a at time t" and $w\ \mathrm{Mod}_t^1 a$ for "w is a first-order (Maelzer) modifier in the environment of a at time t." Then

$$\begin{aligned} w\ \mathrm{Mod}_t^1 a =_{\mathrm{Df}} (\exists x)\Big[&\{[(\xi_t wx \vee \xi_t wa) \supset x\mathrm{Cent}_t a]\ \& \\ &[(\sim\xi_t wx \vee \sim\xi_t wa) \supset \sim x\mathrm{Cent}_t a]\} \\ &\vee \{[(\sim\xi_t wx \vee \sim\xi_t wa) \supset x\mathrm{Cent}_t a]\ \& \\ &[(\xi_t wx \vee \xi_t wa) \supset \sim x\mathrm{Cent}_t a]\}\Big]. \end{aligned}$$

The modifiers of higher order are successively "further" from a (not necessarily spatially but in an ecological sense). Write $w\ \mathrm{Mod}_t^n a$ for "w is a modifier of order n in the environment of a at time t." Then

$$\begin{aligned} w\ \mathrm{Mod}_t^{n+1} a =_{\mathrm{Df}} (\exists x)\Big[&\{[(\xi_t wx \vee \xi_t wy) \supset x\ \mathrm{Mod}_t^n a]\ \& \\ &[(\sim\xi_t wx \vee \sim\xi_t wy) \supset \sim x\ \mathrm{Mod}_t^n a]\} \\ &\vee \{[(\sim\xi_t wx \vee \sim\xi_t wy) \supset x\ \mathrm{Mod}_t^n a]\ \& \\ &[(\xi_t wx \vee \xi_t wy) \supset \sim x\ \mathrm{Mod}_t^n a]\}\Big], \end{aligned}$$

$n = 1, 2, 3, \ldots$; y is either a or a modifier of order $\leq(n - 1)$ for $n > 1$.

So to classify an object w as a first-order modifier we must be able to find an object x that is, or is not, an element of the centrum, depending on the presence or absence

This is the abstract of the talk you presented at the meeting of the Association for Symbolic Logic held in Perth, Australia, May 1983. It will be printed in the Journal of Symbolic Logic as part of the summary of that meeting.

B. S. NIVEN, *The structure of the environment.*

Symbolic definitions of the environments of an animal and a human are given. The defining equations for the animal case include four primitive terms specific to the theory of ecology. An extra primitive is added in the case of a human to provide for a human's perception of the world. The definitions include conditional statements in which consideration is given only to the case that the statement is true. The gross structure of the environment consists of two sets of objects (an object is a measurable lump of matter or energy), called the "centrum" and the "web". Formally, the web contains an infinite number of objects called "modifiers"; consideration is given to only a small finite number of these modifiers both in the construction of envirograms and in the formal definitions of "community" and "ecosystem". Two envirograms displaying the structure of the environment are presented in the animal case for the three-spined stickleback (*Gasterosteus aculeatus*) and the wandering snail (*Lymnaea peregra*). The interpretation of the primitive term "animal" is given as including all those animals ranging from the sponges to the nonhuman primates which are normally studied by zoologists. The first envirogram for a human is described. The main use of the work in the overall formalization project is as a strategy for developing axioms and rules of inference for a new calculus. This calculus will be used for prediction of future states of animal and human communities and ecosystems. The ecosystem, formally defined in terms of the environment, is a category; an implication of this statement is that the axioms and theorems of the algebra of categories can be incorporated into the new calculus. Furthermore the task of developing theorems about ecosystems is now reduced to that of developing theorems about certain kinds of categories undergoing specific changes in time.

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Logical Synthesis of an Animal's Environment: Sponges to Non-human Primates.
I. Primitive Terms and Definitions

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Abstract

This paper is the first in a series on the environment of the freshwater sponge, *Spongilla lacustris*, the rat tapeworm, *Hymenolepis diminuta*, the common octopus, *Octopus vulgaris*, the cane toad, *Bufo marinus*, and the chimpanzee, *Pan troglodytes*. A new version is given of the formal symbolic definition of total environment, which was published by Niven (*Erkenntnis*, 1982, **17**, 307–20). Informal defining equations are then presented, with examples from the environments of the five species of the study.

Introduction

The search for a precise notion of 'environment' is recorded in the ecology literature for at least 50 years. Haskell (1940) discusses some earlier attempts and then presents a sophisticated semiformal definition of 'environment' as a mathematical manifold. In 1954, Andrewartha and Birch suggest a simple informal definition. The same two authors, in 1984, give an analysis of 'environment' based on the formal symbolic definition of Niven (1982).

In this series of six papers, a new version of the 1982 definition is given, followed by applications to the total environment of five species: the freshwater sponge, *Spongilla lacustris*, the rat tapeworm, *Hymenolepis diminuta*, the common octopus, *Octopus vulgaris*, the cane toad, *Bufo marinus*, and the chimpanzee, *Pan troglodytes*.

In this paper, the first in the series, the formal symbolic version of the new definition is given. Informal, partly symbolic versions of the defining equations are then presented. A number of examples from the environments of the five animals of the study show precisely how the informal defining equations should be used to classify objects in the environment.

An improved version of the 1982 definition is desirable, firstly, because of certain philosophical difficulties associated with the use of the subjunctive conditional in the 1982 definition and, secondly, because of practical difficulties in applying the original formal symbolic defining equations. The new version yields the same subsets of objects within the environment; thus, the analysis of Andrewartha and Birch (1984) is still valid.

The construction of the definition follows the guidelines laid down by Church (1956) and other modern logicians. First, the universe of discourse is specified. This is followed by a list of the primitive terms and their interpretations. Finally, the formal symbolic defining equations are presented. A glossary of symbols is available in the Appendix of this paper.

The application to a particular species of animal is greatly aided by the use of an 'envirogram'. This is a diagram, introduced by Andrewartha and Birch (1984), that displays the objects in the environment in their correct compartments. A disadvantage of this diagram is that it does not reflect the non-linearity of the mathematics. Envirograms are presented for each of the five animals in this study.

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Universe of Discourse

A universe of discourse consists of those things with which the discussion is concerned. They are the 'individuals' of the system. In the present context, these are the substantive objects familiar to physical scientists: chunks of matter, or chunks of energy.

The restriction to such substantive objects has the advantage of avoiding the confusion inherent in discussions about continuous rates. For instance, the effect of 'temperature' on an animal is dependent on which part of the temperature scale we specify; very low temperatures may be inimical to the animal, whereas some higher range is not. It is impossible to give a precise classification of 'temperature' within the environment of an animal. If, instead, we fix attention on some discrete chunk of thermal energy, a 'lump of heat energy' of a specified size, it becomes possible to classify that particular object precisely.

Primitive Terms

In a formal theory, certain notions are taken as primitive and all further notions that are introduced in the development of the theory are defined in terms of the primitive ones. The primitive terms themselves are not defined. They are made intelligible by pointing to them or explaining them informally. Such explanation, by signs or other language, is called interpretation.

In the definition of environment, four primitive terms are used that are special to the system. They are 'An', 'Off', 'H' and 'ξ'. Their interpretations follow.

'$\mathrm{An}(x)$' is used to mean that x is an animal. We may regard living organisms as being plants, animals or protists. Apart from a few rare occasions, it is quite clear in the field or laboratory to which of these three categories the organism of interest belongs. In the theory described here, the organism of main interest is, in all cases, assumed to be an animal. It may have living organisms that are not animals in its environment.

By '$x\,\mathrm{Off}_t y$', I mean x is an offspring of y at time t (for the first time).

By '$\xi_t xy$', I mean that object x is brought into close physical proximity with object y at time t, evoking immediately in y some physical, physiological or behavioural response or a change of position in space, and that no other object reduces or enhances this effect of x on y, i.e. that x affects y directly. The subindex t is replaced by τ when the action takes place during an interval of time τ. Judgement as to whether or not a (significant) response occurs is made by the ecologist; thus, certain actions of the animal of interest would normally be ignored. For example, if the animal gazes at some object, this is a response of the animal to the presence of the object and, doubtless, some sort of physiological or biochemical process is evoked; however, normally, an action of this type would be regarded by the ecologist as trivial and ignored. Also, the 'closeness' of x and y will depend on the situation. Among mammals, contact is normally necessary for procreation. This is not necessary among fishes, nor indeed it is necessary when a farmer uses artificial insemination to improve his livestock.

'$\mathrm{H}_t(x)$' is a positive real number that is a non-decreasing function of:

(i) the expectation of life of x at birth or on entering its present stage of the life cycle, and

(ii) the probability that x will have an offspring.

It is assumed that it is possible to estimate (i) and (ii). This has been done for humans. Life expectation and fecundity have also been estimated for some other animals: see, for example, Caughley (1966) for mammals, and Mertz *et al.* (1965) and Park *et al.* (1961) for the *Tribolium* beetle. 'H' should not be confused with 'Darwinian fitness'—a different concept, which applies to several generations. 'H' applies to the present generation only in the particular circumstances that are of interest.

The Conditional in the Definition

All defining equations incorporate statements of the form '$A \mid B$', to be read 'A given that B' where A and B are sentences. Variations in the standard form include sentences like '$\sim A$' (the negation of A) and '$A \vee C$' (either A or C, where C also is a sentence). B is a sentence of the kind 'ξ_t(object)(animal)', where ξ is the interaction primitive referred to above. Since the classification of the object is of interest only if we can say for certain that 'ξ(object)(animal)' is possible at time t, or that such an event certainly does not occur, a large class of sentences of this kind are irrelevant. For example, if we are dealing with an octopus, the event 'ξ(Taj Mahal)(octopus)' would be irrelevant to a discussion of the environment of the animal.

Formal Symbolic Definition of Total Environment

The environment of a subject animal a at time t is a structured set of objects. There are two subsets, called the 'centrum of animal a at time t', $\mathrm{C}_t a$, and the 'web of animal a at time t', $\mathrm{W}_t a$. Objects in the centrum affect the subject animal directly; objects in the web affect the subject animal indirectly, *via* the centrum.

The centrum is further divided into four subsets, called the resources, mates, predators and malentities of the subject animal a, all at time t. The formal definitions are:

$$\begin{aligned}
r\,\mathrm{Res}_t a &=_{\mathrm{df}} [\{\mathrm{H}_t(a) > \mathrm{H}_{t-}(a)\} \mid \xi_t ra] \;\&\; [\mathrm{An}(r) \supset \{\mathrm{H}_t(r) \leqslant \mathrm{H}_{t-}(r)\} \mid \xi_t ra]\\
m\,\mathrm{Mat}_t a &=_{\mathrm{df}} \mathrm{Prob}[(\exists x)(x\,\mathrm{Off}_{\mathrm{t}+\beta} a \;\&\; x\,\mathrm{Off}_{t+\beta} m) \mid \xi_t ma] > 0\\
p\,\mathrm{Pred}_t a &=_{\mathrm{df}} [\{\mathrm{H}_t(a) < \mathrm{H}_{t-}(a)\} \;\&\; \{\mathrm{H}_t(p) > \mathrm{H}_{t-}(p)\} \mid \xi_t pa]\\
c\,\mathrm{Mal}_t a &=_{\mathrm{df}} [\{\mathrm{H}_t(a) < \mathrm{H}_{t-}(a)\} \mid \xi_t ca] \;\&\; [\mathrm{An}(c) \supset \{\mathrm{H}_t(c) \leqslant \mathrm{H}_{t-}(c)\} \mid \xi_t ca]\,.
\end{aligned}$$

The interval of time β in the definition of a mate is the gestation time. A predator must be an animal.

The centrum is the set of objects that are resources, mates, predators or malentities. Formally:

$$\mathrm{C}_t a =_{\mathrm{df}} \{x\colon x\,\mathrm{Res}_t a \vee x\,\mathrm{Mat}_t a \vee x\,\mathrm{Pred}_t a \vee x\,\mathrm{Mal}_t a\}\,.$$

The web consists of a structured set of objects called modifiers. Zero-order modifiers are elements of the centrum. First-order modifiers are objects that modify zero-order modifiers; second-order modifiers modify first-order modifiers, and so on. The modifiers of order greater than zero are also divided into two sets called positive and negative modifiers, depending on whether their presence or absence causes the lower-order modifier to appear in the system. Formally:

$$\begin{aligned}
w\,\mathrm{Mod}_t^{+(n+1)} a &=_{\mathrm{df}} (\exists x)[\{x\,\mathrm{Mod}_t^n a \mid (\xi_t wx \vee \xi_t wy)\} \;\&\; \{\sim x\,\mathrm{Mod}_t^n a \mid \sim(\xi_t wx \vee \xi_t wy)\}]\\
w\,\mathrm{Mod}_t^{-(n+1)} a &=_{\mathrm{df}} (\exists x)[\{x\,\mathrm{Mod}_t^n a \mid \sim(\xi_t wx \vee \xi_t wy)\} \;\&\; \{\sim x\,\mathrm{Mod}_t^n a \mid (\xi_t wx \vee \xi_t wy)\}]
\end{aligned}$$

$n = 0, 1, 2 \ldots$; y is either a or a modifier of order $< n$; $\mathrm{Mod}_t^n a =_{\mathrm{df}} \mathrm{Mod}_t^{+n} a \vee \mathrm{Mod}_t^{-n} a$.

The total environment of the subject animal is the union of the centrum and the web in which the structure of the four subsets of the centrum and their attached modifier chains is preserved.

Informal Defining Equations and Examples

Resources

Resources are objects, such as items of food, that are such that when the subject animal interacts with the object in the sense of the interaction primitive ξ, the 'H' of the animal is increased. In the case that the object is itself an animal, H(object) is decreased or unchanged. For example, the chimpanzee is known to eat bark (Nishida 1976) and ants (McGrew 1974). The formal defining equation for a resource is:

$$r\,\mathrm{Res}_t a =_{\mathrm{df}} [\{\mathrm{H}_t(a) > \mathrm{H}_{t-}(a)\} \mid \xi_t ra] \;\&\; [\mathrm{An}(r) \supset \{\mathrm{H}_t(r) \leqslant \mathrm{H}_{t-}(r)\} \mid \xi_t ra]\,.$$

Informally, for a single, specific chimpanzee and a particular piece of bark,

(bark)Res(chimpanzee) $=_{\mathrm{df}}$ H(chimpanzee) is increased | ξ(bark)(chimpanzee) .

The second part of the definition is not used because the piece of bark is not an animal. We assume that the bark is nutritious so that the chimpanzee's life expectancy is increased and thus H(chimpanzee) is increased. The subindex t is not used in the informal equation.

The following informal defining equation is for a particular ant as a resource:

(ant)Res(chimpanzee) $=_{\mathrm{df}}$ H(chimpanzee) is increased and
H(ant) is decreased | ξ(ant)(chimpanzee) .

In this case, H(ant) is decreased because the ant is eaten, so its life expectancy drops abruptly. Once again, we assume that the ant is nutritious, so the chimpanzee's life expectancy is increased.

Since chimpanzees prefer a particular temperature range, any specific chunk of heat energy corresponding to a particular temperature within that range constitutes a resource. The informal defining equation is:

(heat)Res(chimpanzee) $=_{\mathrm{df}}$ H(chimpanzee) is increased | ξ(heat)(chimpanzee) .

In this case, H(chimpanzee) increases because both expectation of life and probability of reproduction are increased.

A resource need not necessarily be an object that is assimilated by the subject animal. The freshwater sponge, *Spongilla lacustris*, must find a suitable piece of substrate, otherwise its expectation of life is drastically reduced. Thus, a particular piece of substrate is classified as a resource. The informal defining equation is:

(substrate)Res(sponge) $=_{\mathrm{df}}$ H(sponge) is increased | ξ(substrate)(sponge) .

An animal may not be a resource of itself. If the defining equation is written down for this case, a contradiction appears; H(animal) is required simultaneously to both increase and decrease or remain unchanged.

Mates

Mates are usually adult members of the same species as the subject animal but of opposite sex. The definition requires that offspring are possible, so a sterile animal would not be classified as a mate (but would, of course, appear in the environment of the subject animal in some other way, probably as a modifier). The formal defining equation is:

$$m \,\mathrm{Mat}_t a =_{\mathrm{df}} \mathrm{Prob}[(\exists x)(x\,\mathrm{Off}_{t+\beta}a \;\&\; x\,\mathrm{Off}_{t+\beta}m) \mid \xi_t ma] > 0 \,.$$

If the subject animal is a female chimpanzee in oestrous at the time of classification, then any one particular adult male chimpanzee (provided it is not sterile) is a mate. The informal defining equation is:

(male chimp)Mat(subject chimp) $=_{\mathrm{df}}$ an offspring of both individuals will be produced with probability greater than zero | ξ(male chimp)(subject chimp).

The same female chimpanzee will not have mates (in this formal sense) in her environment at a time when she is not in oestrous.

The defining equation allows for self-reproduction. For example, the rat tapeworm, *Hymenolepis diminuta*, customarily self-reproduces (Burt 1980). For a subject animal that is one particular tapeworm, the informal definition is:

(tapeworm)Mat(tapeworm) $=_{\mathrm{df}}$ an offspring of the individual will be reproduced with probability greater than zero | ξ(tapeworm)(tapeworm) .

The interaction primitive ξ is used here in the sense that the subject animal is interacting with itself.

If m is a mate of animal a, then it follows from the symmetry of the definition that a is a mate of m.

Predators

A predator is an animal that benefits from eating the subject animal. The formal definition is:

$$p\,\mathrm{Pred}_t a =_{\mathrm{df}} [\{\mathrm{H}_t(a) < \mathrm{H}_{t-}(a)\} \mathbin{\&} \{\mathrm{H}_t(p) > \mathrm{H}_{t-}(p)\} \mid \xi_t pa] .$$

Resh (1976) gives details of predacious caddisflies of freshwater sponges, which ingest whole particles of sponge. The informal defining equation is:

$$\begin{gathered}\text{(caddisfly)Pred(sponge)} =_{\mathrm{df}} \text{H(sponge) is decreased and} \\ \text{H(caddisfly) increased} \mid \xi\text{(caddisfly)(sponge)} .\end{gathered}$$

An animal may not be a predator of itself; the definition incorporates the contradiction that H(animal) both increases and decreases simultaneously in this case.

Malentities

A malentity is an object that is inimical to the subject animal, often by accident; in the case that the malentity is itself an animal, it does not benefit from the encounter. The formal defining equation is:

$$c\,\mathrm{Mal}_t a =_{\mathrm{df}} [\{\mathrm{H}_t(a) < \mathrm{H}_{t-}(a)\} \mid \xi_t ca] \mathbin{\&} [\mathrm{An}(c) \supset \{\mathrm{H}_t(c) \leqslant \mathrm{H}_{t-}(c)\} \mid \xi_t ca] .$$

In the Foster Gardens in Hawaii, cane toads, attracted by the movement, eat the blossoms that fall from the strychnine trees and die of strychnine poisoning (Alexander 1964). The informal defining equation is:

$$\text{(blossom)Mal(toad)} =_{\mathrm{df}} \text{H(toad) is decreased} \mid \xi\text{(blossom)(toad)} .$$

Snails and other crawling or browsing animals sometimes damage sponges accidentally. In this case, the object is another animal, which acts as a malentity in the environment of the sponge. The malentity is unaffected by the encounter. The informal definition is:

$$\begin{gathered}\text{(snail)Mal(sponge)} =_{\mathrm{df}} \text{H(sponge) is decreased and H(snail) is} \\ \text{unchanged} \mid \xi\text{(snail)(sponge)} .\end{gathered}$$

An animal may formally be a malentity of itself; in this case, H(animal) must decrease due to some biochemical, say, interaction within the animal; in practice, this is an unlikely event.

First-order Modifiers

A first-order modifier modifies an object in the centrum of the subject animal, i.e. it modifies a resource, a mate, a predator or a malentity. A positive first-order modifier acts so as to include the object within the centrum; a negative first-order modifier causes the object to disappear from the centrum.

The formal defining equation for a positive first-order modifier is:

$$w\,\mathrm{Mod}_t^{+1} a =_{\mathrm{df}} (\exists x)[\{x \in \mathrm{C}_t a \mid (\xi_t wx \vee \xi_t wy)\} \mathbin{\&} \{{\sim} x \in \mathrm{C}_t a \mid {\sim}(\xi_t wx \vee \xi_t wy)\}] .$$

Cane toads, as noted above, are attracted by the movement of the blossoms from the strychnine trees. Thus, kinetic energy is a modifier of this malentity in the sense that a toad is unlikely to strike at a blossom lying unmoving on the ground. Thus, a particular chunk of kinetic energy is a first-order modifier of the malentity. The informal definition is:

> (kinetic energy)Mod^{+1}(toad) $=_{\text{df}}$ ($\exists$ blossom) such that [(blossom)Mal(toad) | ξ(kinetic energy)(blossom) and ~(blossom)Mal(toad) | ~ξ(kinetic energy)(blossom)].

The formal definition for a negative first-order modifier is:

$$w\,\text{Mod}_t^{-1}a =_{\text{df}} (\exists x)[\{x \in C_t a \mid \sim(\xi_t wx \vee \xi_t wy)\} \;\&\; \{\sim x \in C_t a \mid (\xi_t wx \vee \xi_t wy)\}]\,.$$

The common octopus, *Octopus vulgaris*, when presented with a crab of species *Dardanus arrosor*, will eat the crab unless it is ‘protected’ by the anemone *Calliactis parasitica*; in the latter case, the crab is never taken (Ross 1971). The anemone is a negative first-order modifier of the crab, which is a resource in the environment of the octopus. The informal defining equation is:

> (anemone)Mod^{-1}(octopus) $=_{\text{df}}$ ($\exists$ crab) such that [(crab)Res(octopus) | ~ξ(anemone)(crab) and ~(crab)Res(octopus) | ξ(anemone)(crab)].

Second-order Modifiers

Second-order modifiers modify first-order modifiers. A positive second-order modifier acts so as to incorporate a first-order modifier into the system; a negative second-order modifier acts so as to exclude the first-order modifier from the system. The formal definition for a positive second-order modifier is:

$$w\,\text{Mod}_t^{+2}a =_{\text{df}} (\exists x)[\{x\,\text{Mod}_t^1 a \mid (\xi_t wx \vee \xi_t wy)\} \;\&\; \{\sim x\,\text{Mod}_t^1 a \mid \sim(\xi_t wx \vee \xi_t wy)\}]\,.$$

Szuch *et al.* (1978) reports that oxygen consumption by *Spongilla lacustris* kept in the light is lower than that by sponges kept in the dark. This difference is probably the result of algal photosynthesis; oxygen produced by endocellular algae reduces the demand on that carried through the aquiferous system. Thus, for a subject sponge, a specific chunk of oxygen is a resource that is modified (negatively) by an individual zoochlorella, which, in turn, is positively modified by a specific chunk of light energy. In the presence of the light energy, the zoochlorella ‘interferes’ with the oxygen resource; in the absence of the light energy, it does not. The two informal defining equations for the modifiers are:

> (zoochlorella)Mod^{-1}(sponge) $=_{\text{df}}$ ($\exists$ oxygen) such that [(oxygen)Res(sponge) | ~ξ(zoochlorella)(sponge) and ~(oxygen)Res(sponge) | ξ(zoochlorella)(sponge)]
>
> (light energy)Mod^{+2}(sponge) $=_{\text{df}}$ ($\exists$ zoochlorella) such that [(zoochlorella)Mod^1(sponge) | ξ(light energy)(zoochlorella) and ~(zoochlorella)Mod^1(sponge) | ~ξ(light energy)(zoochlorella)].

The formal definition of a negative second-order modifier is:

$$w\,\text{Mod}_t^{-2}a =_{\text{df}} (\exists x)[\{x\,\text{Mod}_t^1 a \mid \sim(\xi_t wx \vee \xi_t wy)\} \;\&\; \{\sim x\,\text{Mod}_t^1 a \mid (\xi_t wx \vee \xi_t wy)\}]\,.$$

The cane toad, *Bufo marinus*, has been introduced to Guam and Ponape Island, with complex ecological consequences (Mead 1961). Among these is the following: a food resource of the toad is young of the Giant African snail; the coconut crab also eats the snail and is thus a negative first-order modifier of the snail in the environment of a subject toad; the monitor lizard eats the crab and is thus a negative second-order modifier. The two informal defining equations for the modifiers are:

> (crab)Mod^{-1}(toad) $=_{\text{df}}$ ($\exists$ snail) such that [(snail)Res(toad) | ~ξ(crab)(snail) and ~(snail)Res(toad) | ξ(crab)(snail)]
>
> (lizard)Mod^{-2}(toad) $=_{\text{df}}$ ($\exists$ crab) such that [(crab)Mod^1(toad) | ~ξ(lizard)(crab) and ~(crab)Mod^1(toad) | ξ(lizard)(crab)].

Discussion

"The less a science has advanced, the more its terminology tends to rest on an uncritical assumption of mutual understanding . . . To be satisfactory . . . a definition . . . not only must fulfill the formal requirement of unambiguous eliminability, but must also conform to the traditional usage in question." (Quine 1967). The formal symbolic definition of environment presented and applied in this series of papers is based on the concept of ". . . 'environment' of the individual, regarding the population as part of the environment rather than as itself having an environment." (Andrewartha and Birch 1954). This concept, with variations and improvements by Browning (1963), Maelzer (1965) and Andrewartha (1971), has been widely accepted. Browning's notion of 'hazard' was renamed 'malentity' by Andrewartha, who included living organisms in this subset of the environment; the subset was then enlarged by Niven (1980) to include animals that were themselves damaged by the encounter with the subject (primary) animal. Maelzer's ideas about objects in the vicinity of an animal that "only modified the value of some resource or other component of environment" were formalised and extended by Niven to give us the definition of the 'web' in the environment of an animal. [The names 'centrum' and 'web' are due to Andrewartha and Birch (1984).]

The range of animals for which the present definition is valid includes (i) the sponge, tapeworm, octopus, toad and chimpanzee of the present series of papers; (ii) the earthworm, coral, sea gooseberry, copepod, waterflea, butterfly, blowfly, mosquito, bee, freshwater snail, terrestrial snail, squid, brachiopod, fish, frog, fulmar, penguin, wallaby, dolphin and gorilla of Niven and Stewart (1981–1983); (iii) the spruce budworm, fruit fly, two limpets, magpie, teal, buffalo, moose and rabbit of Andrewartha and Birch (1984). The two latter authors also use the definition for *Homo sapiens* as subject animal. However, the formal symbolic definition of environment was originally constructed for non-human animals and 'culture' was not taken into account. Although it can be argued that even a sponge may be said to possess 'culture' in some sense, or at least an awareness of the universe around it, particularly other sponges of the same species, the animal is not able to communicate clearly its awareness to the human investigator. On the other hand, human culture and its interaction with the human environment can be directly communicated to the investigator and is clearly of great importance in human ecology. The present author, therefore, prefers to leave the question of the human environment open until a satisfactory mathematical definition of 'culture' is constructed (work on this point is proceeding).

In the present study, a human has sometimes been classed as an animal in the sense of the primitive term 'An' and included in the environment of some subject animal. The definition of predator formally includes the parasites. Purely for convenience, non-animal pathogens are currently also being included in this class of objects. No investigations as to the 'environment of a plant' have been undertaken.

Ecology may be defined as "the study of living organisms at the level of the population and community . . ." (Southwood 1980). A connecting link between the concepts of population and community is provided by the modifier chains in the environment of an individual animal. The objects in the modifier chains are precisely those objects that connect animals within a community. For example, as shown above, a monitor lizard appears in the environment of an individual cane toad as a negative second-order modifier. The lizard is connected to the toad (in an ecological sense) by a crab and a snail. If now we focus attention on an individual monitor lizard as the subject animal, we find that the toad is a malentity in the lizard's environment, since lizards will eat the toad and die from the poison. Now, if we look at this community of animals as a whole, the very existence of the community is dependent precisely on these interactions; sets of animals that are not linked by such modifier chains cannot be said to form a community. In this sense, therefore, the structure of the environment provides us with the structure of the community. A population is the set of mates and mates of mates of our original subject animal; a formal definition of community is given in Niven (1988). In the case of both population and community, we usually confine our attention to animals within some particular habitat.

The centrum is complete in the sense that all possible changes of 'H' are taken into account for both subject animal and object under consideration. Thus, if H(subject animal) increases when the interaction occurs, the object is classified either as a resource or a mate; if H(subject animal) decreases, then the object is either a predator or a malentity. In the case that H(subject animal) is unaffected by the interaction, the object does not belong to the centrum (it may, of course, belong to the web). The cases in which H(object) increases are those in which the object is a mate or a predator; the object is a resource or a malentity when H(object) is decreased or unchanged.

The use of the conditional '|' in all definitions implies that the environment of an animal, as defined in this series of papers, is independent of the animal's habitat. In ordinary English we would refer to 'potential resources', 'potential mates', 'potential predators', 'potential malentities' and 'potential modifers'. This device allows classification of an object that at that time need not necessarily be in the vicinity of the subject animal.

The envirogram is useful because it shows exactly what is known about the environment of an animal and precisely where new knowledge fits in. It is simple to construct. There is no need to acquire knowledge about the subject animal in any particular order: items are entered in their correct place on the envirogram as they are brought to the attention of the investigator.

In addition to being of use in the practical classification of an animal's environment, the definition given in this paper is being used to provide the axiom asserting the existence of an identity morphism in new ecological mathematics. A mathematical object that sends an individual animal back to itself, just as multiplying by the unit in ordinary arithmetic sends a number back to itself, is an essential ingredient of useful mathematics. Details are given in Niven (1983, 1988). Also, the functional relations of 'resource', ···, 'modifier' used to define niche and community have yielded practical methods of classifying animal niches and animal communities (Niven 1988, unpublished data).

The definition is also being used by workers in computing science, in particular, the ECO group in the Department of Artificial Intelligence at Edinburgh University are using it as a basis for writing software (Robertson 1986; Muetzelfeldt *et al.* 1987). Also, it has been shown by Abel and Niven (unpublished data) that the Z specification language can be used for the environment definition and that the community classification can then be derived automatically by computer.

Finally, the five species of animal that I have included in this series are a subset of the 25 species studied in the 27 booklets of Niven and Stewart (1981–1983). The original 25 were chosen because they were well known, the information was easily accessible and the range of animal phyla was well represented. Details of that choice are given in the Revised General Introduction, No. XXVII, of the booklets. When choosing a subset for the present papers, I first included the sponge and chimpanzee as being on the extremes of the phyla range. The tapeworm was included because it was the only parasite. Among the 'higher' invertebrates, the octopus is much better known than the brachiopod or squid and has been of interest for a longer period than either of the two snails, certainly back to the time of Aristotle. I had difficulty in deciding which of the non-primate vertebrates to include: the confusion with the taxonomy of *Rana pipiens* militated against the inclusion of that species; neither penguin nor wallaby was of great ecological interest; ultimately I included the cane toad because a special study of the animal has been made at Griffith University by a number of workers and the information is thus very readily accessible. The five species of this series present various problems: the question as to what exactly constitutes a sponge individual subject animal, the peculiar life style of the tapeworm, the 'cultural' aspects of chimpanzee life, and so on.

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References

Alexander, T. R. (1964). Observations on the feeding behaviour of *Bufo marinus* (Linne). *Herpetologica* **20**, 225–9.

Andrewartha, H. G. (1971). 'Introduction to the Study of Animal Populations.' 2nd Edn. (Chapman and Hall: London.)

Andrewartha, H. G., and Birch, L. C. (1954). 'The Distribution and Abundance of Animals.' (University of Chicago Press: Chicago.)

Andrewartha, H. G., and Birch, L. C. (1984). 'The Ecological Web: More on the Distribution and Abundance of Animals.' (University of Chicago Press: Chicago.)

Browning, T. O. (1963). 'Animal Populations.' (Hutchinson: London.)

Burt, M. D. B. (1980). Aspects of the life history and systematics of *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 1–57. (Academic Press: New York.)

Caughley, G. (1966). Mortality patterns in mammals. *Ecology* **47**, 906–18.

Church, A. (1956). 'Introduction to Mathematical Logic.' (Princeton University Press: Princeton, New Jersey.)

Haskell, E. F. (1940). Mathematical systematization of 'environment', 'organism' and 'habitat'. *Ecology* **21**, 1–16.

Maelzer, D. A. (1965). A discussion of components of environment in ecology. *J. Theor. Biol.* **8**, 141–62.

McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *J. Hum. Evol.* **3**, 501–8.

Mead, A. R. (1961). 'The Giant African Snail: a Problem in Economic Malacology.' (University of Chicago Press: Chicago.)

Mertz, D. B., Park, T., and Youden, W. J. (1965). Mortality patterns in eight strains of flour beetles. *Biometrics* **21**, 99–114.

Muetzelfeldt, R., Robertson, D., Uschold, M., and Bundy, A. (1987). Computer-aided construction of ecological simulation programs. IMACS International Symposium on AI, Expert Systems and Languages in Modelling and Simulation. Barcelona, Spain.

Nishida, T. (1976). The bark-eating habits in primates, with special reference to their status in the diet of wild chimpanzees. *Folia Primatol.* **25**, 277–87.

Niven, B. S. (1980). The formal definition of the environment of an animal. *Aust. J. Ecol.* **5**, 37–46.

Niven, B. S. (1982). Formalization of the basic concepts of animal ecology. *Erkenntnis* **17**, 307–20.

Niven, B. S. (1983). Two different animals may not have the same environment. *J. Theor. Biol.* **105**, 369–70.

Niven, B. S. (1988). The ecosystem as an algebraic category: a mathematical basis for theory of community and ecosystem in animal ecology with examples from the ecology of the cephalopod *Octopus vulgaris* and R. L. Kitching's water-filled treehole communities. *Coenosis* **5**, in press.

Niven, B. S., and Stewart, M. G. (1981–1983). 'The Precise Environment of Some Well-known Animals.' Vols I–XXVII. (School of Environmental Studies, Griffith University: Nathan, Qld.)

Park, T., Mertz, D. B., and Petrusewicz, K. (1961). Genetic strains of *Tribolium*: their primary characteristics. *Physiol. Zool.* **34**, 62–87.

Quine, W. V. (1967). Truth by convention. In 'Philosophical Essays for Alfred North Whitehead'. pp. 90–124. (Russell and Russell: New York.)

Resh, V. H. (1976). Life cycles of invertebrate predators of freshwater sponge. In 'Aspects of Sponge Biology'. (Eds F. W. Harrison and R. R. Cowden.) pp. 229–314. (Academic Press: New York.)

Robertson, D. (1986). Ecological ideas in formal notation. Blue Book Note 337, University of Edinburgh.

Ross, D. M. (1971). Protection of hermit crabs (*Dardanus* spp.) from octopus by commensal sea anemones (*Calliactis* spp.) *Nature (Lond.)* **230**, 401–2.

Southwood, T. R. E. (1980). Ecology—a mixture of pattern and probabilism. In 'Conceptual Issues in Ecology'. (Ed. E. Saarinen.) pp. 203–14. (Reidel: Dordrecht.)

Szuch, E. J., Studier, E. H., and Sullivan Jr, R. B. (1978). The relationship of light duration to oxygen consumption in the green, freshwater sponge *Spongilla lacustris*. *Comp. Biochem. Physiol. A Comp. Physiol.* **60**, 221–4.

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Appendix

$>$	greater than
$<$	less than
$\leqslant$	less than or equal to
x_t	x at time t
x_{t-}	x just before time t
$A \mid B$	A given that B
$\sim$	negation
$\in$	element of
$\supset$	subjunctive conditional; read '$x \supset y$' as 'if x then y'
$=_{\mathrm{df}}$	definition; read '$x =_{\mathrm{df}} y$' as 'x is interchangeable with y' or 'x is equal by definition to y'
&	conjunction; read 'A & B' as 'A and B'
$\vee$	disjunction; read '$A \vee B$' as 'A or B' (or both)
$\exists$	existential quantifier; read '$\exists x$' as 'there is at least one x (such that) ...'

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Logical Synthesis of an Animal's Environment: Sponges to Non-human Primates.
II.* The freshwater sponge, *Spongilla lacustris*

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Abstract

The environment of the freshwater sponge *S. lacustris* is classified according to the defining equations given in the first paper of this series. An envirogram displaying objects in the environment in their correct place is presented. Notes on the envirogram include informal versions of the appropriate defining equations that are used for the classification.

Introduction

Sponges are sessile multicellulates of only slightly differentiated form. True muscle and nerve cells are absent. Variations in cell form (and function) are present, but no true organs are formed (Grzimek 1974).

Spongilla lacustris is a freshwater sponge with a world-wide distribution (Grzimek 1974); however, most of the information presented here was taken from work done in North America. A characteristic North American annual cycle for *S. lacustris* is given briefly in note 20—sexual reproduction in the spring following the germination of overwintering gemmules, vegetative growth until late autumn, then colonial decay and gemmulation. However, there are localities where tissue production and gemmulation occur at all times of the year.

Bergquist (1978) provides a list of cell types in sponges and deals in detail with the physiological changes that occur during development. Gilbert and Simpson (1976) report on *S. lacustris* development in a bog pond in the U.S.A., and Saller and Weissenfels (1985) on early development of *S. lacustris*.

Throughout the United States, *S. lacustris* occurs commonly in both lotic and lentic habitats. Characteristically, the animal takes one of two forms: (i) the green form, the colour being caused by symbiotic intracellular zoochlorellae, and (ii) the aposymbiont white form. In addition, cases have been reported in which *S. lacustris* has formed symbiotic 'colonies' with bryozoans (see notes 7, 11, 15).

The taxonomy of *S. lacustris* seems to be fairly well established. Poirrier (1976) discusses the matter in some detail.

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'What counts as a sponge individual?' can be tantalisingly difficult question (Grzimek 1974; Bergquist 1978). There are many reasons for the difficulty, for example:

(i) body morphology and size vary drastically;
(ii) newly settled larvae—and the largest adults—can fuse together in the course of vegetative growth (see note 12); is the resultant mass a new individual?
(iii) gemmulation can be viewed alternatively as an adaptive overwintering mechanism or as a means of asexual reproduction;
(iv) age and natural death are extremely hard to determine; what might be termed a sponge death due to old age usually has the following sequence of events: the central part thins and holes appear, but the edges continue to live until they break away; such edge pieces may re-establish elsewhere on the substrate;
(v) sponge cells, in many respects, maintain an almost protozoan independence; nevertheless, the entire cell mass combines to pump sufficient water to effect all essential exchanges;
(vi) sponge cells show remarkable mobility and a general ability to differentiate and redifferentiate to fill various functional roles;
(vii) against the last two points, which might be used to argue that a sponge individual is a single cell, a functional sponge mechanically dislocated by being rubbed through a sieve shows a remarkable ability to reassemble itself. If such an operation is performed on several species mixed together, the reassemblages remain species-specific.

There have been four major theories concerning the recognition of sponge individuals. The first two have been abandoned as serious alternatives, and the fourth is coming increasingly into favour (Bergquist 1978).

(i) An individual is a single cell;
(ii) an individual is a choanocyte (collar cell);
(iii) an individual is an osculum, the exhalant cells draining to it, and the sector of the inhalant surface and canal system that feeds the related choanocyte chambers;
(iv) an individual is all the substance bounded by a continuous pinacoderm.

Although in this paper we have adopted the fourth viewpoint, the formalised system we use to generate an envirogram is sufficiently flexible to produce an envirogram consistent with each of the theories. For theories (ii) and (iii), this would, fairly trivially, only involve qualifying each entry with 'per choanocyte chamber' or 'per osculum'.

An envirogram for theory (i) would be radically different. We attempted to assemble such an envirogram, but the available information (of a type that would usually be classed as 'biochemistry' or 'physiology') was too sparse. However, to illustrate briefly, consider the following:

Let us take as our individual an archaeocyte cell in the mesohyl:

(i) it would be responsible for obtaining its own oxygen;
(ii) for food resources, choanocytes would be first-order modifiers, which would in turn be modified by all the cells from the porocytes lining the inhalant canal openings down to the choanocyte chamber;
(iii) similarly, excretory functions would be modified by spherulous cells and all the cells leading from the choanocyte chamber to the osculum;
(iv) a modifier chain, in which the co-operation of other cells was required, would also have the 'skeleton' (spicules) and scleroblasts as modifiers.

The reason for the formalised system's flexibility in this respect is the primitive term 'An' (animal). In the present series of papers, 'An' is interpreted as any animal in the range of the phyla from sponge to non-human primate. Nevertheless, a formalised language is inherently flexible; the language can still be useful under various interpretations of 'An' and the other primitive terms. It is possible to change the interpretation of one or more primitive terms, while definitions, axioms, rules of inference, and theorems remain unchanged.

The Envirogram

The envirogram for *S. lacustris* (Fig. 1) displays objects in their correct logical place in the environment. This type of diagram was originally developed by Andrewartha and Birch (1984) using an early formulation of the environment definition by Niven (1982). It enables workers on the animal to relate their own results to those of others and may be used as a guide to further experimentation or observation.

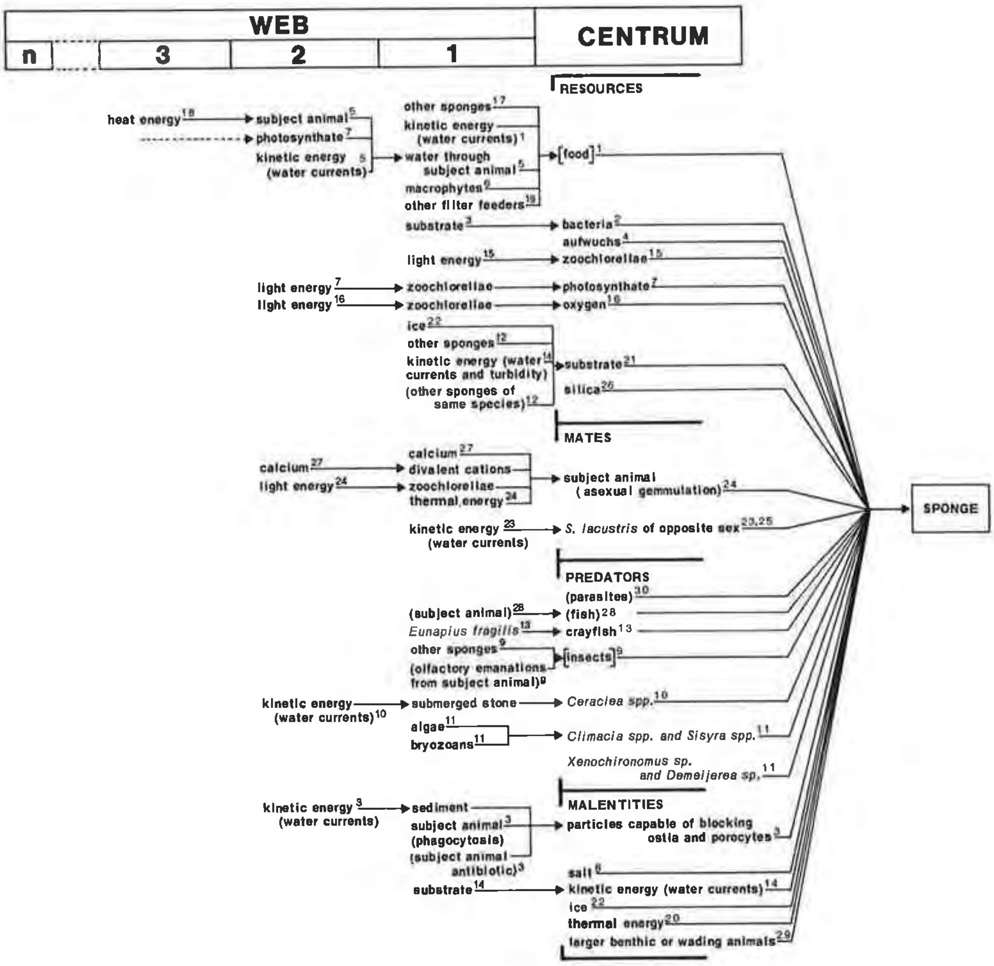

Fig. 1. Envirogram for *Spongilla lacustris*.

The subject animal for the envirogram is an individual in the sense given above. Reports from the literature about objects in the environment of sponges of this species have been combined; thus, the envirogram presented here is a concatenation of many individual envirograms for large numbers of individual sponges observed in many different places at various times. The numbers on the envirogram refer to the notes that follow. These numbers appear in no particular order. The various parts of the envirogram were constructed in an entirely haphazard order as the literature became available. The square brackets indicate a set of objects. Thus, '[food]' refers to a set of food objects, and '[insects]' to a set of insects. The parentheses are used not only for explanatory purposes, e.g. 'kinetic energy (water currents)', but also when there is some doubt about the classification, e.g. '(olfactory emanations from subject animal)'.

A semiformal version of the appropriate defining equations (see part I of this series) is given at the end of each note. The following symbols are used:

(i) $=_{\mathrm{df}}$: 'is equal by definition to', or, more strictly, the form '$x =_{\mathrm{df}} y$' means 'x is to be interchangeable with y'.

(ii) ∃ : the existential operator of formal logic. Read '∃ fish' as 'there exist a fish' or 'there is at least one fish', or, more informally, 'we can find a fish'. In this paper, expressions such as '∃ fish' are always followed by the words 'such that'.

(iii) |: '$x \mid y$' means 'x occurs (will occur), assuming y'. This is the symbol used for conditional events (and conditional probabilities). The expression '$A \mid B$' may be read 'event A occurs, given that event B occurs'; it refers to 'event A under the condition that B', or 'event A under the hypothesis that B'. The use of the conditional in the definitions implies that the environment of the subject animal is independent of its habitat. Thus, an object that is reported in Sweden, say, as being a food object and hence classified as a resource of that particular subject sponge is also classified as a resource of a subject sponge in Denmark; in ordinary English it is a *potential* resource. Similarly, mates, predators, malentities and modifiers are all *potential* mates, etc.

Notes on the Envirogram

1. There are almost no hard data on sponge nutrition. Bacteria, unicellulates, zooplankton, phytoplankton, yeasts, and colloidal organic matter are mentioned by various authors (see note 2) (Grzimek 1974; Harrison and Cowden 1976; Bergquist 1978; Frost 1978*a*).

S. lacustris is not a mobile animal, so it depends largely on external factors to bring food resources within its limited range. The principal external factor is kinetic energy (water currents), which, in effect, provides volumes of nutrient-containing water for the sponge to filter, and removes already filtered water. Other external factors are the movements of any mobile animals or protists that the sponge consumes. (The above considerations can be generalised for all classes of the centrum.)

All of the sponge's food must be suspended or dissolved in water. A current of water is set up by the flagella of the choanocytes within the sponges, and, "in effect, the arrangement of inhalant ostia, canals, prosopyles, choanocyte collar tentacles, and intertentaculae mucous reticulum place a series of sieves of decreasing mesh size in the path of the water current" (Bergquist 1978). The only selective restriction on particle intake is the passive one afforded by ostia size (see also note 3), although individual cells are capable of distinguishing between digestible and indigestible substances. Presumably, indigestible particles are ejected *via* the outflow ostia. It is generally agreed that *S. lacustris* can filter particles within the size range 0·1–50 μm. The sponge uses two methods to capture particles once they have entered the canal system: first, mobile archaeocytes phagocytose particles in the 2–5-μm range directly – this helps to prevent canal occlusion (see note 3); secondly, secondary capture occurs at the choanocyte collar, where particles within the range 0·1–1·5 μm are trapped in the collar tentacles. Very little digestion takes places in the choanocytes, as particles are not retained for more than 3 h before being passed on to other cells. In the diet of three marine sponges, about 80% of the particulate material used was of a size likely to be taken up mainly by choanocytes.

A third method of capturing particles operates at the external surface of the sponge, where exopinacocytes phagocytose larger particles. However, reports deal only with the uptake of non-nutritive particles under laboratory conditions, and the importance of this method for nutrition is not known.

Strictly speaking, the formal versions of the defining equations should be written down for every individual element of the set of food objects. We give here, for a single individual bacterium, an informal version, which is satisfactory for construction of an envirogram. Notice that the second term in the conditonal is not needed for this particular case because the interpretation of 'An' excludes bacteria. Were they counted as animals, then the clause 'and H(bacterium) is decreased' should be added.

(bacterium)Res(sponge) $=_{\mathrm{df}}$ H(sponge) is increased | ξ(bacterium)(sponge)

The following informal defining equation is for a specific bounded quantity of kinetic energy contained in a current of water, abbreviated k.e., which acts as a modifier of a bacterium food resource.

(k.e.)Mod^{+1}(sponge) $=_{\mathrm{df}}$ ($\exists$ bacterium) such that [(bacterium)Res(sponge) | ξ(k.e.)(bacterium) and ~(bacterium)Res(sponge) | ~ξ(k.e.)(bacterium)]

(Frost 1978*a*, 1978*b*, 1980*a*, 1980*b*, 1981)

2. The best data with respect to sponge nutrition concerns bacteria. It is known that the Demospongidae extract bacteria from their aquiferous system and retain them with high efficiency—about 96%. For example, in the laboratory, Frost (1978*a*) showed that *S. lacustris* efficiently filtered *Rhodotorula glutinis* (average diameter 3·9 µm), *Chlamydomonas reinhardti* (6·6 µm) and *Escherichia coli* (2 by 1 µm) from tanks.

The uptake of bacteria by the marginal cells of the basal pinacoderm, using a method of filopodial extension and subsequent phagocytosis, has been reported for the freshwater sponge *Corvomeyenia carolinensis* and also a marine species. If *S. lacustris* used this method, it could be added to the three methods of nutritional uptake mentioned in note 1.

For some sponges living in organically rich estuaries, it has been shown that the uptake of bacteria could satisfy their entire nutritional requirements.

It is possible that *S. lacustris* supports a population of bacteria within the matrix of the sponge. The effect of the bacteria, if any, is not known.

An informal version of the defining equation for a bacterium as a resource is given at the end of note 1. The provision of bacteria by the substrate implies that the substrate may act as a positive first-order modifier:

(substrate)Mod^{+1}(sponge) $=_{\mathrm{df}}$ ($\exists$ bacterium) such that [(bacterium)Res(sponge) | ξ(substrate)(bacterium) and ~(bacterium)Res(sponge) | ~ξ(substrate)(bacterium)].

(Frost 1976*a*, 1976*b*)

3. Large particles (i.e. greater than 50 µm, see note 1) in suspension are a danger to all sponges because they can block the delicate filter system for long periods—as also can very high concentrations of smaller particles. Such blockages affect the sponge in at least the following three ways:

(i) direct damage: for this reason, we classify particles as malentities;
(ii) by causing a reduction of water flow, particles will cause a proportional reduction in nutrient uptake; thus, particles are second-order modifiers of food (they modify water flow);
(iii) similarly, water flow is prerequisite for the provision of oxygen and the removal of carbon dioxide; thus, particles are also second-order modifiers of oxygen (see also note 16).

For economy of space, we have placed only (i) on the envirogram; all subsequent modifiers also apply to (ii) and (iii), thus extending the envirogram to modifiers of the fourth order.

Any source of particles is potentially dangerous—pieces of the substrate, detritus, living organisms, etc. We group these together as 'sediment', a first-order modifier. Almost invariably, 'sediment' will be disturbed and carried by 'kinetic energy (water currents)', a second-order modifier.

Clearly, it is to the subject animal's advantage to maintain its external surface as free of particles as possible. Note 1 gives details of the phagocytosis of particles; in this way, the subject animal acts as a first-order modifier. A second mechanism may contribute to the maintenance of a clear aquiferous system. Frost (1976*b*) reports a significantly smaller build-up of aufwuchs (see also note 4) on the surface of *S. lacustris* as opposed to the surface of nearby macrophytes. It is known that some marine sponges have an antibiotic effect on organisms; this explanation is suggested, though not proved, for *S. lacustris*. Thus, we have tentatively classified 'subject animal (antibiotic)' as a first-order modifier of particles as malentities.

Since a particle is not an animal, the second term in the conditional is excluded from the defining equation for a malentity. The informal defining equation for an individual particle with diameter greater than 50 μm is:

$$(\text{particle})\text{Mal}(\text{sponge}) =_{\text{df}} \text{H}(\text{sponge}) \text{ is decreased} \mid \xi(\text{particle})(\text{sponge})\,.$$

The sponge is a negative first-order modifier of itself by phagocytosis. The informal defining equation is:

$$\begin{aligned}&(\text{sponge})\text{Mod}^{-1}(\text{sponge}) =_{\text{df}} (\exists \text{ particle}) \text{ such that } [(\text{particle})\text{Mal}(\text{sponge}) \mid \\ &\sim \xi(\text{sponge})(\text{particle}) \text{ and } \sim(\text{particle})\text{Mal}(\text{sponge}) \mid \xi(\text{sponge})(\text{particle})]\,.\end{aligned}$$

(Frost 1976*b*; Storr 1976)

4. Most freshwater sponges, including *S. lacustris*, have a relatively aufwuchs-free epithelium. The phagocytic ability of pinacocytes is almost certainly responsible, possibly aided by an antibiotic effect of the sponge on organisms (see note 3).

The phagocytosis of aufwuchs will contribute to sponge nutrition. In general, aufwuchs will include diatoms, fungi and filamentous algae. Frost (1976*b*) reports the following filamentous algal forms collected from *S. lacustris*: *Mougeotia* sp. and *Spirogyra* sp. were most common; *Bulbochaeta* sp., *Oedogonium* sp. and *Zygnema* sp. were also observed.

The informal defining equation for an individual diatom as a resource is:

$$(\text{diatom})\text{Res}(\text{sponge}) =_{\text{df}} \text{H}(\text{sponge}) \text{ is increased} \mid \xi(\text{diatom})(\text{sponge})\,.$$

Since a diatom is not interpreted here as being an animal, the second term in the conditional does not apply.

5. Given that all sponge food resources must be in suspension, in a given locality the quantity of food that becomes available to a sponge will depend on the quantity of water passing through the animal. Many authors have attempted to calculate water transport rates for *S. lacustris*; methods and conclusions vary greatly. Frost (1976*a*) regards $0{\cdot}0118$ ml s^{-1} ml^{-1} as a good estimate.

Several factors can affect water transport rates. It is generally agreed that water flow through a sponge is augmented by external current flow across the osculum; however, authors disagree on the magnitude of the effect. This is apparently why most sponges in a moving environment are tubular and upright, or, if not upright, are oriented perpendicular to the prevailing water current.

The subject animal is capable of regulating water flow, as evidenced by its response to certain stimuli. On mechanical or electrical stimulation, or with thermal (note 18) or light stimuli, the whole body, or at least a portion of it, is contracted, the osculum and pores first and the canal system last. The mechanism of the response is not known.

The informal defining equation for a particular bounded quantity of water acting as a positive first-order modifier on a specified individual diatom that is a food resource is:

$$\begin{aligned}&(\text{water})\text{Mod}^{+1}(\text{sponge}) =_{\text{df}} (\exists \text{ diatom}) \text{ such that } [(\text{diatom})\text{Res}(\text{sponge}) \mid \\ &\xi(\text{water})(\text{diatom}) \text{ and } \sim(\text{diatom})\text{Res}(\text{sponge}) \mid \sim \xi(\text{water})(\text{diatom})]\,.\end{aligned}$$

The informal defining equation for the sponge acting as a positive second-order modifier in its own environment by regulating whether or not that particular bounded quantity of water passes through the sponge is:

$$\text{(sponge)Mod}^{+2}\text{(sponge)} =_{\text{df}} (\exists \text{ water) such that [(water)Mod}^{1}\text{(sponge)} \mid \xi\text{(sponge)(water) and } \sim\text{(water)Mod}^{1}\text{(sponge)} \mid \sim\xi\text{(sponge)(water)]} .$$

The sponge may also be thought of as a negative second-order modifier in its own environment as follows:

$$\text{(sponge)Mod}^{-2}\text{(sponge)} =_{\text{df}} (\exists \text{ water) such that [(water)Mod}^{1}\text{(sponge)} \mid \sim\xi\text{(sponge)(water) and } \sim\text{(water)Mod}^{1}\text{(sponge)} \mid \xi\text{(sponge)(water)]} .$$

(Frost 1976*a*; Reiswig 1976; Storr 1976)

6. It is not uncommon for *S. lacustris* to live in close association with macrophytes. The water plants provide a good surface for aufwuchs and are thus likely to contribute to the maintenance of nutritionally rich water.

In addition, *S. lacustris*, not infrequently, uses macrophytes as a substrate (see note 21). Frost (1976*b*) reports the sponge living close to or on the following macrophytes: *Nymphaea odorata*, *Nuphar advena* and four species of *Utricularia*.

The informal defining equation for *Nymphaea* as a positive first-order modifier of a food object, abbreviated f.o., is:

$$(\textit{Nymphaea})\text{Mod}^{+1}\text{(sponge)} =_{\text{df}} (\exists \text{ f.o.) such that [(f.o.)Res(sponge)} \mid \xi(\textit{Nymphaea})\text{(f.o.) and } \sim\text{(f.o.)Res(sponge)} \mid \sim\xi(\textit{Nymphaea})\text{(f.o.)]} .$$

7. *S. lacustris* (and many other freshwater sponges) may contain intracellular algae (zoochlorellae) as symbionts. Those sponges containing algae will usually be green, whereas those without are usually white. The presence of algae depends largely on the light conditions in which the sponge lives—i.e. if in dark conditions, under rocks, etc., the sponge is less likely to contain algal symbionts. Algae may be present in a sponge from the beginning if it derives from the gemmulation of an algae-containing parent. Otherwise, suitable algae can be filtered and phagocytosed, but not digested.

The exact relationship between the symbionts is not known. However, studies on *S. lacustris* have indicated that algal photosynthate is transferred from the alga to the host sponge, thus potentially benefitting the sponge by augmenting its nutrition. This result is in keeping with results from other freshwater invertebrates containing unicellular algal symbionts; in general, both growth rates and survival under starvation conditions are significantly improved.

S. lacustris with algal symbionts is an active, efficient photosynthetic system, with a calculated efficiency of 5·4%. Suitable light conditions are required. Gross primary productivity is linearly related to water temperature. It is suggested that the presence of algae, with the effects mentioned above, will reduce the need for active feeding and food uptake by the sponge (see also notes 15, 16 and 24).

The informal defining equations for photosynthate, abbreviated p.s.ate, as a resource, a zoochlorella as a positive first-order modifier of the photosynthate, and light energy as a positive modifier of the zoochlorella (and thus a positive second-order modifier of the sponge), follow:

$$\text{(p.s.ate)Res(sponge)} =_{\text{df}} \text{H(sponge) is increased} \mid \xi\text{(p.s.ate)(sponge)} .$$

The second term in the conditional is not used because the photosynthate is not an animal.

$$\text{(zoochlorella)Mod}^{+1}\text{(sponge)} =_{\text{df}} (\exists \text{ p.s.ate) such that [(p.s.ate)Res(sponge)} \mid \xi\text{(zoochlorella)(sponge) and } \sim\text{(p.s.ate)Res(sponge)} \mid \sim\xi\text{(zoochlorella)(sponge)]}$$

(light energy)Mod^{+2}(sponge) $=_{\mathrm{df}}$ ($\exists$ zoochlorella) such that
[(zoochlorella)Mod^{1}(sponge) | ξ(light energy)(zoochlorella) and
$\sim$(zoochlorella)Mod^{1}(sponge) | $\sim\xi$(light energy)(zoochlorella)]

(Szuch *et al.* 1978; Williamson and Williamson 1979; Frost and Williamson 1980)

8. *S. lacustris* is exclusively a freshwater species. Attempts to introduce the sponge to brackish water in both field and laboratory have failed. There is some evidence to suggest that the species can withstand brief exposure to salinities well above those in which it is capable of long-term survival.

We have therefore classified salt (i.e. dissolved in water) as a malentity. The informal defining equation is:

(salt)Mal(sponge) $=_{\mathrm{df}}$ H(sponge) is decreased | ξ(salt)(sponge) .

The second term in the conditional is not used, because salt is not an animal.

(Poirrier 1976)

9. *S. lacustris*, characteristically, has an abundance of commensals, both on its surface and in its tissue and canal systems. There has been speculation that sponges have evolved defensive mechanisms (difficulties of spicule digestion, antibiotic effects, metabolic poisons, etc.), enabling them to be free of predators; this hypothesis is false.

The ability to feed on freshwater sponge is exhibited by certain species in single families of three insect orders: the Trichoptera (see note 10), the Neuroptera and the Diptera (both in note 11). Benthic invertebrates relate to freshwater sponges in two ways other than the predator–prey relation. First, the sponge can serve as a substrate for many aquatic insects; secondly many organisms, including protozoans, nematodes, oligochaetes and water mites, use the vascular system and irregular surfaces of the sponge as suitable permanent habitats. The organisms forming these last two associations will occur as modifiers of food resources in the sponge's environment.

From available information, it appears that there is little host specificity among insect sponge predators. Thus, the presence of other sponges (first-order modifiers) will modify insect predators in two ways: first, the proximity of other sponges will increase the probability of predators finding the subject sponge; however, secondly, this effect may be offset by the predatory load being spread over more sponges.

In addition, it seems likely that olfactory emanations (first-order modifiers) from sponges may provide the mechanism by which insect predators locate sponge hosts; this is not definitely established.

(insect)Pred(sponge) $=_{\mathrm{df}}$ [H(sponge) is decreased and H(insect) is increased] |
ξ(insect)(sponge)

(other sponge)Mod^{-1}(sponge) $=_{\mathrm{df}}$ ($\exists$ insect) such that [(insect)Pred(sponge) |
$\sim\xi$(other sponge)(insect) and $\sim$(insect)Pred(sponge) | ξ(other sponge)(insect)]

(Resh 1976*a*, 1976*b*; Williamson and Williamson 1979)

10. Listed in Table 1 are the predacious caddisflies of freshwater sponges, given by Resh (1976*a*). All are from the genus *Ceraclea* (Order: Trichoptera, Family: Heptoceridae). Resh also comments that atypical occurrences of caddisflies of the families Polycentropodidae and Limnephilidae have been reported in freshwater sponges.

All members of the fulva group (see Table 1) are obligatory sponge feeders and have corresponding morphological adaptations. The senilis group appears to have both facultative and obligate species of sponge feeders and have less pronounced morphological adaptations. The single member of the nigronervosa group appears to be an obligate sponge feeder, but has little in the way of morphological adaptation.

There are two basic life-history patterns exhibited by caddisflies that ingest sponges. *C. resurgens* is typical of the first: it has a univoltine pattern (i.e. one generation per annual cycle). Adults emerge, mate and oviposit during a brief period in the spring. Eggs released on the water surface sink and adhere to submerged stones. After hatching, the larva locates a sponge host; water currents increase the search area and possibly also bear olfactory stimuli from the sponge. Following development, the larva overwinters as a prepupa and emerges the following spring. *C. transversa*, which is typical of the second life-history pattern, has two periods of emergence, mating and so on. The first cohort is similar to *C. resurgens*. The second cohort emerges in mid-summer through autumn. Larvae must overwinter as active detritus feeders after colonial sponges have deteriorated in late autumn to overwinter as gemmules (see note 24).

Table 1. Predacious caddisflies of freshwater sponges

Species	Distribution
Fulva group:	
Ceraclea biwaensis (Tsuda & Kuwayama)	Japan
Ceraclea alces (Ross)	North America
Ceraclea resurgens (Walker)	North America
Ceraclea transversa (Hagen)	North America
Ceraclea fulva (Rambur)	Western Palearctic Region
Ceraclea albimacula (Rambur)	Western Palearctic Region
Ceraclea cama (Flint)	North America
Ceraclea vertreesi (Denning)	North America
Ceraclea latahensis (Smith)	North America
Ceraclea alboguttata (Hagan)	Western Palearctic Region
Senilis group:	
Ceraclea senilis (Burmeister)	Western Palearctic Region
Ceraclea spongillovorax (Resh)	North America
Nigronervosa group:	
Ceraclea nigronervosa (Retzuis)	Transcontinental Palearctic Region, North America

The swarming behaviour of *C. nigronervosa* is described by Solem (1978), and a detailed study of this species was undertaken by Solem and Resh (1981). They report as follows: "The life cycle of *C. nigronervosa* is closely linked to the phenology of the freshwater sponge. All larval instars collected (second through fifth instars) feed on the sponge during its summer proliferation stage. Larvae form non-feeding pre-pupae when the sponge undergoes gemmulation in autumn." They also report that it seems likely that *C. nigronervosa* is an obligate sponge feeder, because the presence or absence of the green alga *Chlorella* sp. in the sponge does not appear to affect the abundance or distribution of *Ceraclea nigronervosa*.

The informal defining equations for an individual *C. resurgens* larva as a predator, a stone as a positive first-order modifer, and a negative second-order modifier, which is kinetic energy in a water current conceived as removing the larva so that it cannot adhere to the stone, are given below. By kinetic energy, abbreviated k.e., is meant a specific bounded quantity of kinetic energy.

$$\text{(larva)Pred(sponge)} =_{\text{df}} \text{H(sponge) is decreased and H(larva) increased} \mid \xi\text{(larva)(sponge)}$$

$$\text{(stone)Mod}^{+1}\text{(sponge)} =_{\text{df}} (\exists \text{ larva}) \text{ such that } [\text{(larva)Pred(sponge)} \mid \xi\text{(stone)(larva) and } \sim\text{(larva)Pred(sponge)} \mid \sim\xi\text{(stone)(larva)}]$$

$$(\text{k.e.})\text{Mod}^{-2}(\text{sponge}) =_{\text{df}} (\exists\ \text{stone})\ \text{such that}\ [(\text{stone})\text{Mod}^{1}(\text{sponge}) \mid \\ \sim\xi(\text{k.e.})(\text{larva})\ \text{and}\ \sim(\text{stone})\text{Mod}^{1}(\text{sponge}) \mid \xi(\text{k.e.})(\text{larva})]$$

(Resh 1976*a*, 1976*b*; Resh *et al.* 1976; Solem and Resh 1981)

11. Spongillaflies of the family Sisyridae (Order: Neuroptera) are commonly found in association with freshwater sponges. The genera *Sisyra* and *Climacia* are known predators.

Unlike the sponge-feeding caddisflies (note 10), sysirid larvae do not ingest whole particles of sponge; rather, they suck fluids from the sponge through their tubular mouthparts (Resh 1976*b*). Besides feeding on sponge, spongillaflies also suck fluids from bryozoans and algae, which are thus first-order modifiers.

Two genera, *Xenochironomus* and *Demeijerea*, of the sponge-feeding midges (Diptera : Chironomidae), are also known to feed on freshwater sponges. In the study by Solem and Resh (1981), over three times as many chironomid larvae were found in a sponge with algae visibly present as in a *Chlorella*-free sponge.

The situation does not seem to be altogether clear; however, informal defining equations are given below for a larva as predator and an individual alga as a negative first-order modifier, in the sense that if the alga is attacked, this 'protects' the sponge.

$$(\text{larva})\text{Pred}(\text{sponge}) =_{\text{df}} \text{H}(\text{sponge})\ \text{is decreased and}\ \text{H}(\text{larva})\ \text{is increased} \mid \\ \xi(\text{larva})(\text{sponge})$$

$$(\text{alga})\text{Mod}^{-1}(\text{sponge}) =_{\text{df}} (\exists\ \text{larva})\ \text{such that}\ [(\text{larva})\text{Pred}(\text{sponge}) \mid \\ \sim\xi(\text{alga})(\text{larva})\ \text{and}\ \sim(\text{larva})\text{Pred}(\text{sponge}) \mid \xi(\text{alga})(\text{larva})]$$

12. Body size within the sponges, including *S. lacustris*, is much less restricted than in any other animal group. Individual sponges growing next to each other can grow together to form a new organism. Sponges are known to produce diffusible surface-active molecules that operate to promote or prevent cell-to-cell adhesion. Such factors, which are strain- or species-specific, provide a simple system of self-recognition, which can lead to fusion or non-fusion.

S. lacustris requires a stable substrate. Other sponges will compete for such space, but fusion with other appropriately 'recognised' *S. lacustris* is one way of protecting the colonised area (see note 21).

The informal defining equations for a particular bounded piece of substrate as a resource, and another sponge (of the same species) as a negative first-order modifier, are given below. On the envirogram, the parentheses surrounding 'other sponges of the same species' indicate that this classification is tentative.

$$(\text{substrate})\text{Res}(\text{sponge}) =_{\text{df}} \text{H}(\text{sponge})\ \text{is increased} \mid \xi(\text{substrate})(\text{sponge})$$

The second term in the conditional is not used, because the piece of substrate is not an animal.

$$(\text{other sponge})\text{Mod}^{-1}(\text{sponge}) =_{\text{df}} (\exists\ \text{substrate})\ \text{such that} \\ [(\text{substrate})\text{Res}(\text{sponge}) \mid \sim\xi(\text{other sponge})(\text{substrate})\ \text{and} \\ \sim(\text{substrate})\text{Res}(\text{sponge}) \mid \xi(\text{other sponge})(\text{substrate})]$$

(Bergquist 1978)

13. In North America, Williamson (1979) reports the predation of freshwater sponges, including *S. lacustris*, by a freshwater crayfish *Orconectes* sp. Both sexes of the crayfish readily consumed both adult and gemmulated *S. lacustris*.

The crayfish also ingests the sponge *Eunapius fragilis*, which is thus classified as a negative first-order modifier.

The informal defining equations for a crayfish as predator, and a sponge *E. fragilis*, which, by being eaten instead of the subject animal, acts as a 'protector' of the subject animal, are:

(crayfish)Pred(sponge) $=_{\mathrm{df}}$ H(sponge) is decreased and H(crayfish) is increased | ξ(crayfish)(sponge)

(*E. fragilis*)Mod^{-1}(sponge) $=_{\mathrm{df}}$ (∃ crayfish) such that [(crayfish)Pred(sponge) | ~ξ(*E. fragilis*)(crayfish) and ~(crayfish)Pred(sponge) | ξ(*E. fragilis*)(crayfish)].

14. Several authors report that strong water currents can damage and break pieces off sponges, particularly branched forms. The substrate and the strength and morphology of the sponge provide the only resistance. The latter, in turn, is influenced by the typical current flow of a locality, e.g. branched forms of *S. lacustris* usually occur only in areas with very slow currents.

In addition, water current and turbidity can affect the choice of substrate during the initial settling stage. *S. lacustris* is not found in areas with very rapid currents. Williamson and Williamson (1979) report congregations of *S. lacustris* on a rock–water interface where the current was well below 0·01 m s^{-1}. However, Harrison (1977) found *S. lacustris* common in a current of 0·342 ft s^{-1} (approximately 0·1 m s^{-1}).

The informal defining equations for a particular bounded amount of kinetic energy, abbreviated k.e., as a malentity, and a particular bounded piece of substrate as a negative first-order modifier, are given below. The substrate is a modifier in the sense that, were it not present, the energy object (water current) would damage the subject sponge.

(k.e.)Mal(sponge) $=_{\mathrm{df}}$ H(sponge) is decreased | ξ(k.e.)(sponge)

Since kinetic energy is not an animal, the second term in the conditional is not used.

(substrate)Mod^{-1}(sponge) $=_{\mathrm{df}}$ (∃ k.e.) such that [(k.e.)Mal(sponge) | ~ξ(substrate)(sponge) and ~(k.e.)Mal(sponge) | ξ(substrate)(sponge)]

(Bergquist 1978; Williamson and Williamson 1979)

15. Note 7 gives some details of the provision of photosynthate by symbiont zoochlorellae to host sponges. The algae will live and reproduce within the host cells, provided light conditions are sufficient. If, for some reason, a sponge with algal symbionts is kept in darkness for a few weeks, it is likely that the algae will be digested; these zoochlorellae appear on the envirogram as food resources.

Possible advantages to the algal symbiont from the association include protection, carbon dioxide, and other inorganic nutrients. In addition to nutrients, the sponge may derive oxygen (note 16) and an automatic removal of waste products.

The informal defining equations below are for a specific individual zoochlorella as a food resource modified by a specific bounded amount of light energy, abbreviated l.e., in such a way that, in the presence of the light energy, the zoochlorella is not a resource, but, in the absence of the light energy, it is a resource.

(zoochlorella)Res(sponge) $=_{\mathrm{df}}$ H(sponge) is increased | ξ(zoochlorella)(sponge)

(l.e.)Mod^{-1}(sponge) $=_{\mathrm{df}}$ (∃ zoochlorella) such that [(zoochlorella)Res(sponge) | ~ξ(l.e.)(sponge) and ~(zoochlorella)Res(sponge) | ξ(l.e.)(sponge)]

(Williamson 1977; Williamson and Williamson 1979; Frost 1983)

16. *S. lacustris* has no special respiratory organs. A continual stream of water is required to transport oxygen into the organism and to remove carbon dioxide. Respiration is by diffusion to individual cells—along the intake canals, at the body surface, and at the collar

tentacles of choanocytes. Every individual needs to be self-sufficient in this respect. Because it is a sedentary animal, oxygen consumption is low, and no more than 20% of the available oxygen is withdrawn from the water flowing through the aquiferous system. Kharchenko and Lyashenko (1986) report that oxygen consumption depends on dry weight.

Szuch *et al.* (1978) report that oxygen consumption by *S. lacustris* kept in the light is lower than that for individuals kept in the dark. This difference is probably the result of algal photosynthesis—oxygen produced by endocellular algae reducing the demand on that carried through the aquiferous system. In normal summer conditions, there exists the potential for the symbiotic system to produce its entire oxygen requirements.

The informal defining equations that follow are for a specific bounded amount of oxygen as a resource modified by an individual zoochlorella, in turn modified by a specific bounded quantity of light energy, abbreviated l.e. In the presence of the zoochlorella, the oxygen is no longer required. In the presence of the light energy, the zoochlorella 'interferes' with the oxygen resource; in the absence of the light energy, it does not.

$$(\text{oxygen})\text{Res}(\text{sponge}) =_{\text{df}} \text{H}(\text{sponge}) \text{ is increased} \mid \xi(\text{oxygen})(\text{sponge})$$

The second term in the conditional is not used, because oxygen is not an animal.

$$(\text{zoochlorella})\text{Mod}^{-1}(\text{sponge}) =_{\text{df}} (\exists \text{ oxygen}) \text{ such that } [(\text{oxygen})\text{Res}(\text{sponge}) \mid \sim \xi(\text{zoochlorella})(\text{sponge}) \text{ and } \sim (\text{oxygen})\text{Res}(\text{sponge}) \mid \xi(\text{zoochlorella})(\text{sponge})]$$

$$(\text{l.e.})\text{Mod}^{+2}(\text{sponge}) =_{\text{df}} (\exists \text{ zoochlorella}) \text{ such that } [(\text{zoochlorella})\text{Mod}^{1}(\text{sponge}) \mid \xi(\text{l.e.})(\text{zoochlorella}) \text{ and } \sim (\text{zoochlorella})\text{Mod}^{1}(\text{sponge}) \mid \sim \xi(\text{l.e.})(\text{zoochlorella})]$$

Table 2. Filtering rates of *Spongilla lacustris*

Date and temperature (°C)	1 October, 13·2			17 October, 9·2		
Sponge volume (ml)	1·6	2·8	3·0	8·6	9·8	7·9
Filtering rate (ml s^{-1} ml^{-1})	0·027	0·023	0·011	0·010	0·010	0·009

17. Any organism that feeds by filtering water will compete for food resources with the subject animal. We have placed 'other sponges' on the envirogram as a first-order modifier of food resources to cover this class. The class includes sponges such as: *Corvomyenia carolinensis*, *Heteromeyenia baileyi*, *Anheteromeyenia ryderi*, *Trochospongilla pennsylvanica* and *Eunapius fragilis* (all present in North America), and many other organisms (see note 19).

The informal defining equation for another (particular) sponge as a first-order modifier of a particular item of food is:

$$(\text{other sponge})\text{Mod}^{-1}(\text{sponge}) =_{\text{df}} (\exists \text{ food}) \text{ such that} [(\text{food})\text{Res}(\text{sponge}) \mid \sim \xi(\text{other sponge})(\text{food}) \text{ and } \sim (\text{food})\text{Res}(\text{sponge}) \mid \xi(\text{other sponge})(\text{food})] .$$

(Harrison 1977)

18. Water temperature is known to affect water transport rates in *S. lacustris*. Table 2 is taken from Frost (1976*a*).

Thermal energy is entered on the envirogram as a modifier of the subject animal, which, in turn, is a second-order modifier in its own environment. The informal defining equation for thermal energy as a positive third-order modifier is given below; for the lower-order modifiers, see note 5.

$$(\text{thermal energy})\text{Mod}^{+3}(\text{sponge}) =_{\text{df}} (\exists \text{ sponge}) \text{ such that } [(\text{sponge})\text{Mod}^{2}(\text{sponge}) \mid \xi(\text{thermal energy})(\text{sponge}) \text{ and } \sim (\text{sponge})\text{Mod}^{2}(\text{sponge}) \mid \sim \xi(\text{thermal energy})(\text{sponge})]$$

19. Many filter feeders, other than sponges, will compete with *S. lacustris* for food resources. The following are just a few examples: the mollusc (*Dreissenia polymorpha*), the waterfleas (*Bosmina longirostrus* and *Daphnia* spp.), the copepod (*Diaptomus oregonensis*).

The informal defining equation for a mollusc that modifies a food resource of the sponge is:

$$\text{(mollusc)Mod}^{-1}\text{(sponge)} =_{\text{df}} (\exists\ \text{food}) \text{ such that } [\text{(food)Res(sponge)} \mid \\ \sim\xi\text{(mollusc)(food) and } \sim\text{(food)Res(sponge)} \mid \xi\text{(mollusc)(food)}]\,.$$

20. Throughout most of North America, *S. lacustris* exhibits the following annual cycle: the change from the overwintering gemmule stage to the definite colonial form of the sponge begins in the spring, with peak abundance and size of the colonies occurring in late summer and early autumn; lower water temperatures in autumn cause deterioration of the colonial sponge until only gemmules remain. Clearly, there is a range of thermal energies that are harmful to the sponge; we classify these as malentities.

Thermal energy also affects reproduction by gemmulation; it is known that gemmules will remain dormant when water temperature is below 4°C (see note 24).

The informal defining equations below are, firstly, for a specific bounded amount of thermal energy (t.e.) as a malentity, and, secondly, for a (different) specific bounded amount of thermal energy as a modifier of the sponge, classified as a mate of itself.

$$\text{(t.e.)Mal(sponge)} =_{\text{df}} \text{H(sponge) is decreased} \mid \xi\text{(t.e.)(sponge)}$$

The second term in the conditional is not used, because thermal energy is not an animal.

$$\text{(t.e.)Mod}^{-1}\text{(sponge)} =_{\text{df}} (\exists\ \text{sponge}) \text{ such that } [\text{(sponge)Mat(sponge)} \mid \\ \sim\xi\text{(t.e.)(sponge) and } \sim\text{(sponge)Mat(sponge)} \mid \xi\text{(t.e.(sponge)}]$$

(Ostrom and Simpson 1978)

21. As individuals, all sponges, including *S. lacustris*, must find attachment space. On the species level, there must be sufficient space to allow development of a sufficient number of individuals, of large enough body size, to sustain reproduction in the population at a viable level. In aquatic habitats, this substrate resource is more frequently limiting than food. Once the resource has been gained, it has to be protected from encroachment by other species (see note 12 re. fusion). *S. lacustris* does not require a hard substratum: it may grow as upright branches from the pond bottom or attached to aquatic macrophytes. Settling larvae of *S. lacustris* prefer a surface that has been precoated with bacterial or algal film. Rock or macrophyte substrates (see note 6) are preferred; nevertheless, the orientation of the particular surface to the prevailing currents is at least as important.

The informal defining equation for a bounded specific piece of substrate as a resource is:

$$\text{(substrate)Res(sponge)} =_{\text{df}} \text{H(sponge) is increased} \mid \xi\text{(substrate)(sponge)}\,.$$

The second term in the conditional is not used, because substrate is not an animal.

(Bergquist 1978; Frost *et al.* 1982)

22. Cases have been reported in which ice scour has removed a sponge species from a location. We classify ice as both a malentity and a modifier of the resource 'substrate'.

The two informal defining equations follow:

$$\text{(ice)Mal(sponge)} =_{\text{df}} \text{H(sponge) is increased} \mid \xi\text{(ice)(sponge)}\,.$$

The second term in the conditional is not used, because ice is not an animal.

$$\text{(ice)Mod}^{-1}\text{(sponge)} =_{\text{df}} (\exists\ \text{substrate}) \text{ such that } [\text{(substrate)Res(sponge)} \mid \\ \sim\xi\text{(ice)(substrate) and } \sim\text{(substrate)Res(sponge)} \mid \xi\text{(ice)(substrate)}]$$

(Bergquist 1978)

23. *S. lacustris*, like all other sponges, can reproduce sexually. Again, like other sponges, *S. lacustris* is hermaphroditic, though in a unique way that ensures that, in any one breeding season, each individual will be either female or male, but not both (see note 25).

During the annual cycle, outlined in note 20, oocyte and sperm production commences shortly after the gemmules are released from dormancy in the early spring. Williamson and Williamson (1979) report a case in which sperm production lasted about 6 weeks. It seems likely that both sperm and oocytes are produced by the redifferentiation of choanocyte cells.

Sperm are released into the exhalant stream, and water currents are necessary to carry the sperm to a position where they will be sucked into the inhalant stream of a female. The sperm are trapped by choanocytes and transferred to eggs in the mesohyl.

Embryos develop into larvae and, when ready for release, move to an exhalant canal. At this stage, we regard the parents as having reproduced successfully.

The informal defining equations below are for a sponge of opposite sex, abbreviated sponge opp. sex, as a mate, and a specific bounded quantity of kinetic energy (within a water current), abbreviated k.e.

> (sponge opp. sex)Mat(sponge) $=_{df}$ an offspring of both individuals will be produced with probability greater than zero | ξ(sponge opp. sex)(sponge)
>
> (k.e.)Mod^{+1}(sponge) $=_{df}$ (∃ sponge opp. sex) such that [(sponge opp. sex)Mat(sponge) | ξ(k.e.)(sponge) and ~(sponge opp. sex)Mat(sponge) | ~ξ(k.e.)(sponge)]

(Williamson and Williamson 1979)

24. Some authors refer to gemmulation directly as a method of asexual reproduction, whereas others write in a way that seems to imply that this is merely an adaptive stage in the life of an individual. Once again, we encounter difficulty with what is to count as an individual sponge (see Introduction).

Gemmules are complex, armoured structures, coated in a thick layer of spongin, embedded with microscleres. These small spherical structures are produced at the onset of winter (when the colonial sponge dies back) and are capable of withstanding freezing and desiccation. When environmental conditions are again favourable, the gemmule hatches and grows quickly. Thus, thermal energy acts as a positive first-order modifier.

With respect to algal symbionts, *S. lacustris* has two forms: the characteristically green symbiotic form, containing intracellular zoochlorellae, and the white aposymbiotic form. The two forms show slight but significant differences in the gemmulation process. The white form gemmulates a few weeks before the green (in late autumn) and produces significantly smaller gemmules; for the white form, the former point confers the disadvantage of a shorter growing season, which "could potentially decrease their ability to reproduce vegetatively and procure food for winter dormancy" (Williamson and Williamson 1979). Both forms hatch at the same time in the spring. It is cautiously suggested that the larger green gemmules are "more viable in nature" (Williamson and Williamson 1979)—i.e. the hatching rate is higher.

Light (photoperiod), both in combination with intracellular zoochlorellae and without, is also suggested as an important triggering mechanism for gemmulation in *S. lacustris*.

S. lacustris gemmules will remain dormant indefinitely if kept at temperatures below 4°C.

The informal defining equation for the sponge as a mate of itself follows. In this definition, the primitive term ξ, followed twice by the subject animal, should be interpreted as the sponge affecting itself in such a way that a physiological change is induced and the gemmule is produced asexually. There is no logical contradiction in using the definition in this way.

> (sponge)Mat(sponge) $=_{df}$ an offspring from the single parent sponge will result with probability greater than zero | ξ(sponge)(sponge)

Thermal energy (t.e.) is a positive first-order modifier:

$$\text{(t.e.)Mod}^{+1}\text{(sponge)} =_{\mathrm{df}} (\exists \text{ sponge}) \text{ such that } [\text{(sponge)Mat(sponge)} \mid \xi\text{(t.e.)(sponge) and } \sim\text{(sponge)Mat(sponge)} \mid \sim\xi\text{(t.e.(sponge)]} .$$

The following informal defining equations are for a zoochlorella as a first-order modifier of the subject animal as a mate of itself, and light energy, abbreviated l.e., as a modifier of a specific individual zoochlorella.

$$\text{(zoochlorella)Mod}^{+1}\text{(sponge)} =_{\mathrm{df}} (\exists \text{ sponge}) \text{ such that } [\text{(sponge)Mat(sponge)} \mid \xi\text{(zoochlorella)(sponge) and } \sim\text{(sponge)Mat(sponge)} \mid \sim\xi\text{(zoochlorella)(sponge)}]$$

It should be remembered that, in the formal version of this defining equation, the instant of time *t* is all important. The definition is correct in the sense that, at time *t*, '∃ sponge', or, less formally, 'it is possible to find a sponge', such that, if the zoochlorella is present, the sponge will produce a gemmule asexually, and without the zoochlorella, it will not. The same sponge may well reproduce asexually without the presence of the zoochlorella at some other time.

$$\text{(l.e.)Mod}^{+2}\text{(sponge)} =_{\mathrm{df}} (\exists \text{ zoochlorella}) \text{ such that } [\text{(zoochlorella)Mod}^{1}\text{(sponge)} \mid \xi\text{(l.e.)(zoochlorella) and } \sim\text{(zoochlorella)Mod}^{1}\text{(sponge)} \mid \sim\xi\text{(l.e.)(zoochlorella)}]$$

(Ostrom and Simpson 1978; Williamson and Williamson 1979; Harrison *et al.* 1981; Frost *et al.* 1982)

25. *S. lacustris* is hermaphroditic, but in a rather unusual way. It has been shown that, in any given reproductive season, an individual sponge will be strictly either male or female. However, of five indviduals, tagged so that they could be reliably identified after their period of winter dormancy, three had changed sex by the following reproductive season, one male becoming a female and two females becoming male; the sex of the other two was unchanged.

"While it is only theorizing to guess at the significance of this behaviour it is possible to see advantages for a sessile organism which disperses by free larvae. An isolated larva can produce an individual which will produce gemmules. Next spring when those gemmules germinate some may change sex. This enables successful fertilization and ensures the spread of the species." (Bergquist 1978).

In their work on white and green forms of *S. lacustris*, Williamson and Williamson (1979) observed male sexual elements in twice as many white sponges as in green; one explanation involves the possibility of antibiosis in zoochlorellae.

The relevant informal defining equation is given at the end of note 23.

26. All freshwater sponges, including *S. lacustris*, are characterised by silica (silicon dioxide) skeleton needles or spicules. Spicules are formed by a cell type called the scleroblast, which deposits silica on an organic 'axial thread'. Such spicules consist of about 92% silicon dioxide, 7% water, and traces of magnesium, potassium and sodium. Because of the contribution of the skeleton to sponge growth, all of these materials will be resources. To obtain silica, *S. lacustris* can only use dissolved silicic acid and not solid quartz.

Several authors suggest that the sharpness of the spicules and their difficulty of digestion afford the sponge protection from some potential predators.

The informal defining equation for silica as a resource is:

$$\text{(silica)Res(sponge)} =_{\mathrm{df}} \text{H(sponge) is increased} \mid \xi\text{(silica)(sponge)} .$$

The second term in the conditional is not used, because silica is not an animal. 'Silica' should be interpreted as a specific bounded quantity of silicic acid.

(Simpson *et al.* 1979)

27. Calcium and divalent cations can play a significant role in the gemmulation process for *S. lacustris* and other freshwater sponges. If kept in pure water, gemmules will hatch, demonstrating that all essential factors, including any essential ions, are contained within the gemmule. Results establish that calcium at concentrations of 5 mM and higher foster germination; however, the presence of sufficient amounts of strontium, barium, zinc or manganese results in an inhibition of germination. Nevertheless, in the latter case, if a sufficient concentration of calcium is also present, any inhibition will be overcome (Ostrom and Simpson 1978).

Informal defining equations for a specific bounded quantity of zinc as a first-order modifier of the subject animal as a mate of itself, and calcium (similarly specific and bounded) as a modifier of zinc, are given below:

$$\begin{aligned}&(\text{zinc})\text{Mod}^{-1}(\text{sponge}) =_{\text{df}} (\exists\ \text{sponge}) \text{ such that } [(\text{sponge})\text{Mat}(\text{sponge}) \mid \\ &\sim \xi(\text{zinc})(\text{sponge}) \text{ and } \sim(\text{sponge})\text{Mat}(\text{sponge}) \mid \xi(\text{zinc})(\text{sponge})]\end{aligned}$$

$$\begin{aligned}&(\text{calcium})\text{Mod}^{-2}(\text{sponge}) =_{\text{df}} (\exists\ \text{zinc}) \text{ such that } [(\text{zinc})\text{Mod}^{1}(\text{sponge}) \mid \\ &\sim \xi(\text{calcium})(\text{zinc}) \text{ and } \sim(\text{zinc})\text{Mod}^{1}(\text{sponge}) \mid \xi(\text{calcium})(\text{zinc})]\,.\end{aligned}$$

28. Pieces of freshwater sponge have occasionally been found in the stomachs of fish; whether the fish were directly predatory is not known, but doubtful. The sharp, indigestible silica skeleton and noxious chemicals have been given as reasons for the sponge's relative freedom from larger predators. Thus, we tentatively classify fish as predators modified by subject animal (skeleton and poisons).

Informal defining equations for one particular fish as a predator, and the subject sponge as a modifier, follow:

$$\begin{aligned}&(\text{fish})\text{Pred}(\text{sponge}) =_{\text{df}} \text{H}(\text{sponge}) \text{ is decreased and } \text{H}(\text{fish}) \text{ is increased} \mid \\ &\xi(\text{fish})(\text{sponge})\end{aligned}$$

$$\begin{aligned}&(\text{sponge})\text{Mod}^{-1}(\text{sponge}) =_{\text{df}} (\exists\ \text{fish}) \text{ such that } [(\text{fish})\text{Pred}(\text{sponge}) \mid \\ &\sim \xi(\text{sponge})(\text{fish}) \text{ and } \sim(\text{fish})\text{Pred}(\text{sponge}) \mid \xi(\text{sponge})(\text{fish})]\,.\end{aligned}$$

29. Snails and other crawling or browsing animals have been reported as occasionally damaging sponges as an accidental adjunct of their normal activities. Presumably, the same sort of damage can be done by wading animals. We group these animals together and classify them as malentities.

In the informal defining equation below, 'larger benthic or wading animal' is abbreviated 'animal'. This is a case in which the malentity is unaffected by the encounter; thus, H(animal) remains unchanged.

$$\begin{aligned}&(\text{animal})\text{Mal}(\text{sponge}) =_{\text{df}} \text{H}(\text{sponge}) \text{ is decreased and } \text{H}(\text{animal}) \text{ is unchanged} \mid \\ &\xi(\text{animal})(\text{sponge})\end{aligned}$$

30. In note 9, a few of the many animals frequently associated with freshwater sponges, including *S. lacustris*, were mentioned. In the absence of better information, it was suggested that many of this group would function in the sponge's environment as at least some modifier of food. Still, without hard data, some authors suggest a parasite–host relationship. Thus, we tentatively group the animals mentioned below as parasites on the envirogram:

(i) larvae from eggs of water mites, including *Unionicula crassipes*, which frequently oviposit on freshwater sponges;
(ii) annelids (roundworms) of the genera *Aelosoma*, *Naïs* and *Chaetogaster*;
(iii) certain predatory ciliates;
(iv) freshwater gammarids (sand fleas) of the family Leucothoidae.

The informal defining equation for a larva acting as a predator in the formal sense is:

$$\text{(larva)Pred(sponge)} =_{df} \text{H(sponge) is decreased and H(larva) is increased} \mid \xi\text{(larva)(sponge)} .$$

(Kahl and Konopacka 1981)

References

Andrewartha, H. G., and Birch, L. C. (1984). 'The Ecological Web: More on the Distribution and Abundance of Animals.' (University of Chicago Press: Chicago.)

Bergquist, P. R. (1978). 'Sponges.' (Hutchinson: London.)

Frost, T. M. (1976*a*). Sponge feeding: a review with a discussion of some continuing research. In 'Aspects of Sponge Biology'. (Eds F. W. Harrison and R. R. Cowden.) pp. 283–98. (Academic Press: New York.)

Frost, T. M. (1976*b*). Investigations of the aufwuchs of freshwater sponges. 1. A quantitative comparison between the surfaces of *Spongilla lacustris* and three aquatic macrophytes. *Hydrobiologia* **50**, 145–9.

Frost, T. M. (1978*a*). In situ measurements of clearance rates for the freshwater sponge *Spongilla lacustris*. *Limnol. Oceanogr.* **23**, 1034–9.

Frost, T. M. (1978*b*). Impact of the freshwater sponge *Spongilla lacustris* on a *Sphagnum* bog-pond. *Verh. Int. Ver. Limnol.* **20**, 2368–71.

Frost, T. M. (1980*a*). Selection in sponge feeding processes. In 'Nutrition in the Lower Metazoa'. (Eds D. G. Smith and Y. Tiffon.) pp. 33–44. (Pergamon Press: New York.)

Frost, T. M. (1980*b*). Clearance rate determinations for the freshwater sponge *Spongilla lacustris*: effects of temperature, particle type and concentration, and sponge size. *Arch. Hydrobiol.* **90**, 330–56.

Frost, T. M. (1981). Analysis of ingested particles within a fresh-water sponge. *Trans. Am. Microsc. Soc.* **100**, 271–7.

Frost, T. M. (1983). Algal symbiosis in freshwater sponges: inter-habitat and inter-species variation in chlorophyll content. *Am. Zool.* **23**, 944 (Abstract).

Frost, T. M., de Nagy, G. C., and Gilbert, J. J. (1982). Population dynamics and standing biomass of the freshwater sponge *Spongilla lacustris*. *Ecology* **63**, 1203–10.

Frost, T. M., and Williamson, C. E. (1980). In situ determination of the effect of symbiotic algae on the growth of the freshwater sponge *Spongilla lacustris*. *Ecology* **61**, 1361–70.

Gilbert, J. J., and Simpson, T. L. (1976). Gemmule polymorphism in the freshwater sponge (*Spongilla lacustris*). *Arch. Hydrobiol.* **78**, 268–77.

Grzimek, B. (Ed.) (1974). 'Grzimek's Animal Life Encyclopedia. Vol. 1.' (van Nostrand Reinhold: New York.)

Harrison, F. (1977). The taxonomic and ecological status of the environmentally restricted spongillid species of North America. III. *Corvomeyenia carolinensis* Harrison 1971. *Hydrobiologia* **56**, 187–90.

Harrison, F. W., and Cowden, R. R. (Eds) (1976). 'Aspects of Sponge Biology.' (Academic Press: New York.)

Harrison, F. W., Rosenberg, E. M., Davis, D. A., and Simpson, T. L. (1981). Correlation of cyclic GMP and cyclic AMP immunofluorescence with cytochemical patterns during dormancy, release and development from gemmules in *Spongilla lacustris* (Porifera, Spongillidae). *J. Morphol.* **167**, 52–64.

Kahl, K., and Konopacka, A. (1981). Oligochaeta inhabiting the colonies of the sponge *Spongilla lacustris* (L.) in the River Gać. *Acta Hydrobiol.* **23**, 243–9.

Kharchenko, T. A., and Lyashenko, A. V. (1986). Oxygen consumption of freshwater sponges. *Gidrobiol. Zh.* **22**, 98–100.

Niven, B. S. (1982). Formalization of the basic concepts of animal ecology. *Erkenntnis* **17**, 307–20.

Ostrom, K. M., and Simpson, T. L. (1978). Calcium and the release from dormancy of freshwater sponge gemmules. *Dev. Biol.* **64**, 332–8.

Poirrier, M. A. (1976). A taxonomic study of the *Spongilla alba*, *S. cenota*, *S. wagneri* species group (Porifera : Spongillidae) with ecological observations of *S. alba*. In 'Aspects of Sponge Biology'. (Eds F. W. Harrison and R. R. Cowden.) pp. 203–14. (Academic Press: New York.)

Reiswig, H. M. (1976). Discussion on external currents and sponge feeding. In 'Aspects of Sponge Biology'. (Eds F. W. Harrison and R. R. Cowden.) pp. 47–8. (Academic Press: New York.)

Resh, V. H. (1976*a*). Life cycles of invertebrate predators of freshwater sponge. In 'Aspects of Sponge Biology'. (Eds F. W. Harrison and R. R. Cowden.) pp. 299–312. (Academic Press: New York.)

Resh, V. H. (1976*b*). Life histories of coexisting species of *Ceraclea* caddisflies (Trichoptera : Leptoceridae): the operation of independent functional units in a stream ecosystem. *Can. Entomol.* **108**, 1303–18.

Resh, V. H., Morse, J. C., and Wallace, I. D. (1976). The evolution of the sponge feeding habit in the caddisfly genus *Ceraclea* (Trichoptera : Leptoceridae). *Ann. Entomol. Soc. Am.* **69**, 937–41.

Saller, U., and Weissenfels, N. (1985). The development of *Spongilla lacustris* from the oocyte to the free larva. Porifera : Spongillidae. *Zoomorphology (Berl.)* **105**, 367–74.

Simpson, T. L., Refolo, L. M., and Kaby, M. E. (1979). Effects of germanium on the morphology of silica deposition in a freshwater sponge. *J. Morphol.* **159**, 343–54.

Solem, J. O. (1978). Swarming and habitat segregation in the family Leptoceridae (Trichoptera). *Norw. J. Entomol.* **25**, 145–8.

Solem, J. O., and Resh, V. H. (1981). Larval and pupal description, life cycle, and adult flight behaviour of the sponge-feeding caddis fly, *Ceraclea nigronervosa* (Retzius), in Central Norway (Trichoptera). *Entomol. Scand.* **12**, 311–19.

Storr, J. W. (1976). Discussion on external currents and sponge feeding. In 'Aspects of Sponge Biology'. (Eds F. W. Harrison and R. R. Cowden.) pp. 46–7. (Academic Press: New York.)

Szuch, E. J., Studier, E. H., and Sullivan Jr, R. B. (1978). The relationship of light duration to oxygen consumption in the green, freshwater sponge *Spongilla lacustris*. *Comp. Biochem. Physiol. A Comp. Physiol.* **60**, 221–4.

Williamson, C. E. (1977). Fluorescence identification of zoochlorellae: a rapid method for investigating algae–invertebrate symbioses. *J. Exp. Zool.* **202**, 187–94.

Williamson, C. E. (1979). Crayfish predation in freshwater sponges. *Am. Midl. Nat.* **101**, 245–6.

Williamson, C. E., and Williamson, G. L. (1979). Life-cycles of lotic populations of *Spongilla lacustris* and *Eunapius fragilis* (Porifera : Spongillidae). *Freshwater Biol.* **9**, 543–53.

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Logical Synthesis of an Animal's Environment: Sponges to Non-human Primates.
III.* The Rat Tapeworm, *Hymenolepis diminuta*

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Abstract

The environment of the rat tapeworm, *H. diminuta*, is classified according to the defining equations given in the first paper of this series. Two envirograms are presented: they display the objects within the environments of larva and adult in their correct places. Notes on the envirograms include informal versions of the appropriate defining equations that are used for the classification.

Introduction

Hymenolepis diminuta, the rat tapeworm, is widely dispersed over the whole world. Its way of life differs markedly from the other animals' of this series in that much of its life is spent within the body of another animal. Unlike the sponge of the previous paper, the life cycle of *H. diminuta* divides clearly into two stages, larva and adult; it is convenient, therefore, to construct two separate envirograms for the animal.

The early larval stage, known as the oncosphere, is taken in this paper to mean a whole unit consisting of a hexacanth larva surrounded by two embryonic envelopes and possessing six hooks and penetration glands (see note 7). Pappas and Leiby (1986) found the length of the oncosphere to vary from 36·5 μm to 41 μm. The early embryology of *H. diminuta*, from the primary oocyte to the formation of the first mesomere, has been followed by means of scanning electron microscopy, histochemistry and light microscopy by Coil (1986). Survival of eggs (as measured by their infectivity to the intermediate host) was found to be age-dependent with an expected value of 11 days when the eggs were retained within the host's faecal pellet (Keymer 1982).

The oncosphere is ingested by an intermediate host. There is steady growth and gradual differentiation from hexacanth larva to mature cysticercoid; the animal remains in the latter stage until it is ingested by the definitive host. The cysticercoid possesses a 'tail' or cercomer, and a protoscolex. Details of the development of the cysticercoid are given by Richards and Arme (1983, 1984). Intermediate hosts of *H. diminuta* are Coleoptera, Lepidoptera, Orthoptera, Siphonaptera, and other arthropods. Burt (1980) lists 66 species, of which 29 are beetles. Keymer (1982) found that older beetles are less susceptible to infection by the tapeworm.

The definitive hosts are many and varied. Burt (1980) lists 99 species that act as definitive hosts, ranging through Canidae, Insectivora, Primates and, in particular, the Rodentia. In the last, he includes five species of *Microtus*, six species of *Apodemus*, 10 species of *Mus*, and nine species of *Rattus*. *R. norvegicus* and *R. rattus* seem to be the most common definitive hosts. Infections of *Homo sapiens* are considered to be accidental and no serious health hazard.

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The top end, or 'head', of the adult tapeworm is called the scolex. It is followed by a long chain of proglottides (segments), which differentiate in the 'neck' region (germitive area) of the animal. Thus, as each proglottis ages, it is found further down the length of the tapeworm; it becomes engorged with fertilised eggs, which develop into oncospheres; these rupture, finally break off, and are eliminated by the host. The adult worm thus maintains a more or less constant length of about 70 cm. However, the size varies with the species of definitive host and the number of worms present. Pappas and Leiby (1986) observed 151–435 proglottides per tapeworm. Details of the development of the adult tapeworm are given by Pappas *et al.* (1983).

"Following ingestion by the rat, the scolex of the cysticercoid evaginates through the surrounding layers, via the evagination canal, and adheres to the lining of the intestine. These surrounding layers and the cercomer are lost at this stage and the neck region starts to produce young proglottides. The cercomer . . . is now understood to be the larval organ primarily responsible for development and metabolism within the cysticercoid, and which has a tegument which differs, ultrastructurally, from the tegument of the scolex and neck region" (M. D. B. Burt, personal communication).

Roberts (1980) writes that the growth rate after infection of the rat (i.e. at the mature cysticercoid stage) is "explosive"—it must "rival or surpass that of any other metazoan tissue, including embryonic and neoplastic. Within 15 days after infection of the rat, a normal *H. diminuta* will have produced up to 2200 proglottides, and will have increased its length by up to 3400 times and its weight by up to 1·8 million times".

The adult tapeworm usually occupies a site in the small intestine of the rat host. There is evidence that it occupies different regions of the intestine at different times. These migrations appear to be a response to the host's feeding habits (Kennedy 1976). There is also evidence that the migration may be correlated with the host's circadian variation of 5-hydroxytryptamine (5-HT) (Cho and Mettrick 1982). The presence of the tapeworm has a marked effect on the gastro-intestinal physiology of the laboratory rat (Arme 1976).

Under natural conditions, the life-span of adult *H. diminuta* is probably as long as the host that harbours it. By artificial passage to successive hosts, an adult tapeworm has been kept alive for 14 years—and may well live longer (Burt 1980). The oncospheres can remain viable for about 6 months after having been passed in the faeces of the definitive host.

The way of life of this remarkable animal is described in the article by Lumsden and Specian (1980), quoting Professor Horace W. Stunkard, as follows: ". . . As archaic as the Palaeozoic, they (tapeworms) are as modern as tomorrow. They have attained the ideal welfare state with all its beneficence; absolute security with an abundance of predigested food, and with a minimum of effort or exertion . . . digestive, respiratory and circulatory organs have been discarded as superfluous, (since) every essential is provided in abundance with no concern for cost or other responsibility. With no need to expend energy for food or shelter, the cestode can get down seriously to the business of reproduction . . ."

The Envirograms

The subject animals for the two envirograms are an adult (Fig. 1) and a larva (Fig. 2). Envirograms for oncosphere and cysticercoid have been combined in the latter case; thus, note 6 in Fig. 2 refers to the oncosphere, and note 7 to the cysticercoid. Reports from the literature about objects in the environment of many individuals have been combined, so the envirograms of Figs 1 and 2 are concatenations of many individual envirograms for large numbers of individual tapeworms observed in different places and at different times. The numbers on the envirograms refer to the notes that follow. These numbers appear in no particular order. The various parts of the envirograms were constructed in an entirely haphazard order as the literature became available. The square brackets indicate a set of objects; thus, '[host's food]' in Fig. 1 refers to a set of food objects of the host. The parentheses are used not only for explanatory purposes, e.g. 'negative ions (pH)', but also in the case that there is some doubt about the classification, e.g. '(oxygen)'. The symbol ϕ on the larva envirogram represents the empty set; larvae do not reproduce. It was distressing to put 'none known' on both envirograms under the heading 'PREDATORS'. Although the material presented in this paper by no means constitutes a complete review, a special effort was made to find reports of predators (including parasites and pathogens) of *H. diminuta.*

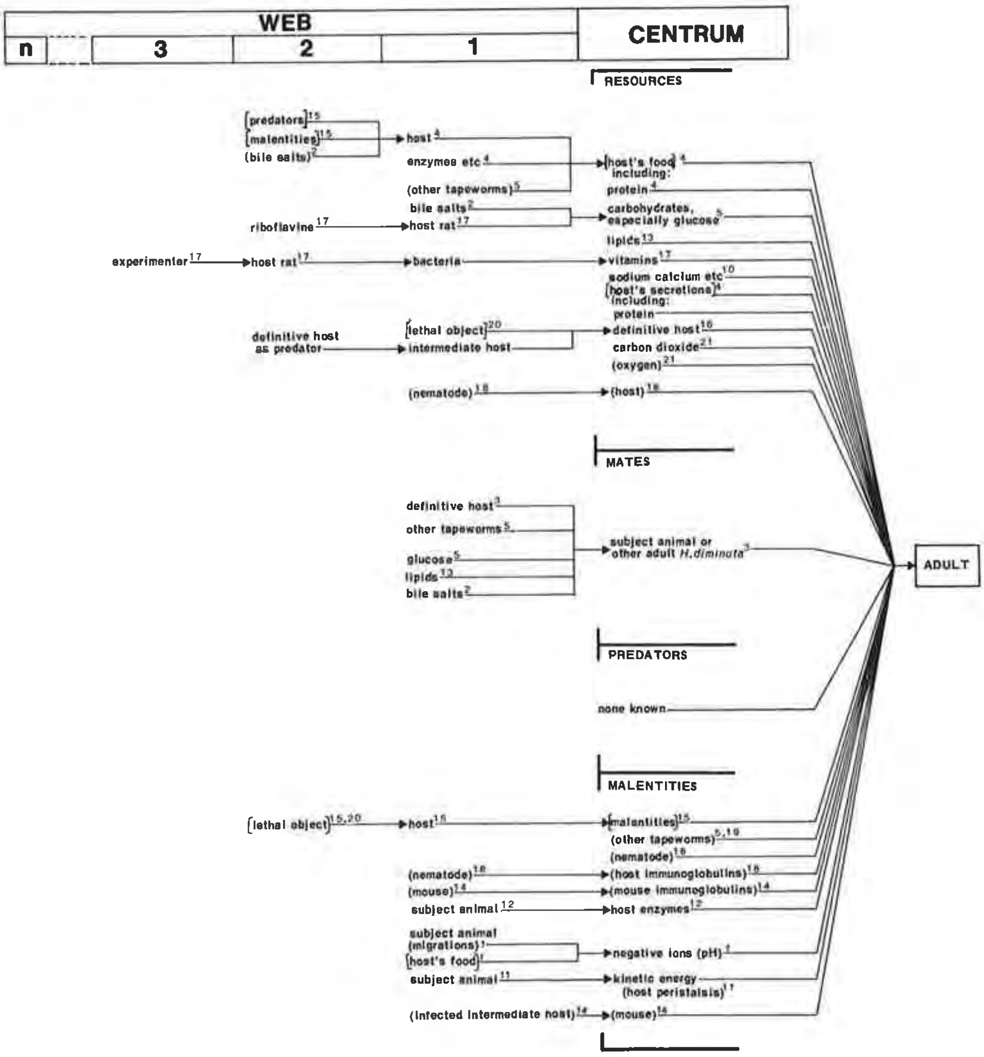

Fig. 1. Envirogram for adult tapeworm.

However, apart from some tentative suggestion that the nematode *Nippostrongylus brasiliensis* may be a predator (see note 18), no such reports were found.

A semiformal version of the appropriate defining equations (see part I of this series) is given at the end of each note. The following symbols are used:

(i) $=_{\mathrm{df}}$: 'is equal by definition to', or more strictly, the form '$x =_{\mathrm{df}} y$' means 'x is to be interchangeable with y'.

(ii) ∃: the existential quantifier of formal logic. Read '∃ fish' as 'there exist a fish' or 'there is at least one fish', or, more informally, 'we can find a fish'. In this paper, expressions such as '∃ fish' are always followed by the words 'such that'.

(iii) |: '$x \mid y$' means 'x occurs (will occur), assuming y'. This is the symbol used for conditional events (and conditional probabilities). The expression '$A \mid B$' may be read 'event A occurs, given that event B occurs'; it refers to 'event A under the condition that B' or 'event A under the hypothesis that B'. The use of the conditional in the definitions implies that the environment of the subject animal is independent of its habitat. Thus, an object that is reported as a resource for the ANU population (in Australia), for example would also be classified as a resource for the OSU population (in the United States).* In ordinary English it is a *potential* resource. Similarly, mates, predators, malentities and modifers are all *potential* mates, etc.

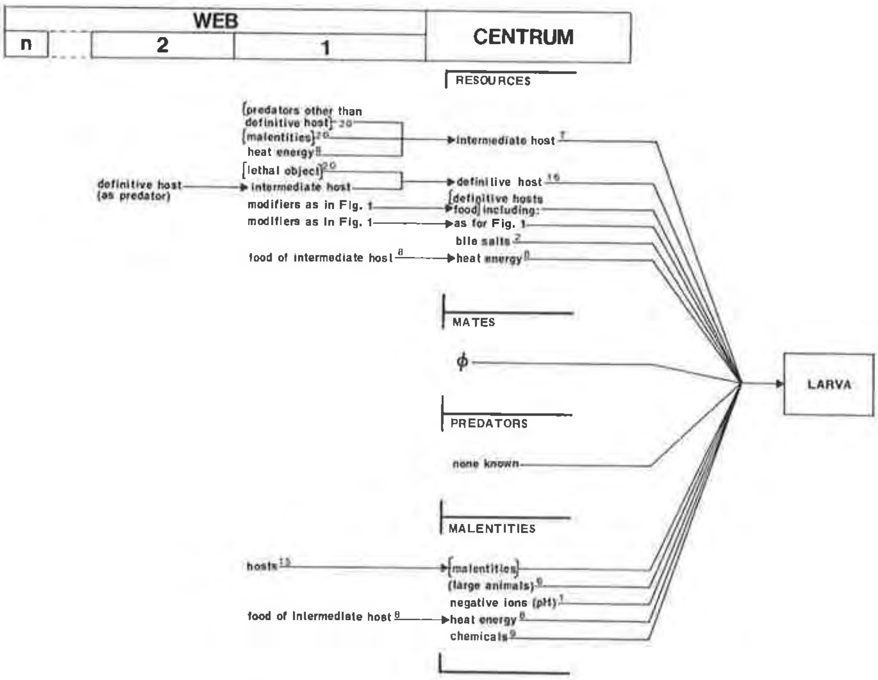

Fig. 2. Envirogram for tapeworm larva.

Notes on the Envirograms

1. Following ingestion by the definitive host, the animal is protected from stomach acids by the outer layers of the cysticercoid during its passage through the host's stomach. If already encysted worms are introduced into the stomach of the definitive host, they will be destroyed, but they can establish themselves if introduced directly into the small intestine (Burt 1980).

According to Mettrick (1980), pH is known to affect the migrations of *H. diminuta*, and the region of the intestine with the lowest pH usually has the highest biomass of the tapeworm. The cestode is, however, capable of inhabiting any part of the intestine. Uglem and Just (1983) found that the animal releases proteins that inhibit trypsin activity;

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*ANU and OSU populations refer to the work of Pappas and Leiby (1986).

furthermore *H. diminuta* is able to change the pH in order to protect itself. The principal determinants of the pH of the contents of the host's gut are the type of food and the time of ingestion.

Informal versions of the defining equations given below are for an adult tapeworm as the subject animal. The object is a particular drop of liquid in the intestine of the host, which has a relatively high pH. The animal itself acts as a modifier of the malentity by migrating or altering the pH. Since a drop of liquid is not an animal, the second term in the definition is excluded from the defining equation for a malentity.

(high pH drop)Mal(tapeworm) $=_{df}$ H(tapeworm) is
decreased | ξ(high pH drop)(tapeworm)

(tapeworm)Mod^{-1}(tapeworm) $=_{df}$ ($\exists$ high pH drop) such that
[high pH drop)Mal(tapeworm) | $\sim\xi$(tapeworm)(tapeworm) and
$\sim$(high pH drop)Mal(tapeworm) | ξ(tapeworm)(tapeworm)]

See also Cho (1984, 1985).

2. Activation and excystment of the larva in the definitive host requires the presence of bile salts. Experiments in which a host rat was made bileless showed that *H. diminuta* either failed to establish itself in the gut or was severely stunted.

Egg production and carbohydrate absorption by the adult tapeworm from bileless hosts are also greatly reduced. Thus, bile salts will be a resource for the larva, and both a modifier of mates and a modifier of carbohydrate (glucose etc.) food resources for the adult. Nevertheless, it is possible that the effect of the absence of bile salts may be indirect—i.e. *via* an effect on the digestion of the host.

The informal defining equation for a specific bounded quantity of bile salts as a resource of the subject larva in the late cysticercoid stage is:

(bile salts)Res(larva) $=_{df}$ H(larva) is increased | ξ(bile salts)(larva)

The informal defining equation for bile salts as a positive first-order modifier of a specific bounded quantity of glucose in the environment of a subject adult tapeworm follows:

(bile salts)Mod^{+1}(tapeworm) $=_{df}$ ($\exists$ glucose) such that
[(glucose)Res(tapeworm) | ξ(bile salts)(glucose) and
$\sim$(glucose)Res(tapeworm) | $\sim\xi$(bile salts)(glucose)]

3. *H. diminuta* is hermaphroditic; each proglottis contains both female and male reproductive organs. Like other tapeworms, self-reproduction seems to be the norm. However, cross-fertilisation is not ruled out. Lumsden and Specian (1980) report that, during copulation, a male protusile organ is inserted into a genital chamber of an "appropriate" proglottis of the same or another tapeworm. Self-insemination within the same proglottis is "not uncommon". The proportion of cross-fertilisations is unknown. In any case, reproduction can take place only within the definitive host, which is therefore a modifier of mates.

The informal defining equations below are for an adult tapeworm as a mate of itself, and a particular definitive host as a positive first-order modifier.

(tapeworm)Mat(tapeworm) $=_{df}$ an offspring of the tapeworm will be produced
with probability greater than zero | ξ(tapeworm)(tapeworm)

(def. host)Mod^{+1}(tapeworm) $=_{df}$ ($\exists$ tapeworm) such that
[(tapeworm)Mat(tapeworm) | ξ(def. host)(tapeworm) and
$\sim$(tapeworm)Mat(tapeworm) | $\sim\xi$(def. host)(tapeworm)]

4. Tapeworms have no mouths or digestive tracts. Under normal circumstances, in both

definitive and intermediate hosts, they do not feed on the host itself, but soak up nutriments, competing with the host for food that has already been processed. This is generally true of both protein and carbohydrate in *H. dininuta*'s diet. However, Mettrick (1980) reports that depriving the host of protein has little effect because the small amount of protein secreted in the digestive juices of the host will still be sufficient for the cestode's growth. Hall (1983) studied weaning rats fed on low-protein diets and infested with tapeworms, and concluded that the effect of low protein on the tapeworms was not significant. The amount of protein contained in the worm burdens was less than 1·5% of the average total intake of the protein-malnourished rats.

Lumsden and Specian (1980) write that, roughly speaking, the body plan of *H. diminuta* may be conceived as "a gut turned inside out . . . While the skin of most organisms serves as insulation from the environment, that of *H. diminuta* . . . promotes nearly all forms of chemical interchange between the environment and the internal tissues, especially the absorption of nutriments". The success of *H. diminuta* in competing with the host mucosa for available nutriments is explained by the fact that, per unit weight, the effective surface area of the tapeworm is greater than that of the intestine by a factor of three or four.

The food eaten by the host is processed and made acidic in the host's stomach; the acid chyme entering the duodenum is a mixture of semi-emulsified fat, protein, polypeptides, carbohydrates including non-hydrolised starch, and water. Enzymes, water, and various secretions from the host's pancreas, liver and intestinal walls are mixed with the chyme, the composition of which varies greatly from time to time, the host contributing the appropriate secretion to facilitate the digestive process. These enzymes (and other secretions) thus act as modifiers of the tapeworm's food; without the presence of the enzymes etc, the class of objects '[host's food]' would not enter the environment of the tapeworm as resources. Note that 'host' occurs as a first-order modifier of the tapeworm's resource 'host's food', because it both provides the food and is a competitor for it.

The following informal defining equations are for a particular object belonging to the class 'host's food' as a resource, and the two ways in which a host modifies that object.

$$\begin{array}{l}\text{(host's food)Res(tapeworm)} =_{\text{df}} \text{H(tapeworm) is increased} \mid \\ \xi\text{(host's food)(tapeworm)}\end{array}$$

The second term in the definition is not used because 'host's food' is not an animal. The informal defining equation for a host as a modifier in the sense that it provides 'host's food' for the tapeworm is:

$$\begin{array}{l}\text{(host)Mod}^{+1}\text{(tapeworm)} =_{\text{df}} (\exists\ \text{host's food) such that} \\ [\text{(host's food)Res(tapeworm)} \mid \xi\text{(host)(host's food) and} \\ \sim\text{(host's food)Res(tapeworm)} \mid \sim\xi\text{(host)(host's food)}]\end{array}$$

The informal defining equation for a host as a modifier in the sense that it 'competes' with the tapeworm for 'host's food' (not the same object as above) is:

$$\begin{array}{l}\text{(host)Mod}^{-1}\text{(tapeworm)} =_{\text{df}} (\exists\ \text{host's food) such that} \\ [\text{(host's food)Res(tapeworm)} \mid \sim\xi\text{(host)(host's food) and} \\ \sim\text{(host's food)Res(tapeworm)} \mid \xi\text{(host)(host's food)}]\end{array}$$

5. *H. diminuta* does not use all carbohydrates. Di- and polysaccharides are not absorbed. The most useful of the carbohydrates is glucose. Galactose is used to a limited extent, but "*H. diminuta* could not be supported on a galactose diet and sucrose; dextrin and maltose were all inferior to glucose in promoting worm growth" (Mettrick 1980). Arme (1976) reports that the tapeworm is impervious to fructose. Younger worms can take up glucose against steeper concentration gradients than older worms.

The rate of development and maturation within the definitive host depends particularly on the carbohydrate (and especially glucose) contents of the host's diet. The presence of other individuals of *H. diminuta* is also known to affect these rates. It is certain that these co-parasites will compete with the subject animal for available carbohydrate (i.e. they will be first-order modifiers). In addition, there may be an 'overcrowding' effect, which, irrespective of mechanism, allows them to be classified as malentities (see note 19).

Roberts (1980) reports that the presence of the acanthocephalan *Moniliformis dubius* has an 'overcrowding' effect similar to the effect observed when additional tapeworms are present (see also note 19). Roberts reports also that, while the 'overcrowding' effect is not well understood, competition for host dietary carbohydrates probably plays some role, and that foods other than carbohydrates are probably also involved.

The following informal definitions are for glucose as a resource and a first-order modifier of mates, the latter in the sense that a tapeworm deprived of glucose is inhibited in its growth and therefore in its reproduction. The object here is a specific measured quantity of glucose.

$$\text{(glucose)Res(tapeworm)} =_{\text{df}} \text{H(tapeworm) is increased} \mid \xi\text{(glucose)(tapeworm)}$$

$$\begin{aligned}&\text{(glucose)Mod}^{+1}\text{(tapeworm)} =_{\text{df}} (\exists\ \text{tapeworm}) \text{ such that}\\&[\text{(tapeworm)Mat(tapeworm)} \mid \xi\text{(glucose)(tapeworm) and}\\&\sim\text{(tapeworm)Mat(tapeworm)} \mid \sim\xi\text{(glucose)(tapeworm)}]\end{aligned}$$

See also Lee and Ip (1986).

6. The oncosphere (early larval stage) has a stiff outer shell, which protects it from damage when it is passed in the faeces of the definitive host. Anything crushing the oncosphere by, say, accidentally chewing it, will be a malentity; I have tentatively classified large animals as malentities, since I think this kind of accident must be not uncommon, even though not reported. 'Large' should be interpreted as relative to the oncosphere.

Unless damaged, an oncosphere can remain viable for about 6 months after having been eliminated from the host.

The informal defining equation for a large animal as a malentity is:

$$\begin{aligned}&\text{(large animal)Mal(tapeworm)} =_{\text{df}} \text{H(tapeworm) is decreased and}\\&\text{H(large animal) is unchanged} \mid \xi\text{(large animal)(tapeworm)}\end{aligned}$$

7. The intermediate host, an arthropod, mechanically ruptures (with its mouthparts) the outer capsule of the oncosphere, thus acting as a resource for the early larval stage of the tapeworm. The oncosphere hooks, in conjunction with the penetration glands, enable the larva to pass through the gut wall of the arthropod and to establish itself.

For some intermediate hosts, the cysticercoids develop more rapidly in females. The reason for this is not clear but Hurd and Arme (1984) suggest that *H. diminuta* may interact with the endocrine system of its beetle host. The age of the intermediate host is also important; Ubelaker (1980) reports that older female intermediate hosts are less frequently infected than young or middle-aged females, while, among males, those of middle age were infected most often.

The informal defining equation for an arthropod as a resource is:

$$\begin{aligned}&\text{(arthropod)Res(larva)} =_{\text{df}} \text{H(larva) is increased and H(arthropod) is}\\&\text{unchanged} \mid \xi\text{(arthropod)(larva)}\end{aligned}$$

The precise response of the arthropod to the presence of *H. diminuta* has not been studied for many of the intermediate hosts. Ubelaker (1980) mentions other workers' results for some beetles: a higher respiratory rate in one case, a higher mortality in others. There is at least the possibility that, in some cases, the host is unaffected. Mettrick and Rahman (1984) found that the strain of parasite, species of intermediate host and the presence of 5-HT were significant. Maema (1986) reported that fecundity of some hosts is affected and

Keymer (1980) found that increasing parasite burden resulted in decreasing fecundity of *Tribolium confusum* hosts. [See also Keymer (1981) and Keymer and Anderson (1979).]

8. The development of the larva is dependent on temperature: within limits, the higher the temperature, the quicker the development. Ubelaker (1980) reports that 30°C is the most favourable temperature for the development of the larva, mature cysticercoids being produced in 8 days. At 20°C, the time increased to 23 days. While temperatures above 30°C result in more rapid development, Ubelaker reports that they also result in a higher incidence of abnormalities; thus, the range of heat energies corresponding to temperatures above 30°C constitutes malentities. Abnormalities due to heat stress can be reduced by changing the diet of the intermediate host (in this case, a beetle) to pure sugar instead of whole wheat flour. Thus, 'food of intermediate host' is a modifier of the malentity 'heat energy'.

The population of larval *H. diminuta* in beetles is increased at higher temperatures, the suggestion being that:

(i) the activity of certain enzymes in the oncospheres is increased, enabling them to increase their penetration and success; thus, heat energy acts here as a resource.

(ii) the beetles eat more at higher temperatures and therefore ingest more oncospheres. Here, heat energy is a modifier of the host, which, in turn, is a modifier of the class of resource '[host's food]' (partially digested, see note 4).

The informal defining equation for a specific bounded amount of heat energy as a modifier of the intermediate host is:

$$\text{(heat)Mod}^{+1}\text{(larva)} =_{\text{df}} (\exists\ \text{host}) \text{ such that } [\text{(host)Res(larva)} \mid \xi\text{(heat)(host) and } \sim\text{(host)Res(larva)} \mid \sim\text{(heat)(host)}]$$

9. Ubelaker (1980) reports that mebendazole at a concentration of 0·1 g per 10 g flour (the medium in which the beetles are kept) retards the development of the cysticercoids within their hosts, while "one gram or higher concentration were lethal to some, but not all, cysticercoids". Triethylene-thiophoramide kills some cysticercoids if the beetle host walks on blotting paper that has been soaked in it for 3 h.

The informal defining equation for a specific bounded quantity of flour containing 0·1 g mebendazole per 10 g flour, abbreviated mebendazole, as a malentity, is:

$$\text{(mebendazole)Mal(larva)} =_{\text{df}} \text{H(larva) is decreased} \mid \xi\text{(mebendazole)(larva)}$$

Since the object is not an animal, the second term in the definition is not used.

10. Whereas the skin of the most organisms insulates them from the environment, that of *H. diminuta* promotes nearly all forms of chemical interchange between the environment and the internal tissues. In addition to protein and carbohydrate absorption, the tapeworm has a sodium transport system, and calcium is required for the activation of muscle tissue (Lumsden and Specian 1980). Presumably, other elements are also required.

The informal defining equation for a specific bounded quantity of calcium as a resource is:

$$\text{(calcium)Res(tapeworm)} =_{\text{df}} \text{H(tapeworm) is increased} \mid \xi\text{(calcium)(tapeworm)}$$

The second term in the definition is not used because calcium is not an animal.

11. The peristaltic contractions of the definitive host's intestine are a constant threat to the tapeworm, which resists explusion by maintaining continuous moderate contraction (tonus) of its muscles. The animal attaches itself to the host by using the two pairs of suckers on its scolex. Also, the topography of the tapeworm is such that it tends to move back up the host's intestine during peristalsis [M. D. B. Burt, personal communication; for a scanning electron micrograph of the terminal proglottides, which illustrates this point, see Lumsden and Specian (1980)].

The informal defining equations that follow are first for a specific bounded quantity of kinetic energy, abbreviated k.e., as a malentity, and, secondly, for the subject tapeworm itself acting as a modifier by resisting the peristaltic contractions of its host.

$$\text{(k.e.)Mal(tapeworm)} =_{\text{df}} \text{H(tapeworm) is decreased} \mid \xi\text{(k.e.)(tapeworm)}$$

The second term in the definition is not used because kinetic energy is not an animal.

$$\text{(tapeworm)Mod}^{-1}\text{(tapeworm)} =_{\text{df}} (\exists\ \text{k.e.}) \text{ such that } [\text{(k.e.)Mal(tapeworm)} \mid \sim\xi\text{(tapeworm)(k.e.) and } \sim\text{(k.e.)Mal(tapeworm)} \mid \xi\text{(tapeworm)(k.e.)}]$$

12. It is necessary for the tapeworm to protect itself against the digestive action of the enzymes of its host; the mechanism for doing this is frequently discussed in the literature; I have entered 'host enzymes' as malentities modified by 'subject animal', on the envirogram, since the potential danger to the tapeworm is so apparent. Christensen *et al.* (1986) found that fresh rat serum severely affected *H. diminuta*. Alghali and Grencis (1986) and Fagbemi and Christensen (1984) studied the effect of interactions in mice between *H. diminuta* and other infective agents. As mentioned in note 1, Uglem and Just (1983) found that the animal releases proteins that inhibit the host's trypsin activity.

The informal defining equations for an enzyme as a malentity, and the subject tapeworm as a modifier, are:

$$\text{(enzyme)Mal(tapeworm)} =_{\text{df}} \text{H(tapeworm) is decreased} \mid \xi\text{(enzyme)(tapeworm)}$$

The second term in the definition is not used because an enzyme is not an animal.

$$\text{(tapeworm)Mod}^{-1}\text{(tapeworm)} =_{\text{df}} (\exists\ \text{enzyme}) \text{ such that } [\text{(enzyme)Mal(tapeworm)} \mid \sim\xi\text{(tapeworm)(tapeworm) and } \sim\text{(enzyme)Mal(tapeworm)} \mid \xi\text{(tapeworm)(tapeworm)}]$$

13. *H. diminuta* absorbs fatty acids, modifies and stores them. At least some are used in egg production. Rat intestines infected with *H. diminuta* have been shown to contain approximately 30% less lipids than uninfested intestines (however, the lipid gradient down the intestine is generally the same) (Mettrick 1980).

The following informal defining equation is for a specific bounded quantity of lipid as a resource:

$$\text{(lipid)Res(tapeworm)} =_{\text{df}} \text{H(tapeworm) is increased} \mid \xi\text{(lipid)(tapeworm)}$$

The second term in the definition is not used because a lipid is not an animal.

14. Although *H. diminuta* in a rat host can survive until the host itself dies, the tapeworm is rejected within 9–14 days by a mouse host. The mechanism for this difference is not completely understood (Hopkins 1980). Formally, there are two alternatives:

(i) the mouse can be classified as a predator or malentity; or
(ii) from a biochemical perspective, the host immunoglobulins can be classified as malentities.

In both cases, an immune response of the mouse is involved.

(i) I tentatively classify the mouse as a malentity, since there is only some evidence that the ejection of the tapeworm causes an increase in H(mouse) [and, certainly, there is a decrease in H(tapeworm)]. An increase in H(mouse) might perhaps occur, for example, because the mouse will no longer lose the protein *secreted* during digestion (see note 4); note that the loss of *ingested* protein is insufficient grounds for classifying the mouse as a malentity because, in this case, the tapeworm is acting as a first-order modifier of the mouse's food, i.e. it is causing only *indirect* harm, and, therefore, the elimination of the tapeworm does not *directly* cause an increase in H(mouse). Of course, the mouse will be a malentity only if it becomes a host of

H. diminuta—i.e. after eating an infected intermediate host. The latter is thus a first-order modifier.

(ii) Mouse immunoglobulins have been observed bound to the outer tegument of the tapeworm; it is possible that the tegumental surface is damaged when this occurs and facilitates ejection. From this point of view, mouse immunoglobulins can be classified as malentities. The mouse will be a first-order modifier (see McCaigue and Halton 1987).

The informal defining equations for a particular mouse as a malentity, and a particular infected intermediate host, abbreviated int. host, as a first-order modifier, are:

(mouse)Mal(tapeworm) $=_{\mathrm{df}}$ H(tapeworm) is decreased and H(mouse) is decreased | ξ(mouse)(tapeworm)

(int. host)Mod^{+1}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ mouse) such that [(mouse)Mal(tapeworm) | ξ(int. host)(mouse) and $\sim$(mouse)Mal(tapeworm) | $\sim\xi$(int. host)(mouse)]

The informal defining equations for some one particular mouse immunoglobulin, abbreviated img., as a malentity, and the mouse as a first-order modifier, are:

(img.)Mal(tapeworm) $=_{\mathrm{df}}$ H(tapeworm) is decreased | ξ(img.)(tapeworm)

The second term in the definition is not used because img. is not an animal.

(mouse)Mod^{+1}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ img.) such that [(img.)Mal(tapeworm) | ξ(mouse)(img.) and $\sim$(img.)Mal(tapeworm) | $\sim\xi$(mouse)(img.)]

For studies of mouse immunisation against *H. diminuta*, see Elowni (1983) and Choromanski (1983). Wakelin (1976) discusses host responses in general.

15. Both the definitive and intermediate hosts provide protection to the tapeworm against a large class of malentities. However, the sword is double-edged, as the tapeworm will almost certainly die if its host is killed (see note 20).

The informal defining equations for some object x as a malentity, and some one specific host as a first-order modifier, are:

(x)Mal(tapeworm) $=_{\mathrm{df}}$ H(tapeworm) is decreased and, if x is an animal, then H(x) is either decreased or unchanged | ξ(x)(tapeworm)

(host)Mod^{-1}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ x) such that [(x)Mal(tapeworm) | $\sim\xi$(host)(x) and $\sim$(x)Mal(tapeworm) | ξ(host)(x)]

16. Because the tapeworm is unable to reproduce unless it is living in a definitive host, the definitive host is a resource [because that part of H(tapeworm) dealing with the probability of reproducing is directly increased]. One might also argue that the definitive host aids reproduction in the tapeworm only because of the food and protection that it provides, and that a laboratory artefact might be sufficient for the purpose. For the present, however, it seems sensible to classify the definitive host as a resource rather than only a modifier; it appears as such on both envirograms (see also note 2). The informal defining equations for the definitive host as a resource, the intermediate host as a first-order modifier (because it is eaten), and the definitive host as a second-order modifier (because it eats the intermediate host), are given below. In order to make them more specific, the intermediate host is taken to be a specific beetle, and the definitive host, a specific rat. Notice that the times (or hosts) cannot be identical in all the defining equations. The subject animal 'tapeworm' here refers to an individual in either the adult or the cysticercoid stage.

(rat)Res(tapeworm) $=_{\mathrm{df}}$ H(tapeworm) is increased and H(rat) is either decreased or unchanged | ξ(rat)(tapeworm) (beetle)Mod^{+1}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ rat) such that [(rat)Res(tapeworm) | ξ(beetle)(rat) and $\sim$(rat)Res(tapeworm) | $\sim\xi$(beetle)(rat)]

(rat)Mod^{+2}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ beetle) such that [(beetle)Mod^{1}(tapeworm) | ξ(rat)(beetle) and $\sim$(beetle)Mod^{1}(tapeworm) | $\sim\xi$(rat)(beetle)]

Although the rat is included twice in this modifier chain, it serves a different function in the two places in the environment of the tapeworm: resource and second-order modifier. The chain 'rat–beetle–rat–beetle . . .' could be repeated, formally speaking, but serves no useful scientific purpose.

17. Establishment and growth of *H. diminuta* are severely inhibited when the host rat is fed a diet deficient in all B vitamins, providing the host is prevented by the experimenter from eating its own faeces. If the rat is allowed to do this (as it is its normal behaviour), the lack of B vitamins in the diet has no effect on the cestode (Roberts 1980). "The worms obtain a sufficient supply of B vitamins (especially vitamin B_6) for normal development, the B vitamins having been produced by the bacterial flora in the large intestine" (L. S. Roberts, personal communication).

When the host rat is fed a diet lacking riboflavine, the tapeworm grows larger, whether or not the host is allowed to eat its faeces. Roberts (1980) suggests that this may be because more glucose is available to the cestode, since the host's glucose absorption is reduced when it is fed on a riboflavine-deficient diet. Riboflavine is thus a modifier of the host rat, which is, in turn, a modifier of glucose as a resource in the tapeworm's environment.

The informal defining equations for the chain 'riboflavine–host rat–glucose' follow:

(glucose)Res(tapeworm) $=_{\mathrm{df}}$ H(tapeworm) is increased | ξ(glucose)(tapeworm)

(rat)Mod^{+1}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ glucose) such that [(glucose)Res(tapeworm) | ξ(rat)(glucose) and $\sim$(glucose)Res(tapeworm) | $\sim\xi$(rat)(glucose)]

(riboflavine)Mod^{+2}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ rat) such that [(rat)Mod^{1}(tapeworm) | ξ(riboflavine)(glucose) and $\sim$(rat)Mod^{1}(tapeworm) | $\sim\xi$(riboflavine)(glucose)]

18. The presence of the nematode *Nippostrongylus brasiliensis* adversely affects *H. diminuta*. I have tentatively classified the nematode as a malentity, since "it would appear that the effects are" either "inhospitable conditions induced by the pathogenic effects of the nematode", or "stimulation by the nematode of the immune response of the host, or both" (Roberts 1980). If the first of these alternatives is correct, then the nematode can be tentatively classified as a malentity because, while H(tapeworm) is decreased, there is no clear evidence that H(nematode) is increased. If there were clear evidence for the latter, the nematode would be classified as a predator. The situation with the second alternative is more complicated (similar to the mouse–mouse immunoglobulin case of note 14). Because of the stimulated immune response, the nematode can be classified as a first-order modifier either of the host as resource, or of host immunoglobulins as malentities. I have put all of the above alternatives on the envirogram; all are in parentheses to indicate tentativeness.

The informal defining equations for a specific host immunoglobulin as a malentity, and a specific nematode as a first-order modifier, follow:

(host img.)Mal(tapeworm) $=_{\mathrm{df}}$ H(tapeworm) is decreased | ξ(host img.)(tapeworm)

The second term in the definition is not used because an immunoglobulin is not an animal.

(nematode)Mod^{+1}(tapeworm) $=_{\mathrm{df}}$ ($\exists$ host img.) such that [(host img.)Mal(tapeworm) | ξ(nematode)(host img.) and $\sim$(host img.)Mal(tapeworm) | $\sim\xi$(nematode)(host img.)]

19. Other tapeworms may sometimes act as malentities in the environment of the subject animal; the mechanism causing the so-called 'crowding' effect (Roberts 1980) is unknown; Roberts writes, "The important developmental implication of the crowding effect is that worms in the host's intestine are, by whatever means, influencing growth, cell division, DNA synthesis, and numerous other physiological parameters of other worms". Insler and Roberts (1980) report some evidence to the effect that the animals may secrete substances that inhibit the growth of neighbouring individuals of *H. diminuta*, although they remark that "demonstration of inhibition has not been completely consistent". However, in a later series of experiments, Roberts and Insler (1982) produced supporting evidence for such a mechanism, including the finding that the properties of certain secretions differed according to the population density.

The informal defining equation for a specific individual tapeworm, other than the subject animal, as a malentity is:

$$\text{(other tapeworm)Mal(tapeworm)} =_{\text{df}} \text{[H(tapeworm) is decreased and H(other tapeworm) is either decreased or unaffected]} \mid \xi\text{(other tapeworm)(tapeworm)}$$

See also Keymer *et al.* (1983), Zavras and Roberts (1984, 1985).

20. Under natural conditions, the life-span of adult *H. diminuta* is probably as long as the host that harbours it. Thus, any object, animate or inaminate, that leads to the demise of the host will also kill the subject animal unless, of course, it is possible for the tapeworm to survive the ingestion of one definitive host by another. Burt (1980) reports that, by artificial passage to successive hosts, an adult tapeworm has been kept alive for 14 years—and may well live longer.

It is also possible that an object lethal to an intermediate host may kill the cysticercoid. Nevertheless, there would seem to be a real possibility of the cysticercoid surviving and the dead intermediate host being eaten by a definitive host.

The informal defining equation for one particular member of the class of lethal objects as a modifier of the host is:

$$\text{(lethal object)Mod}^{-1}\text{(tapeworm)} =_{\text{df}} (\exists \text{ host}) \text{ such that [(host)Res(tapeworm)} \mid \sim\xi\text{(lethal object)(host) and } \sim\text{(host)Res(tapeworm)} \mid \xi\text{(lethal object)(host)]}$$

21. *H. diminuta*'s energy metabolism is usually anaerobic; this involves the breakdown of glucose and the fixation of CO_2. Nevertheless, aerobic energy metabolism is not precluded (Fioravanti and Saz 1980). Carbon dioxide is the gas most abundant in the intestinal lumen, reaching partial pressures as high as 680 mm Hg. Reports on the oxygen content of the rat gut differ, but, according to Mettrick (1980), it is probably about 40–50 mm Hg in places. the partial pressures of both gases are higher in parasitised than in unparasitised guts.

The informal defining equation for carbon dioxide as a resource is:

$$(CO_2)\text{Res(tapeworm)} =_{\text{df}} \text{H(tapeworm) is increased} \mid \xi(CO_2)\text{(tapeworm)}$$

The second term in the definition is not used because carbon dioxide is not an animal. [See also Ovington and Bryant (1981).]

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References

Alghali, S. T. O., and Grencis, R. K. (1986). Immunity to tapeworms: Intraspecific cross-protective interactions between *Hymenolepis citelli*, *Hymenolepis diminuta* and *Hymenolepis microstoma* in mice. *Parasitology* **92**, 665–74.

Arai, Hisao P. (1980). Migratory activity and related phenomena in *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 615–37. (Academic Press: London.)

Arme, C. (1976). Feeding. In 'Ecological Aspects of Parasitology'. (Ed. C. R. Kennedy.) pp. 75–97. (North-Holland: Amsterdam.)

Burt, M. D. B. (1980). Aspects of the life history and systematics of *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 1–57. (Academic Press: London.)

Cho, C. H. (1984). Study of the effects of insulin on the migration of *Hymenolepis diminuta* in rats. *J. Helminthol.* **58**, 291–4.

Cho, C. H. (1985). Pancreatic secretion is the migratory cue for *Hymenolepis diminuta* in rat small intestine. *J. Helminthol.* **59**, 319–22.

Cho, C. H., and Mettrick, D. F. (1982). Circadian variation in the distribution of *Hymenolepis diminuta* (Cestoda) and 5-hydroxytryptamine levels in the gastro-intestinal tract of the laboratory rat. *Parasitology* **84**, 431–41.

Coil, W. H. (1986). The early embryology of *Hymenolepis diminuta* (Cestoda). *Proc. Helminthol. Soc. Wash.* **53**, 38–47.

Elowni, E. E. (1983). *Hymenolepis diminuta* immunogenicity of the strobilate worm. *Z. Parasitenkd.* **69**, 501–6.

Fioravanti, Carmen F., and Saz, Howard J. (1980). Energy metabolism of adult *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 463–504. (Academic Press: London.)

Hall, A. (1983). Dietary protein and the growth of rats infected with the tapeworm *Hymenolepis diminuta*. *Br. J. Nutr.* **49**, 59–66.

Hopkins, C. A. (1980). Immunity and *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 551–614. (Academic Press: London.)

Hurd, H., and Arme, C. (1984). *Tenebrio-molitor* Coleoptera effect of metacestodes of *Hymenolepis diminuta* Cestoda on hemolymph amino-acids. *Parasitology* **89**, 245–52.

Insler, G. D., and Roberts, L. S. (1980). Developmental physiology of cestodes. XV. A system for testing possible crowding factors in vitro. *J. Exp. Zool.* **211**, 45–54.

Keymer, A. (1980). The influence of *Hymenolepis diminuta* on the survival and fecundity of the intermediate host, *Tribolum confusum*. *Parasitology* **81**, 405–21.

Keymer, A. (1981). Population dynamics of *Hymenolepis diminuta* in the intermediate host. *J. Anim. Ecol.* **50**, 941–50.

Keymer, A. (1982). The dynamics of infection of *Tribolium confusum* by *Hymenolepis diminuta*: the influence of exposure time and host density. *Parasitology* **84**, 157–66.

Keymer, A. E., and Anderson, R. M. (1979). The dynamics of infection of *Tribolium confusum* by *Hymenolepis diminuta*: the influence of infective-stage density and spatial distribution. *Parasitology* **79**, 195–207.

Keymer, A., Crompton, D. W. T., and Singhvi, A. (1983). Mannose and the crowding effect of *Hymenolepis diminuta* in rats. *Int. J. Parasitol.* **13**, 561–70.

Lee, C. G. L., and Ip, Y. K. (1986). Effect of host fasting and subsequent refeeding on the glycogan metabolizing enzymes in *Hymenolepis diminuta* (Cestoda). *Biol. Bull. (Woods Hole)* **171**, 417–25.

Lumsden, Richard Dick, and Specian, Robert (1980). The morphology, histology, and fine structure of the adult stage of the cyclophyllidean tapeworm *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 157–280. (Academic Press: London.)

Maema, M. (1986). Experimental infection of *Tribolium confusum* (Coleoptera) by *Hymenolepis diminuta* (Cestoda): host fecundity during infection. *Parasitology* **92**, 405–12.

McCaigue, M. D., and Halton, D. W. (1987). Immunological damage to *Hymenolepis diminuta* following a challenge infection in C57 mice. *Int. J. Parasitol.* **17**, 795–804.

Mettrick, D. F. (1980). The intestine as an environment for *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 281–356. (Academic Press: London.)

Mettrick, D. F., and Rahman, M. S. (1984). Effects of parasite strain and intermediate host species on carbohydrate intermediary metabolism in the rat tapeworm *Hymenolepis diminuta*. *Can. J. Zool.* **62**, 355–61.

Ovington, K. S., and Bryant, C. (1981). The role of carbon dioxide in the formation of end-products by *Hymenolepis diminuta*. *Int. J. Parasitol.* **11**, 221–8.

Pappas, P. W., and Leiby, D. A. (1986). Variation in the sizes of eggs and oncospheres and the numbers and distribution of testes in the tapeworm, *Hymenolepis diminuta*. *J. Parasitol.* **72**, 383–91.

Pappas, P. W., Narcisi, E. M., and Rentko, V. (1983). Alterations in brush border membrane proteins and membrane bound enzymes of the tapeworm *Hymenolepis diminuta* during development in the definitive host. *Mol. Biochem. Parasitol.* **8** 317–24.

Richards, K. S., and Arme, C. (1983). The rostellar tegumentary cytoplasm of the metacestode of *Hymenolepis diminuta* Cyclophyllidea Cestoda. *Parasitology* **86**, 83–8.

Richards, K. S., and Arme, C. (1984). Maturation of the scolex syncytium in the metacestode of *Hymenolepis diminuta* with special reference to microthrix formation. *Parasitology* **88**, 341–50.

Roberts, Larry S. (1980). Development of *Hymenolepis diminuta* in its definitive host. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 357–423. (Academic Press: London.)

Roberts, L. S., and Insler, G. D. (1982). Development physiology of cestodes. XVII. Some biological properties of putative 'crowding factors' in *Hymenolepis diminuta*. *J. Parasitol.* **68**, 263–9.

Ubelaker, John E. (1980). Structure and ultrastructure of the larvae and metacestodes of *Hymenolepis diminuta*. In 'Biology of the Tapeworm *Hymenolepis diminuta*'. (Ed. H. P. Arai.) pp. 59–156. (Academic Press: London.)

Uglem, G. L., and Just, J. J. (1983). Trypsin inhibition by tapeworms anti enzyme secretion of pH adjustment? *Science (Wash. D.C.)* **220**(4592), 79–81.

Wakelin, D. (1976). Host responses. In 'Ecological Aspects of Parasitology'. (Ed. C. R. Kennedy.) pp. 115–41. (North-Holland: Amsterdam.)

Zavras, E. T., and Roberts, L. S. (1984). Developmental physiology of cestodes: Characterization of putative crowding factors in *Hymenolepis diminuta*. *J. Parasitol.* **70**, 937–44.

Zavras, E. T., and Roberts, L. S. (1985). Developmental physiology of cestodes: Cyclic nucleotides and the identity of putative crowding factors in *Hymenolepis diminuta*. *J. Parasitol.* **71**, 96–105.

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Logical Synthesis of an Animal's Environment: Sponges to Non-human Primates.
IV.* The Common Octopus, *Octopus vulgaris*

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Abstract

The environment of the octopus, *O. vulgaris*, is classified according to the defining equations given in the first paper of this series. An envirogram displaying the objects within the environment in their correct place is presented. Notes on the envirogram include informal versions of the appropriate defining equations that are used for the classification.

Introduction

Unlike the sponge and tapeworm of parts II and III in this series, *Octopus vulgaris* has long been known to interact with humans, particularly in Mediterranean lands. Aristotle (1965) refers to it in some detail and pottery from Minoan and Mycenean civilisations is often decorated with naturalistic and stylised representations of the octopus (Cotterell 1979). The environment definition is unsuitable for the human environment (see part I), nevertheless it is convenient to classify people in the environment of an octopus by treating them like other animals in that the primitive term H applies; this has been done in the present study, so that 'fisherman' and 'pearl diver' appear on the envirogram in their appropriate places, thus pointing the way to future use of the classification in applied problem-solving. The ability of the octopus to squeeze through extremely small spaces and its tendency to lurk in crannies is well known to Mediterranean fishermen (see notes 23 and 24).

All cephalopods are active, fast-moving molluscs. They are marine and die quickly in fresh water. They have tentacles with suction discs, which are used for seizing prey. They have two gills, two kidneys and three hearts, two to pump de-oxygenated blood through the gills and the third to pump oxygenated blood through the body. The blood is blue; the colour is from the copper-containing compound that holds the oxygen. An adult octopus will sometimes deliberately leave the water, but not for long, nor does it travel great distances. However, it has been seen seizing a crab on rocks out of the water, and if kept cool can live up to 48 h out of water.

O. vulgaris lives mainly in tropical and subtropical waters. Details of the distribution of the animal are given in a review by Mangold (1983*b*) who provides a world map showing distribution. More recently, extra details of distribution off Brazil and Spain are given by Haimovici and Andriquetto (1986) and Sanchez (1986). The animal is a coastal species, living between the surface and a depth of 100–150 m (Mangold 1983*b*). The larvae may travel considerable distances while in the planktonic stage. Mileikovsky (1971) writes "Pelagic larvae of *Octopus vulgaris* drifted over distances ranging from 40–70 to 200–250 miles across the English Channel from North-Western France to South England".

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*Part III, *Aust. J. Zool.*, 1988, **36**, 1–14.

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Octopus eggs are between 1 and 3 mm long. Immediately upon hatching (after 4–5 weeks), the young octopus, now 2–3 mm in length, enters the planktonic stage. This stage lasts a maximum of 3 months, after which the animal will settle out of the planktonic stage at a length of about 1 cm. The growth of newly settled animals is rapid; on average, in 40 days at 25°C in the laboratory, they will increase their size by a factor of 10. After 2 years, the animal will weigh about 5 kg and apparently usually dies at this weight (see note 7). However, occasionally, individuals weighing 25 kg have been found (Wells 1978). The life span for *O. vulgaris* is given by Mangold (1983*a*) as 15–18 months. The largest specimens span 10 ft, with bodies 9 inches across. They are generally found in deeper water than are the smaller individuals. The maximum (reliable) depth record for *O. vulgaris* is about a quarter of a mile. Mangold (1983*a*) reports that animals of the same size in the laboratory and in the sea may be of different ages. Thus, determination of age in natural populations is difficult. For details of age estimates, see the review by Mangold (1983*b*). Adult individuals of *O. vulgaris* swim backwards, but a young animal, up to a week after hatching, will swim backwards or forwards with equal facility. An octopus can also swim by contracting the web-like basal membranes. They characteristically 'glide–crawl' in their usual habitat. An individual with a 2-ft span has been reported as moving at 8 mph. During migration, *O. vulgaris* travels quite significant distances at 4 mph. Each expelled jet drives the octopus 6–8 ft.

Among cephalopods, the common octopus has a particularly virulent poison (see note 3). The animal captures its prey by seizing it with suckered arms or enveloping the prey in its web.

O. vulgaris is colour-blind (Messenger 1977). There is no evidence that the animal can respond to sound (Young 1971).

The Envirogram

Three envirograms have been superimposed (Fig. 1); the subject animals are an adult individual of *O. vulgaris*, a planktonic larva, indicated by $\{\ldots\}$ on the diagram, and an egg, indicated by $\{\{\ldots\}\}$. This superimposition has been done to save space. Since nearly all available information is from studies of adults, the two envirograms for larva and egg are extremely sparse. The envirogram for an adult is, in turn, a concatenation of many individual envirograms for many adult individuals of *O. vulgaris* observed by various workers at different times and places.

Numbers on the envirogram refer to the notes that follow. They appear in no particular order. The various parts of the envirogram were constructed in an entirely haphazard order as the literature became available. The square brackets indicate a set of objects; thus '[food]' refers to a set of food objects, and '[macroscopic predators including larger octopodes]' to a set of such predators. The parentheses are used to indicate that there is some doubt about the classification, e.g. '(starfish)' classified as a predator seems to be a rather unusual case (see note 15).

Semiformal versions of the appropriate defining equations are given in the notes. The following symbols are used:

(i) $=_{\mathrm{df}}$: 'is equal by definition to', or, more strictly, the form '$x =_{\mathrm{df}} y$' means 'x is to be interchangeable with y'.

(ii) $\exists$: the existential quantifier of formal logic. Read '$\exists$ fish' as 'there exists a fish' or 'there is at least one fish', or, more informally, 'we can find a fish'. In this paper, expressions such as '$\exists$ fish' are always followed by the words 'such that'.

(iii) $|$: '$x \mid y$' means 'x occurs (will occur), assuming y'. This is the symbol used for conditional events (and conditional probabilities). The expression '$A \mid B$' may read 'event A occurs, given that event B occurs'; it refers to 'event A under the conditions that B', or 'event A under the hypothesis that B'. Thus, an object that is reported as a resource for *O. vulgaris* in the Mediterranean, for example, would also be classified as a resource for *O. vulgaris* off the coast of Brazil. In ordinary English it is a *potential* resource. Similarly mates, predators, malentities and modifiers are all *potential* mates, etc.

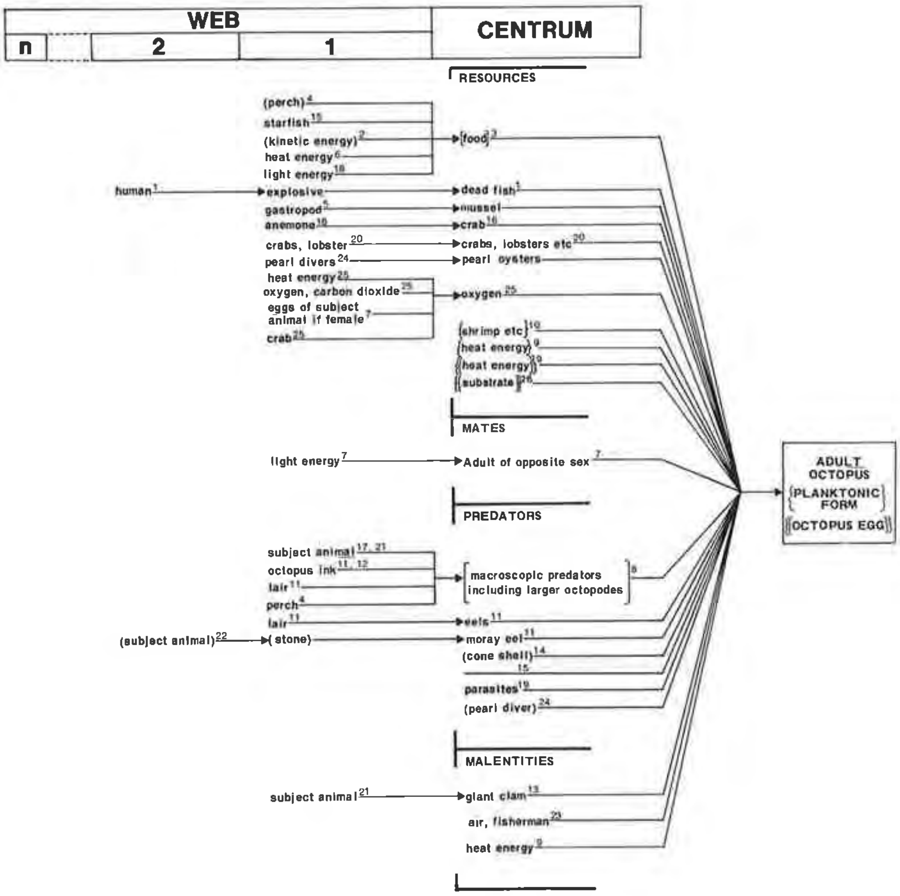

Fig. 1. Envirogram for the octopus.

Notes on the Envirogram

1. Wells (1978) reports the octopus feeding on fish killed by an explosion at sea. In this case, the explosive material acts as a modifier of a food resource and the human acts as a modifier of the explosive, and is thus a second-order modifier in the environment of the subject octopus. The informal versions of the defining equations are:

$$\text{(dead fish)Res(octopus)} =_{\text{df}} \text{H(octopus) is increased} \mid \xi\text{(dead fish)(octopus)}$$

Since a dead fish is an inanimate object, the second part of the definition is not used.

$$\text{(explosive)Mod}^{+1}\text{(octopus)} =_{\text{df}} (\exists \text{ dead fish) such that [(dead fish)Res(octopus)} \mid \xi\text{(explosive)(dead fish) and } \sim\text{(dead fish)Res(octopus)} \mid \xi\text{(explosive)(dead fish)]}$$

$$\text{(human)Mod}^{+2}\text{(octopus)} =_{\text{df}} (\exists \text{ explosive) such that [(explosive)Mod}^{1}\text{(octopus)} \mid \xi\text{(human)(explosive) and } \sim\text{(explosive)Mod}^{1}\text{(octopus)} \mid \sim \xi\text{(human)(explosive)]}$$

2. According to Wells (1978), the animal nearly always attacks live prey, and motionless potential food is usually ignored unless touched. Visually detected movement in prey may be an important factor in triggering a response in the animal. Nevertheless, blind specimens feeding and behaving normally have been reported in aquaria. Also, many prey that are eaten, even in the laboratory, do not move (e.g. bivalves) (R. F. Ambrose, personal communication) (see note 3 for more details of food).

Kinetic energy, abbreviated k.e., is tentatively classified as a modifier of the class [food]. The informal defining equation for some particular food object is:

$$\begin{aligned}&(\text{k.e.})\text{Mod}^{+1}(\text{octopus}) =_{\text{df}} (\exists\,\text{food}) \text{ such that } [(\text{food})\text{Res}(\text{octopus}) \mid \xi(\text{k.e.})(\text{food})\\ &\text{and } \sim(\text{food})\text{Res}(\text{octopus}) \mid \sim\xi(\text{k.e.})(\text{food})]\end{aligned}$$

3. In the laboratory, an octopus will eat crabs (see also notes 16, 20), lobsters, bivalves, gastropods, and fish if it can corner them. It will also eat other members of the same species if not well matched in size or pre-occupied with mating. Shells and exoskeletons scattered around known lairs indicate that the octopus' diet in the wild is similar. However, *O. vulgaris* has been observed to ignore live fish in the sea, presumably because they cannot be cornered. Crabs appear to be the favourite food, especially in the Channel Islands. R. F. Ambrose (personal communication) remarks, "Crabs seem to be the favourite food everywhere. Octopuses often hunt 'speculatively' by feeling under rocks and in cracks; all the hunting I have observed in the field has been of this sort". Mangold (1983*a*) writes, "Given the choice of live crustaceans (mainly crabs), shelled molluscs or fish, *O. vulgaris* . . . from the Banyuls area invariably take the crabs and ignore other food items at all growth stages. If no crabs are offered, . . . (the octopus) . . . will accept molluscs and/or fish, but only after several days or weeks of starvation. Bivalves are preferred over gastropods". Mangold then quotes similar observations by other authors working in the Catalonian Sea, the northern coast of the western Mediterranean, and the north-west African coast. Nixon and Budelman (1984) report that the polychaete scaleworm (*Hermione hystrix*) is sometimes eaten by *O. vulgaris*. In a 1-year study in the Catalonian Mediterranean, Guerra (1978) found that 80% of the food intake was Crustacea, 12% fish, and 8% cephlopods. Further details are provided by Mangold (1983*b*).

The adult *O. vulgaris* is probably an opportunistic feeder, but is most likely to forage away from its lair between dusk and dawn. It seems likely that at least some of the prey captured in these often quite lengthy excursions may be eaten away from the lair.

In captivity, the normal food-gathering method is a visually directed, jet-propelled pounce. Observations of the octopus feeding in the wild are rare and almost always involve an unknown interference effect by the observer. Nevertheless, it is generally assumed that gathering behaviour is similar in the wild.

The octopus will hold the prey, live, in its web, retreat to its lair, then poison the prey by secretions from its salivary glands. There is circumstantial evidence that the animal uses some form of external digestion before internal digestion. Wells (1978) records that *O. vulgaris* saliva contains many pharmacologically active substances, including dopamine, tyramine, octopamine, 5-hydroxytryptamine, histamine, acetylcholine and taurine. 'Cephalotoxin' appears to be a glycoprotein. Ghiretti (1960) describes a detailed analysis of *O. vulgaris* saliva: "The saliva . . . (injected into a crab) . . . produced first a phase of over-excitability followed by a quiet phase and then paralysis".

If there is any disturbance in the vicinity, the octopus will raise its head from the lair; sometimes, the animal alternately raises and lowers its head, suggesting that it may determine distance by parallax.

On seeing prey, the octopus characteristically changes colour to reddish brown. Where several prey are available, the animal will go on collecting, for example crabs—even if this results in earlier captures escaping from its web. Finally, the octopus will poison all of the crabs before settling down to eat them singly.

In preying upon gastropods, the octopus is reported by Wodinsky (1978) in the Caribbean to bore a hole in the shell, inject toxin, then pull out and consume the affected snail. *O. vulgaris* has a typical molluscan radula and a parrot-like beak of tanned protein. It is widely reported as using the radula to bore holes in shellfish, after which substances from the salivary gland are used to kill the shellfish and loosen muscle attachments. However, Wodinsky reports that a brooding female will not bore a hole in a gastropod shell, but instead "expend a great amount of energy pulling the living snail out by force—she then scarcely eats the snail". The feeding behaviour of brooding, reproducing females undergoes other substantial changes; intake decreases by:

(i) 70% of normal intake per meal,
(ii) 65% of normal number of meals.

According to Hamada (1974), in Japan, the octopus never bores holes in a molluscan shell. It shows greater appetite for bivalves than snails. "Some gastropods, that have a calcareous operculum or that withdraw too deeply into their shells to be reached by the octopus' mouth, were not eaten, although they were seized by the octopus and carried into the nest". The scars left on the shells clearly indicate that the octopus knew the position most easily accessible for biting. Any prey that was too large to be bitten by the octopus' beak was never eaten. No nudibranches or echinoderms were eaten. Pilson and Taylor (1961), working in the laboratory, report observations of *Octopus bimaculides* and *O. bimaculatus* drilling holes in the shells of molluscan prey. Arnold and Arnold (1969), also working in the laboratory, found that *O. vulgaris*, when offered the conch *Strombus raninus*, quickly grasped it with one or more arms, checked for occupancy by inserting an arm tip into the aperture, and passed the shell under the web to the mouth. The shell was rasped repeatedly with the radula, repositioned, and rasped again. It was penetrated at an approximate maximal rate of $1{\cdot}25\ \mathrm{mm\ h^{-1}}$. There was a marked preference for individual animals to bore in a particular sector of the spire.

The informal defining equation for a particular conch as a food resource of the subject octopus is:

$$\text{(conch)Res(octopus)} =_{\mathrm{df}} \text{H(octopus) is increased} \mid \xi\text{(conch)(octopus)}$$

4. Kayes (1974) reports that, around Malta, the perch *Serranus scriba* often follows the octopus on its foraging expeditions. The fish is conspicuous where the octopus is not, thus giving away the latter's position to potential prey (which can then seek shelter) and to potential predators. In the light of Ambrose's remarks (personal communication below), the perch is only tentatively classified as a modifier of food.

Ambrose (personal communication) remarks, "The perch following an octopus probably benefits by feeding on small organisms that are 'flushed' as the octopus moves along. Octopus prey organisms probably do not have sufficiently acute vision to be warned by *Serranus*". If these statements are true, then the octopus is acting as a first-order modifier of food resources in the environment of the perch. The perch, however, is acting mainly as a modifier of predators of the octopus.

The informal defining equation for the perch as a positive first-order modifier of some particular predator of the subject octopus is:

$$\begin{aligned}&\text{(perch)Mod}^{+1}\text{(octopus)} =_{\mathrm{df}} (\exists\ \text{predator) such that [(predator)Pred(octopus)} \mid \\ &\xi\text{(perch)(octopus) and } \sim\text{(predator)Pred(octopus)} \mid \sim\xi\text{(perch)(octopus)]}\end{aligned}$$

5. The predatory gastropod *Ocenatra* sp. eats the mussels *Mytilus* spp., also food for *O. vulgaris*. Both the gastropod and the octopus drill through the shells of the mussels with their raduli (Simpson *et al.* 1957).

The informal defining equations are:

$$\text{(mussel)Res(octopus)} =_{\mathrm{df}} \text{H(octopus) is increased} \mid \xi\text{(mussel)(octopus)}$$

(gastropod)Mod^{-1}(octopus) $=_{\mathrm{df}}$ ($\exists$ mussel) such that [(mussel)Res(octopus) $|$
$\sim\xi$(gastropod)(mussel) and $\sim$(mussel)Res(octopus) $|$ ξ(gastropod)(mussel)]

6. In Naples harbour, a natural habitat, the water temperature varies from 25°C in summer (July, August) to 15°C or less in mid-winter. All individuals of *O. vulgaris* eat less in winter and some even lose weight. Starvation causes emaciation but not debilitation; the animal will remain alert after losing 40% of its body weight.

Wells (1978) suggests that time for digestion seems to depend only on temperature. Data are far from conclusive, but the suggestion is consistent with information from other poikilotherms. The size of the meal is not important, but Wells (1978) remarks that the animal is evidently sensitive to the presence of food in the crop. After feeding, there is an increase in the tendency to attack objects seen, which rises to a maximum after about half an hour and then declines progressively. The rise and fall correlate with the weight of the crop over the same period.

The informal defining equation for some particular measured quantity of heat energy acting as a positive first-order modifier of a particular food object is:

(heat)Mod^{+1}(octopus) $=_{\mathrm{df}}$ ($\exists$ food) such that [(food)Res(octopus) $|$
ξ(heat)(octopus) and $\sim$(food)Res(octopus) $|$ $\sim\xi$(heat)(octopus)]

7. Although not reflected in the catch, it is believed that the sex ratio for *O. vulgaris* is 1 : 1 (Wells 1978; Mangold 1983*b*).

Sperm are packed into spermatophores and are ejected after copulation into the mantle cavity of the female. Mating often occurs when the females are immature. Only females ready to lay eggs consistently fend off the males. There is little evidence for specifically sexual display, but it is likely that either subtle visual or chemotactile cues are used in recognising the opposite sex. Packard (1961) reports sucker display in encounters between the sexes. [See also Mangold (1983*b*).]

Females lay eggs in strings and attach them to the roofs of their lairs; if there is no roof, as in an aquarium, they attach them to the sides. They lay up to 500 000 eggs in strings of many hundreds; this may take a week or more. Average egg size is 1–3 mm. The female then broods the eggs for 4–6 weeks (at 22–23°C). During this time, she continually directs jets of water over the eggs. She rarely leaves them, seldom feeds, and becomes emaciated (see note 3). Respiration increases during this period, and intruding rubbish and animals (including those normally eaten) are pushed away to arms' length.

Shortly after the eggs hatch, the female dies. This seems to be universal for the animals; males grow at the same rate as females, and it appears that most males also die by the end of their second year. Mangold (1983*b*) reports that a female is unlikely to spawn a second time.

Hatanaka (1979) reports that, off the north-west coast of Africa, males larger than 50 cm in total length carry spermatophores in all seasons. Most females larger than 70 cm in total length are mature in the spawning seasons, while those less than 50 cm are usually immature. "Several parameters are thought to influence the process of sexual maturation in cephalopods, namely light, temperature and food availability at different stages of the life cycle" (Mangold 1983*a*, 1983*b*).

Informal defining equations are given for a mate in the case that the subject octopus is female, and for a particular quantity of light energy acting as a modifier of the mate:

(male octopus)Mat(subject female) $=_{\mathrm{df}}$ an offspring of both individuals will be produced with probability greater than zero $|$ ξ(male octopus)(subject female)

(light)Mod^{+1}(subject female) $=_{\mathrm{df}}$ ($\exists$ male octopus) such that
[(male octopus)Mat(subject female) $|$ ξ(light)(subject female) and
$\sim$(male octopus)Mat(subject female) $|$ $\sim\xi$(light)(subject female)]

Full details of mating behaviour are given by Mangold (1983*b*) and Guerra (1975).

8. In the laboratory, when a new octopus is introduced, a resident male will immediately flush 'dark' and act aggressively. If the intruder is a male, a fight will ensue and the smaller will generally be killed and eaten. If the intruder is a female, she will generally submit and copulation (see note 7) will follow (Wells 1978; Mangold 1983*b*). It is not known what occurs when two females are thrust together.

In the informal defining equations below, a large male intruder is assumed to act as a predator of a smaller resident male; the latter, which is taken to be the subject animal, acts as a negative modifier in its own environment by flushing 'dark' and acting aggressively.

$$\text{(intruder)Pred(octopus)} =_{\text{df}} \text{H(octopus) is decreased and H(intruder) is increased} \mid \xi\text{(intruder)(octopus)}$$

$$\text{(octopus)Mod}^{-1}\text{(octopus)} =_{\text{df}} (\exists\ \text{intruder}) \text{ such that } [\text{(intruder)Pred(octopus)} \mid {\sim}\xi\text{(octopus)(octopus) and } {\sim}\text{(intruder)Pred(octopus)} \mid \xi\text{(octopus)(octopus)}]$$

9. The development of the eggs takes about 28 days at 22°C (Wells 1978). The planktonic stage may last up to 3 months in the cold waters of the English Channel (i.e. at the northern limit of the range of *O. vulgaris*), but is usually much shorter. Wells reports Japanese work in which the larvae were raised at 25°C in the laboratory and settled 33–40 days after hatching.

The informal defining equation is for a specific quantity of heat energy corresponding to a temperature of 25°C acting as a resource for the subject larva.

$$\text{(heat)Res(larva)} =_{\text{df}} \text{H(larva) is increased} \mid \xi\text{(heat)(larva)}$$

10. During the 'planktonic stage'—after hatching but before settling on the substrate as an adult—the young octopus feeds on plankton. In the laboratory, larvae have been raised on live shrimp larvae, *Palaemon serrifer*, fragments of crab meat and, finally, as the larvae settle to the bottom, whole small crabs.

The informal defining equation is for a particular shrimp larva as a food resource for the subject larva.

$$\text{(shrimp)Res(larva)} =_{\text{df}} [\text{H(larva) is increased and H(shrimp) is decreased}] \mid \xi\text{(shrimp)(larva)}$$

11. Large eels, including the common moray, *Gymnothorax mordax*, the giant moray, *Enchelynassa* spp., and conger eels, *Conger* spp., are the most important predators of *O. vulgaris*.

Whereas both the sight of a common moray and its 'smell' will alert an octopus, alarm can only be engendered by a combination of both stimuli. The ejection of ink, generally black, is the only means of defence. If necessary, several successive ejections can be made—up to six have been observed. Moray eels have poor eyesight, and a trace of octopus ink in the water is sufficient to send them into a hunting frenzy. However, high concentrations of ink will paralyse the olfactory sense of the eels; this has been observed in aquaria but whether it occurs even partially in a natural habitat is unknown. Although high concentrations of ink in enclosed waters are reported by Lane (1960) to be fatal to some species of octopus, there seems to be some doubt about this (R. F. Ambrose, personal communication).

Eels will swallow a small octopus whole. A larger octopus will often fasten its legs around the eel's head, but, by gymnastic contortions, the eel usually succeeds in eating the octopus. A very large octopus is often eaten arm by arm—the eel grasping and twisting them off successively. During the short pauses while each arm is consumed, the octopus may escape (see note 21).

The lair of the octopus enhances its chance of surviving in two ways. Firstly, the possibility of detection is reduced. Secondly, the lair affords a certain amount of protection and some possibility, therefore, of escape from an attacking eel. Lairs are usually well separated. The octopus sometimes moves medium-sized rocks into an ‘extension’ of the lair if the natural terrain does not provide enough protection. However, Bierens De Haan (1929) shows that the octopus will as readily collect transparent as opaque objects to fashion a lair. The octopus also shows no preference between the ‘hide’ give by two parallel sheets of glass and two similarly placed pieces of slat. He concludes that, in building a lair, the octopus is not seeking to hide itself. [Nevertheless, Richard Aronson has found that *O. briareus* does not like transparent homes as much as opaque ones (R. F. Ambrose, personal communication).]

The informal defining equations for a particular eel as a predator, and the lair of the subject animal as a negative first-order modifier are:

$$\begin{aligned}&(\text{eel})\text{Pred}(\text{octopus}) =_{\text{df}} [\text{H}(\text{octopus}) \text{ is decreased and}\\ &\text{H}(\text{eel}) \text{ is increased}] \mid \xi(\text{eel})(\text{octopus})\end{aligned}$$

$$\begin{aligned}&(\text{lair})\text{Mod}^{-1}(\text{octopus}) =_{\text{df}} (\exists \text{ eel}) \text{ such that } [(\text{eel})\text{Pred}(\text{octopus}) \mid\\ &\sim \xi(\text{lair})(\text{octopus}) \text{ and } \sim(\text{eel})\text{Pred}(\text{octopus}) \mid \xi(\text{lair})(\text{octopus})]\end{aligned}$$

12. In addition to its anaesthetising uses (see note 11), octopus ink has other defensive effects. Firstly, the ink can provide a screen behind which the octopus will change colour and dart swiftly away. Secondly, the ink can produce the effect of decoy; particularly with a small octopus, the ink may remain in a concentrated blob about the size of the animal’s body while it changes colour and escapes.

The informal defining equation for the subject animal’s ink as a negative first-order modifier of a particular eel as a predator is:

$$\begin{aligned}&(\text{ink})\text{Mod}^{-1}(\text{octopus}) =_{\text{df}} (\exists \text{ eel}) \text{ such that } [(\text{eel})\text{Pred}(\text{octopus}) \mid\\ &\sim \xi(\text{ink})(\text{octopus}) \text{ and } \sim(\text{eel})\text{Pred}(\text{octopus}) \mid \xi(\text{ink})(\text{octopus})]\end{aligned}$$

13. In northern Australia, an octopus has been observed with one arm caught in a giant clam, probably *Tridacna* sp. The octopus was later seen swimming away with only seven arms (see note 21) (Lane 1960).

The clam, since it does not benefit from the encounter, is classified as a malentity and the subject octopus as a modifier, since its action in losing an arm modifies the effect of the clam’s assault. The informal defining equations are:

$$\begin{aligned}&(\text{clam})\text{Mal}(\text{octopus}) =_{\text{df}} \text{H}(\text{octopus}) \text{ is decreased and}\\ &\text{H}(\text{clam}) \text{ is unchanged} \mid \xi(\text{clam})(\text{octopus})\end{aligned}$$

$$\begin{aligned}&(\text{octopus})\text{Mod}^{-1}(\text{octopus}) =_{\text{df}} (\exists \text{ clam}) \text{ such that } [(\text{clam})\text{Mal}(\text{octopus}) \mid\\ &\sim \xi(\text{octopus})(\text{octopus}) \text{ and } \sim(\text{clam})\text{Mal}(\text{octopus}) \mid \xi(\text{octopus})(\text{octopus})]\end{aligned}$$

14. Lane (1960) records, from northern Australia, a reported encounter in a collecting bucket between a cone shell, *Conus textile*, and *O. vulgaris*. The gastropod, which is poisonous, injects its venom through a radula tooth, which is modified to form a hypodermic needle. The octopus put an arm into the shell, but withdrew it after 20 s, became violently agitated and shed the arm, which was broken off near the body. The octopus died the following night. It was suggested that similar encounters would be frequent in the natural habitat. *Conus textile* is classified tentatively as a predator, not a malentity, because it characteristically hunts its prey this way.

The informal defining equation for *Conus* as a predator is:

$$\begin{aligned}&(\textit{Conus})\text{Pred}(\text{octopus}) =_{\text{df}} [\text{H}(\text{octopus}) \text{ is decreased and } \text{H}(\textit{Conus}) \text{ is increased}] \mid\\ &\xi(\textit{Conus})(\text{octopus})\end{aligned}$$

15. Many echinoderms have dietary overlap with the octopus, particularly the starfish (Asteroidae), which consume many shellfish.

Lane (1960) reports two unusual cases in which an octopus was paralysed by starfish. In the case in which the brittle star, *Ophicocoma echinata*, was involved, the octopus died. The effect seemed to be well known to local fishermen.

I have tentatively classified starfish as a predator, since the octopus would probably be consumed if it were paralysed after an attack in the wild. However, in its natural habitat, it seems likely that an octopus would be able to avoid debilitating contacts.

Ambrose (personal communication) suggests that "In one of Lane's cases, there was probably no toxin involved . . . In the case of the brittle star, the brittle star may not have been capable of eating the octopus (most of the species of which I am aware could not). I consider starfish to be extremely unlikely predators of octopuses, based on my experiences in the Mediterranean, Caribbean and Northern Pacific".

The informal defining equation for a starfish as a negative first-order modifier of some specific object of food (a resource) is:

$$\begin{aligned}&(\text{starfish})\text{Mod}^{-1}(\text{octopus}) =_{\text{df}} (\exists\ \text{food}) \text{ such that } [(\text{food})\text{Res}(\text{octopus}) \mid \\ &\sim \xi(\text{starfish})(\text{food}) \text{ and } \sim(\text{food})\text{Res}(\text{octopus}) \mid \xi(\text{starfish})(\text{food})]\end{aligned}$$

16. Grzimek (1974) describes the relationship between the pagurid *Eupagurus prideauxi* and the anemone *Adamsia palliata*, in which the anemone provides protection for the crab from predation, in particular by a fish or octopus. Ross and von Boletzky (1979) report an association between the pagurid *Dardanus arrosor* and the anemone *Calliactis parasitica*; they comment that, after a long confinement in an aquarium not containing an octopus, the crab "loses its activity towards its symbiotic actinium *C. parasitica*". However, in the presence of *O. vulgaris* (and other cephalopods), the activity is restored. Although visual cues are insufficient, effluent from a tank containing an octopus will revive the activity. Ross (1971) reports that, when single crabs of species *D. arrosor* or *D. callidus* with and without their commensal anemone *C. parasitica* were exposed to *O. vulgaris*, "In every case, the octopus attacked, usually at once. All *Dardanus* without *Calliactis* were eventually ingested. None of those with *Calliactis* were even taken". Similar trials with *Pagurus prideauxi* and *Adamsi palliata* showed that this pagurid was not protected by its anemone.

The informal defining equations for a particular specimen of *Dardanus* as food, and a particular specimen of *Calliactis* as a negative first-order modifier are:

$$\begin{aligned}&(\textit{Dardanus})\text{Res}(\text{octopus}) =_{\text{df}} [\text{H}(\text{octopus}) \text{ is increased and} \\ &\text{H}(\textit{Dardanus}) \text{ is decreased}] \mid \xi(\textit{Dardanus})(\text{octopus})\end{aligned}$$

$$\begin{aligned}&(\textit{Calliactis})\text{Mod}^{-1}(\text{octopus}) =_{\text{df}} (\exists\ \textit{Dardanus}) \text{ such that} \\ &[(\textit{Dardanus})\text{Res}(\text{octopus}) \mid \sim \xi(\textit{Calliactis})(\textit{Dardanus}) \text{ and} \\ &\sim(\textit{Dardanus})\text{Res}(\text{octopus}) \mid \xi(\textit{Calliactis})(\textit{Dardanus})]\end{aligned}$$

17. The octopus is able to change its colour to match its surroundings, thus assisting it to escape the attention of predators. Packard and Sanders (1969) give a general account, with good photographs, of the various body patterns of the animal in the Bay of Naples. The same authors (1971) also provide a more detailed account of colour changes, with sketches and photographs describing defensive and attack modes.

The informal defining equation for the subject animal acting as a negative first-order modifier in its own environment by changing its colour pattern in the presence of an eel (classified as a predator) is:

$$\begin{aligned}&(\text{octopus})\text{Mod}^{-1}(\text{octopus}) =_{\text{df}} (\exists\ \text{eel}) \text{ such that } [(\text{eel})\text{Pred}(\text{octopus}) \mid \\ &\sim \xi(\text{octopus})(\text{octopus}) \text{ and } \sim(\text{eel})\text{Pred}(\text{octopus}) \mid \xi(\text{octopus})(\text{octopus})]\end{aligned}$$

18. Kayes (1974) made hourly inspections, day and night, for 11 days and found that *O. vulgaris* hunts virtually throughout the night, with only brief excursions away from its lair during the day.

The informal defining equation for a specific measured quantity of light energy, abbreviated l.e., acting as a negative first-order modifier on a particular crab classified as a resource is:

$$(\text{l.e.})\text{Mod}^{-1}(\text{octopus}) =_{\text{df}} (\exists\ \text{crab}) \text{ such that } [(\text{crab})\text{Res}(\text{octopus}) \mid \sim \xi(\text{l.e.})(\text{octopus}) \text{ and } \sim(\text{crab})\text{Res}(\text{octopus}) \mid \xi(\text{l.e.})(\text{octopus})]$$

19. Hochberg (1983) reviews the literature on the parasites of cephalopods. For *O. vulgaris*, the following are recorded:

(i) an iridovirus has been associated with lesions on the arms and mantle;
(ii) filamentous fungal thalli, possibly *Aspergillus*, penetrate throughout the renal appendages and cause considerable damage to the host tissue (rare);
(iii) two species of the sporozoan *Aggregata* have been identified;
(iv) the vermiform ciliate *Chromidina coronata* attaches to the appendages within the renal or renal-pancreatic coela;
(v) *O. vulgaris* possibly functions merely as a paratenic host to the trypanorhynchs (cestodes) *Nybelina lingualis*, *Tetrabothriorhynchus octopodiae* and *Tetrarhynchus megabothrium*;
(vi) the copepod *Octopicola superbus* has been found in *O. vulgaris*, but no damage to the octopus has been reported.

The informal defining equation for an iridovirus as a predator is:

$$(\text{iridovirus})\text{Pred}(\text{octopus}) =_{\text{df}} [\text{H(octopus) is decreased and H(iridovirus) is increased}] \mid \xi(\text{iridovirus})(\text{octopus})$$

20. Crabs are able to shed their claws and sometimes escape this way, thus acting as first-order modifiers of themselves regarded as a resource for the octopus.

Lobsters (*Homarus* spp., Weber 1975) and fiddler crabs (Portunidae) both resist (fight back) attempted octopus predation. This is atypical, most crabs being strangely quiescent. Crabs that are eaten include *Carcinus* spp. The octopus also eats abalone (*Haliotis* spp.), clam (*Chione* spp.), scallop (*Pecten circularis requisulcatus*), and the little-neck clam (*Protothaca jedoensis*).

During the winter of 1899, a plague of *O. vulgaris* occurred in the English Channel and along the French coast. Many fishermen were forced to find other work as oysters, abalone and many varieties of fish became very scarce, undoubtedly due to predation by the octopus. Estimates were that there was an 18% fall in the number of lobsters and a 32% fall in the number of crabs compared with the previous year: 1922 and 1950–51 were also plague years, but not to the same extent (Lane 1960).

According to Ambrose and Nelson (1983), from studies in the Mediterranean off the coast of France, *O. vulgaris* consumes at least 22 molluscan and several crab species. Molluscs comprised an estimated 80% of the animals' diet. The most frequently encountered species in the field, the bivalves *Venus verracosa* and *Pitaria chione*, and the abalone *Haliotis tuberculata*, were also estimated to be most frequent in the diet of *O. vulgaris*. The distribution of octopus drill holes on the two bivalve species was non-random; in the abalone, the distribution was indistinguishable from random (see also note 3).

The informal defining equation for a particular crab as a resource is:

$$(\text{crab})\text{Res}(\text{octopus}) =_{\text{df}} [\text{H(octopus) is increased and H(crab) is decreased}] \mid \xi(\text{crab})(\text{octopus})$$

21. *O. vulgaris* can apparently shed a limb at will, and can suffer severe injuries and mutilation and yet survive. Regeneration of many parts is possible. In one instance, one-third of an arm was broken off and was observed to be fully regenerated and functional, although thinner, after 6 weeks (Lane 1960).

The informal defining equation for the subject octopus acting as a negative first-order modifer, in its own environment, of an eel as a predator by shedding a limb is:

$$\begin{gathered}\text{(octopus)Mod}^{-1}\text{(octopus)} =_{\text{df}} (\exists \text{ eel}) \text{ such that } [\text{(eel)Pred(octopus)} \mid \\ \sim \xi\text{(octopus)(octopus) and } \sim\text{(eel)Pred(octopus)} \mid \xi\text{(octopus)(octopus)}]\end{gathered}$$

22. Lane (1960) reports having seen a film of an individual *O. vulgaris* holding a stone as a shield against the attacks of a moray eel. The stone, modified by the subject animal, has been tentatively included on the envirogram. The classification is tentative, since other workers have expressed doubts that *O. vulgaris* would, in fact, behave in such a way.

The informal defining equations are:

$$\begin{gathered}\text{(eel)Pred(octopus)} =_{\text{df}} [\text{H(octopus) is decreased and} \\ \text{H(eel) is increased} \mid \xi\text{(eel)(octopus)}\end{gathered}$$

$$\begin{gathered}\text{(stone)Mod}^{-1}\text{(octopus)} =_{\text{df}} (\exists \text{ eel}) \text{ such that } [\text{(eel)Pred(octopus)} \mid \\ \sim \xi\text{(stone)(octopus) and } \sim\text{(eel)Pred(octopus)} \mid \xi\text{(stone)(octopus)}]\end{gathered}$$

$$\begin{gathered}\text{(octopus)Mod}^{+2}\text{(octopus)} =_{\text{df}} (\exists \text{ stone}) \text{ such that } [\text{(stone)Mod}^{1}\text{(octopus)} \mid \\ \xi\text{(octopus)(stone) and } \sim\text{(stone)Mod}^{1}\text{(octopus)} \mid \sim \xi\text{(octopus)(stone)}]\end{gathered}$$

23. The habit of the octopus of lurking in crannies often leads to capture by fishermen using kegs, pots, etc, or to death from exposure to the air, since the animal tends not to abandon the pot even when it is being raised. In this case, the fisherman (or a measured quantity of air) kills the animal accidentally and is thus classified as a malentity (see also note 24).

The informal defining equation for a specific measured quantity of air is:

$$\text{(air)Mal(octopus)} =_{\text{df}} \text{H(octopus) is decreased} \mid \xi\text{(air)(octopus)}$$

24. The animals are often killed by pearl divers because they open pearl oysters. Pearl divers are classified in two ways in the environment of the octopus.

(i) The diver is a first-order modifier of the resource 'pearl oyster'.

(ii) Tentatively, the pearl diver is either a malentity or a predator of the octopus. It may be argued that many pearl divers do, in fact, eat the animal after killing it in the course of their duties. In this case, it would seem natural to classify the human as a predator.

The informal defining equation for the diver as a first-order modifier of the resource 'pearl oyster' is:

$$\begin{gathered}\text{(diver)Mod}^{-1}\text{(octopus)} =_{\text{df}} (\exists \text{ pearl oyster}) \text{ such that} \\ [\text{(pearl oyster)Res(octopus)} \mid \sim \xi\text{(diver)(pearl oyster) and} \\ \sim\text{(pearl oyster)Res(octopus)} \mid \xi\text{(diver)(pearl oyster)}]\end{gathered}$$

25. Experiments on oxygen uptake at 15°C showed that the ventilation rate is increased by lack of oxygen or by excess carbon dioxide: 51 times per minute at 2·5 kg O_2 pressure and 12 times per minute at 8 kg O_2 pressure. Oxygen consumption increases with temperature (Wells 1978). Details of metabolic costs in *O. vulgaris* are given in Mangold (1983*a*): "The capture, ingestion, digestion and assimilation of a prey (crab) causes an increase in oxygen uptake that lasts about 6 hours and peaks during the 1st to 3rd hour after capture . . . There is also a long-term effect of feeding. Feeding a starved octopus in the 300 to 500 g size range a 20 g crab each day results in a progressive rise in oxygen consumption over the first 2 to 4 days following the first meal. Small animals do treble their oxygen uptake, larger ones double it . . . The size of the meal greatly affects oxygen consumption."

The informal defining equations for a particular measured quantity of oxygen as a resource, which is modified by a particular measured quantity of heat energy, are:

$$\text{(oxygen)Res(octopus)} =_{\text{df}} \text{H(octopus) is increased} \mid \xi\text{(oxygen)(octopus)}$$

$$\begin{gathered}\text{(heat)Mod}^{+1}\text{(octopus)} =_{\text{df}} (\exists\ \text{oxygen}) \text{ such that } [\text{(octopus)Res(octopus)} \mid \\ \xi\text{(heat)(octopus) and } \sim\text{(oxygen)Res(octopus)} \mid \sim\xi\text{(heat)(octopus)}]\end{gathered}$$

[See also Wells *et al.* (1983).]

26. Eggs are always attached to a substrate. "On sandy or muddy bottom, eggs are laid in empty mollusc shells or in man-made objects such as cans, tins, bottles, tyres, boots and amphorae. In the aquarium, the egg strings are stuck to the wall of the tank if no suitable home is provided" (Mangold 1983*b*). Thus, a substrate is a necessity for an increase in H(egg) and therefore is classified as a resource:

$$\text{(substrate)Res(egg)} =_{\text{df}} \text{H(egg) is increased} \mid \xi\text{(substrate)(egg)}$$

See also note 7.

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References

Ambrose, R. F., and Nelson, B. V. (1983). Predation by *Octopus vulgaris* in the Mediterranean. *Mar. Ecol. (Publ. Stn. Zool. Napoli I)* **4**, 251–61.

Aristotle (1965). 'Historia Animalium, Books IV, V.' (Translated by A. L. Peck.) (William Heineman: London.)

Arnold, J. M., and Arnold, K. O. (1969). Some aspects of hole-boring predation by *Octopus vulgaris*. *Am. Zool.* **9**, 991–6.

Bierens De Haan, J. A. (1929). 'Animal Psychology for Biologists.' (University Press: London.)

Cotterell, A. (1970). 'The Minoan World.' (Michael Joseph Ltd: London.)

Ghireti (1960). Toxicity of octopus saliva against crustacea. *Ann. N.Y. Acad. Sci.* **90**, 726–41.

Grzimek, B. (Ed.) (1974). 'Grzimek's Animal Life Encyclopedia, Vol. 3.' (van Nostrand Reinhold: New York.)

Guerra, A. (1975). Determinación de las diferentes fases del desarrollo sexual de *Octopus vulgaris* Lamarck, mediante un índice de madurez. *Invest. Pesq.* **39**, 397–416.

Guerra, A. (1978). Sobre la alimentación y el comportamiento alimentario de *Octopus vulgaris*. *Invest. Pesq.* **42**, 351–64.

Haimovici, M., and Andriquetto, F. J. M. (1986). Cephalopods in bottom trawl fishing off South Brazilian coast. *Arq. Biol. Technol. (Curitiba)* **29**, 473–95.

Hamada, S. (1974). Feeding behaviour of *Octopus vulgaris* Cuvier on molluscs. *Venus Jpn. J. Malacol.* **33**(3), 138–43.

Hatanaka, H. (1979). Spawning seasons of common octopus (*Octopus vulgaris*) off the northwest coast of Africa. *Bull. Jpn. Soc. Sci. Fish.* **45**(7), 805–10.

Hochberg, F. G. (1983). The parasites of cephalopods: a review. *Mem. Nat. Mus. Victoria* **44**, 109–45.

Hyman, L. H. (1940). 'The Invertebrates, Vol. 1, Protozoa through Ctenophora.' (McGraw-Hill: New York.)

Kayes, R. J. (1974). The daily activity pattern of *Octopus vulgaris* in a natural habitat. *Mar. Behav. Physiol.* **2**, 337–43.

Lane, F. W. (1960). 'Kingdom of the Octopus.' (Sheridan House: New York.)

Lapan, Elliot A. (1975). Studies on the chemistry of the octopus renal system and an observation on the symbiotic relationship of the dicyemid mesozoa. *Comp. Biochem. Physiol. A Comp. Physiol.* **52**(4), 651–7.

Laubier-Bonichon, A., and Mangold, K. (1975). Sexual maturation in male *Octopus vulgaris* (Cephalopoda : Octopoda) in relation to photosexual reflex. (In French.) *Mar. Biol. (Berl.)* **29**(1), 45–52.

Mangold, K. (1983*a*). Food, feeding and growth in cephalopods. *Mem. Nat. Mus. Victoria* **44**, 81–93.

Mangold, K. (1983*b*). *Octopus vulgaris.* In 'Cephalopod Life Cycles'. (Ed. P. R. Boyle.) pp. 335–64. (Academic Press: London.)

Messenger, J. B. (1974). Reflecting elements in cephalopod skin and their importance for camouflage. *J. Zool. Proc. Zool. Soc. Lond.* **174**(3), 387–95.

Messenger, J. B. (1977). Evidence that *Octopus* is colour blind. *J. Exp. Biol.* **70**, 49–55.

Mileikovsky, S. A. (1971). Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol. (Berl.)* **10**, 193–213.

Nixon, M., and Budelmann, B. U. (1984). Scale-worms occasional food of octopus. *J. Molluscan Stud.* **50**, 39–42.

Packard, A. (1961). Sucker display of *Octopus. Nature (Lond.)* **190**, 736.

Packard, A., and Sanders, G. D. (1969). What the octopus shows to the world. *Endeavour (Engl. Ed.)* **28**, 92–9.

Packard, A., and Sanders, G. D. (1971). Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Anim. Behav.* **19**, 780–90.

Pilson, M. E. Q., and Taylor, P. B. (1961). Hole drilling by *Octopus. Science (Wash. D.C.)* **134**, 1366–8.

Ross, D. M. (1971). Protection of hermit crabs (*Dardanus* spp.) from octopus by commensal sea anemones (*Calliactis* spp.). *Nature (Lond.)* **230**, 401–2.

Ross, D. M., and von Boletzky, S. (1979). The association between the pagurid *Dardanus arrosor* and the actinian *Calliactis parasitica*: recovery of activity in inactive *D. arrosor* in the presence of cephalopods. *Mar. Behav. Physiol.* **6**(3), 175–84.

Sanchez, P. (1986). Bathymetric distribution and abundance of some cephalopods in the Catalan Sea Northeast Spain. *Invest. Pesq.* **50**, 237–46.

Simpson, G. C., Pittendrich, C. S., and Tiffany, L. H. (1957). 'Life: An Introduction to Biology.' (Routledge and Kegan Paul: London.)

Wells, M. J. (1978). 'Octopus: Physiology and Behaviour of an Advanced Invertebrate.' (Chapman and Hall: London.)

Wells, M. J., O'Dor, R. K., Mangold, K., and Wells, J. (1983). Feeding and metabolic rate in *Octopus vulgaris. Mar. Behav. Physiol.* **9**, 305–18.

Wodinsky, J. (1978). Feeding behaviour of broody female *Octopus vulgaris. Anim. Behav.* **26**(2), 803–13.

Young, J. Z. (1971). 'The Anatomy of the Nervous System of *Octopus vulgaris*.' (The Clarendon Press: Oxford.)

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Logical Synthesis of an Animal's Environment: Sponges to Non-human Primates.
V.* The Cane Toad, *Bufo marinus*

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Abstract

The environment of the cane toad *Bufo marinus* is classified according to the defining equations given in the first paper of this series. Envirograms are presented, displaying objects in the environment of adult, tadpole and egg in their correct places. Notes on the envirograms include informal versions of the appropriate defining equations that are used for the classification.

Introduction

Of the five animal species of this series, the cane toad, *Bufo marinus*, has the biggest impact on human society. Toad pollution of water sources, dissemination of eggs of human parasites, and attacks on bees, domestic pets, food animals and animals of religious significance (such as goannas among some human groups in Australia) are all matters for concern (Freeland 1984). In a substantial report covering many aspects of the animal's ecology, van Beurden (1980*b*) found that human-aided spread is common.

The toad's natural range is in South and Central America. However, it has been introduced to many countries, usually in an attempt to control pests of the sugarcane industry. The dates of introduction to various countries are given in Easteal (1981). Details of the introduction and spread in Australia from 1935 to 1979 are given in Boughton and Sabath (1980). The attempt at biological control has not always been successful and the animal itself has sometimes become a pest. The toad shows a marked ability to thrive in a wide variety of habitats. Covacevich and Archer (1975) cite the following range in Queensland alone: frontal dunes of ocean beaches; inland border of coastal mangroves; highly acidic areas of coastal wallum; *Melaleuca* swamps; open grassland; open sclerophyll forest; highland closed forest; dry, sparse, open plains; wet and dry creek beds; and coastal towns and cities. Harding and Catterall (1983) give details of the movement patterns of the animal in SE. Queensland. The toad is usually a lowland animal, found below 1000 m, according to Zug and Zug (1979), the maximum height for population survival probably being determined by thermal tolerance limits. Zug and Zug also remark that they suspect that forests are marginal areas. Van Beurden and Grigg (1980) report a spread of *B. marinus* along the coast of New South Wales and inland at rates which are sometimes as high as 3 km per year. However, capture–mark–release–recapture data from van Beurden (1978) in Queensland indicate that the resident adult toad moves little from day to day or month to month.

The animal is large, the females commonly having a snout–vent length of 120 mm. Individuals of over 200 mm have been reported (Zug and Zug 1979; M. J. Tyler, pers. comm.). Life tables are not available. However, Pemberton (1949) reports a captive toad living 15 years, during which time it ate an estimated 72 000 cockroaches.

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The main purpose of these papers is to demonstrate that the mathematical definition of an animal's environment given in the first paper (Niven 1987) applies widely, specifically to the five species of the series: sponge, tapeworm, octopus, toad and chimpanzee, and by extension to all species within the animal phyla from the sponges to the non-human primates. For this reason all objects named in the literature as relating to the subject animal's environment have been classified, including in the present paper such bizarre objects as ping-pong balls, lighted cigarette ends and strychnine flowers (see notes 7 and 8). It is not the intention of these papers to choose 'important' objects in the environment, but rather to show that the mathematical definition yields a classification which applies universally.

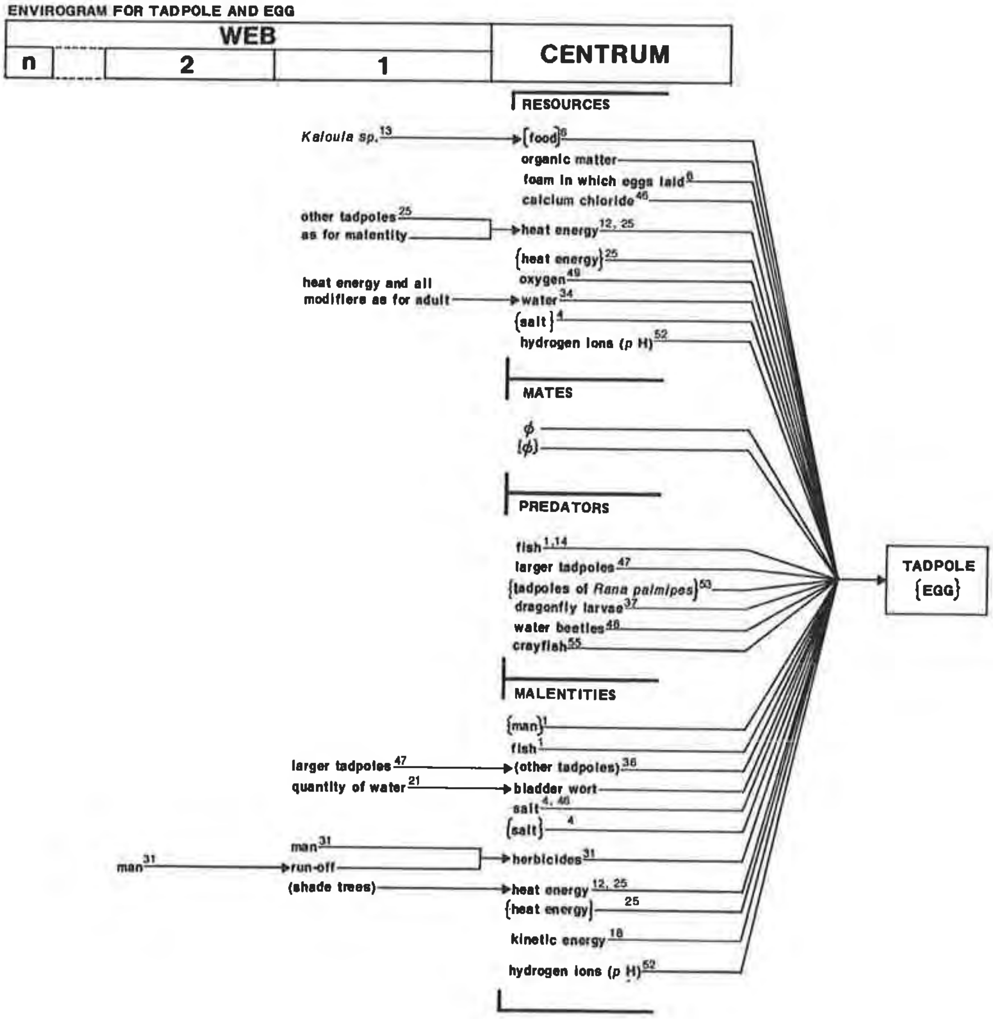

Fig. 1. Envirogram for *Bufo marinus* tadpole and egg.

The situation is similar in animal taxonomy; we classify *Brachionus angularis* as a rotifer and *Bufo marinus* as a vertebrate without regard to their 'importance' in the scheme of things, and in particular without regard to the fact that far more attention has been paid

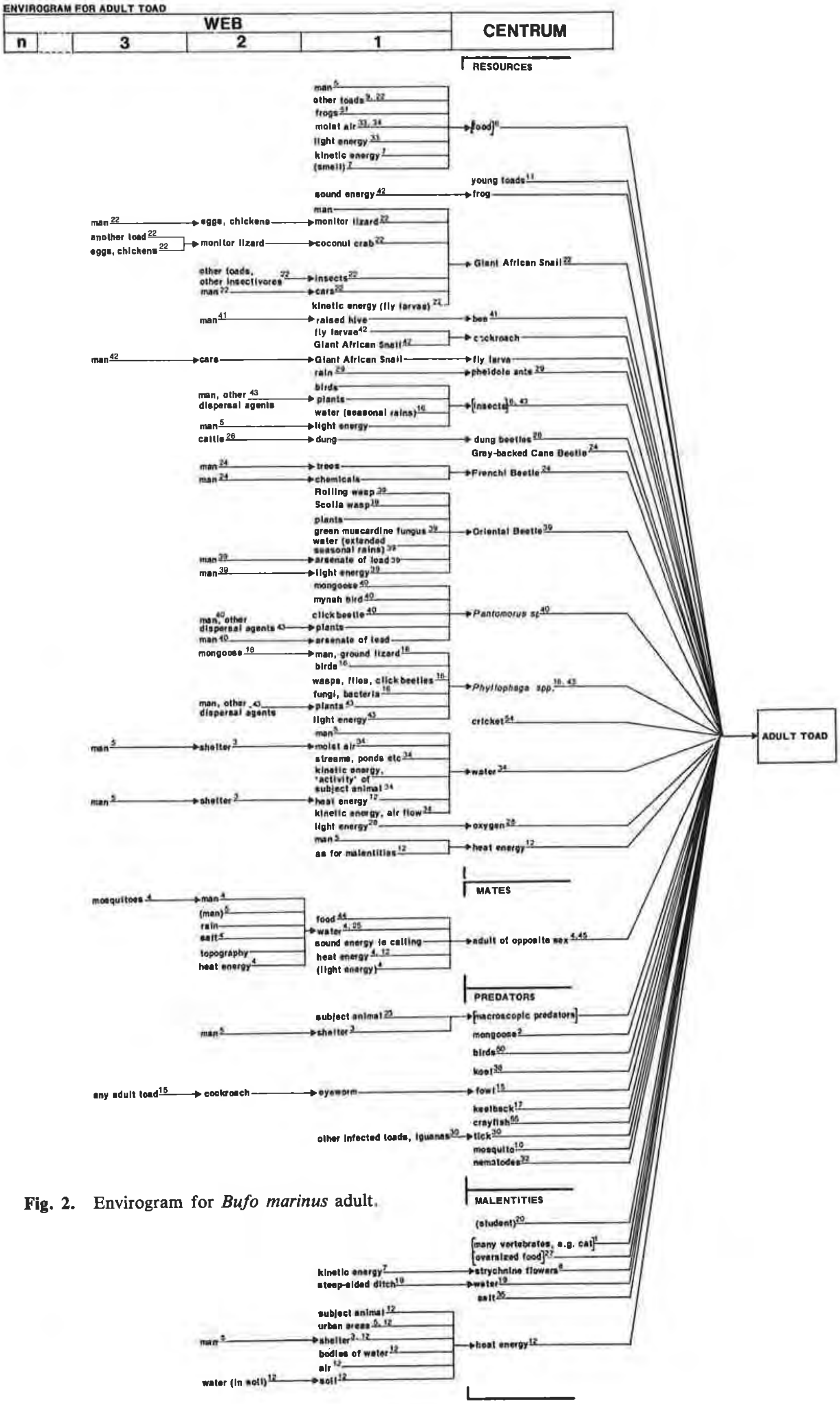

Fig. 2. Envirogram for *Bufo marinus* adult.

in the zoological literature to *B. marinus*. Similarly a zoologist may choose to work with only those items in the environment of particular interest at the time.

The Envirograms

Three envirograms are presented in this paper, for an adult toad, a tadpole, and an egg. The tadpole and egg envirograms have been superimposed in order to save space. The subject animal may be specifically a female or male toad, or a large or small tadpole; the particular case is specified in the relevant note. Since many reports on the animal have been combined, each envirogram is a concatenation of many envirograms for different individuals in different places at different times.

The numbers on the envirograms refer to the notes which follow. These numbers appear in no particular order. The various parts of the envirograms were constructed in an entirely haphazard order as the literature became available. The square brackets indicate a set of objects. Thus, '[many vertebrates, e.g. cat]' refers to the cats, dogs, pigs, rats and so on mentioned in note 1. Tentative classification is indicated by round brackets, for instance '(student)' implies that a student is only tentatively classified as a malentity; details are given in note 20.

A semi-formal version of the appropriate defining equations (see Niven 1987) is given at the end of each note. The following symbols are used.

(i) $=_{\mathrm{df}}$: 'is equal by definition to'

(ii) $\exists$: the existential operator of formal logic. Read '$\exists$ cockroach' as 'there exists a cockroach' or 'there is at least one cockroach', or, more informally, 'we can find a cockroach'. In this paper, expressions such as '$\exists$ cockroach' are always followed by the words 'such that'.

(iii) $|$: '$x \mid y$' means 'x' occurs (will occur), assuming 'y'. This is the symbol used for conditional events (and conditional probabilities). The expression '$A \mid B$' may be read 'Event A occurs, given that event B occurs'; it refers to 'event A under the conditions that B', or 'event A under the hypothesis that B'. Thus an object which is reported as a resource for *B. marinus* in Fiji would also be classified as a resource for *B. marinus* in Australia. In ordinary English it is a *potential* resource. Similarly mates, predators, malentities and modifiers and all *potential* mates, etc.

Notes on the Envirograms

1. Humans and many other vertebrates have been known to mouth or ingest *B. marinus* and either die or become ill. Licht (1967) reports the death of some members of a Peruvian family after eating soup containing eggs of the toad. At least the following cases of death among animals have been recorded: domestic cats and dogs; pigs; rat (*Rattus rattus*), western native cat (*Dasyurus geoffroii*); land mullet (*Egernia bungana*); goannas (*Varanus* spp.); slaty grey snake (*Stegonatus cucullatus*); brown tree snake (*Boiga irregularis*); red-billed black snake (*Pseudechis porphyriacus*); death adder (*Acanthophis antarcticus*); brown snake (*Pseudonaja textilis*); tiger snake (*Notechis scutatus*); crows (*Corvus* spp.); kookaburra (*Dacelo gigas*); Tasmanian devil (*Sarcophilus harrissi*); and turtle (*Kinosternon* sp.).

In addition to references given below, see also Lever (1937, 1945), Buzacott (1939), La Rivers (1948), Watson (1960), Mead (1961), Allen and Neill (1956), Adams (1967), Licht and Low (1968), Frauca (1974), Pippet (1975), and Tyler (1975, 1976).

In all cases, the animals listed above suffered from the effects of the poisonous milky secretions from the toad's parotoid glands. Knowles and Levin (1964) give Marino bufagin, bufotoxin and bufotenine as the active constituents. The mixture has a digitalis-like action: according to M. J. Tyler (pers. comm.), the secretions also include adrenaline and noradrenaline, but the predominant component is 5HT (5-hydroxytryptamine), otherwise called serotonin. Blair (1947) reports that, on occasions, the toad is capable of squirting its poison up to 15 inches (*c.* 0·48 m). Chen and Chen (1933) report that the regeneration by the toad of its poisonous secretion after expression is apparently quite slow. One toad weighing 254 g gave 0·71 g fresh secretion at the first expression and only 0·48 g at the second expression 76 days later.

Abel and Macht (1912) report that *B. marinus* is resistant, but not totally so, to its own poison. Under its influence, the toad becomes sluggish.

Clearly, any animal species which is poisoned through contact with *B. marinus* is in considerable danger, unless it learns to avoid toads. In all areas into which the toad has been introduced, there have been reports of native species being affected, e.g. Covacevich and Archer (1975) suggest that *Dasyurus* spp. (the marsupial 'cats' of Australia) are retreating to areas not populated by the toad. Alcala (1957) reports, however, that domestic cats in the Philippines have learned to avoid the toads.

Zug and Zug (1979) observe that young toads are distasteful but not toxic and thus the likelihood of death by predation is greater during this stage than it is for the adults, both because of smaller body size and lack of toxicity. Pearse (1980*a*, *b*) has shown that, at least with respect to some fish, i.e. the purple-spotted gudgeon (*Hypseleotris galli*), the tadpole is toxic. The mosquito fish (*Gambusia affinis*), a native of Mexico like *B. marinus*, did not relish the tadpoles, but recovered from minor effects.

Since the animal that eats the toad does not thrive but is adversely affected, it is classified as a malentity. The informal defining equation for a cat as a malentity is:

$$\text{(cat)Mal(toad)} =_{\text{df}} \text{H(toad) is decreased and H(cat) is decreased} \mid \xi\text{(cat)(toad)}.$$

2. Baldwin *et al.* (1952) report from Hawaii that, in 11 days, five mongooses ate 20 adult *B. marinus* with apparent relish and no ill effects. Also, Simmonds (1957) in Fiji records the mongoose as a predator. The informal defining equation is:

$$\text{(mongoose)Pred(toad)} =_{\text{df}} \text{H(toad) is decreased and H(mongoose) is increased} \mid \xi\text{(mongoose)(toad)}.$$

3. *B. marinus* is primarily, though not exclusively, nocturnal. During the day, the species characteristically seeks cover (shelter) in thick growths of vegetation beneath rotting organic matter, within clods in ploughed fields, in holes, and under houses. Alcala (1957) comments that *B. marinus* tends not to penetrate primary forest. He adds that the toad is most abundant in savannah country, grasslands, cultivated areas, and near human habitation (see note 5). On Barbados, Mungomery (1936*a*) observes that the elimination of available daytime shelter resulted in a decrease in the toad population. Tyler (1975) reports that the toad is having difficulty in maintaining its population partly because of the clearing of suitable day and dry-period shelter. Zug and Zug (1979) suggest that toads reduce water loss by retreating to sheltered areas during the day and at other times of low humidity. They suggest also that subadults and adults compete for sheltered retreats. The latter point is made more strongly by Straughan (1966), who suggests that juveniles are forced to migrate because of occupation by adults of suitable sheltering sites; this leads to the dispersal of the animal.

If the suggestion given by Zug and Zug is correct, then 'shelter', which in a particular case is some particular object, modifies moist air and thermal energy, which in turn modify water as a resource (see note 34). An object which provides shelter is thus a second-order modifier. 'Shelter' is also a negative first-order modifier of 'heat energy' as a malentity. In this latter sense, the informal defining equation is:

$$\text{(shelter)Mod}^{-1}\text{(toad)} =_{\text{df}} (\exists\ \text{heat}) \text{ such that } [\text{(heat)Mal(toad)} \mid \sim\xi\text{(shelter)(toad)} \text{ and } \sim\text{(heat)Mal(toad)} \mid \xi\text{(shelter)(toad)}].$$

Here, 'heat' should be understood to mean a particular 'chunk' of heat energy.

4. *B. marinus* is an opportunistic breeder, requiring only appropriate bodies of water into which the female, who nearly always carries mature eggs, lays. Almost any body of water, whether standing or running, fresh or brackish, will probably be satisfactory. The Queensland Museum has a photograph of eggs laid in salt water (in the wild), but it is not known if they survived and developed. Also, water in which the toad is found, even on a beach, may be fresh; M. J. Tyler (pers. comm.) writes, 'Covacevich and Archer (1975) talk about *B. marinus* on Rainbow Beach etc. On Rainbow Beach this may not be salt water. I found tadpoles and babies there in water flowing towards the sea from banks. I took water samples and found the chloride level so low as to indicate that this was a freshwater source'. Nevertheless, Ely (1944) conducted laboratory experiments which showed eggs could survive and develop normally in solutions containing up to 20% seawater. A solution containing 15% seawater (about 0·5% salt) seemed to be the most favourable medium, since the eggs developed more quickly than in either a 10% seawater solution (see note 25 on rapid development) or in tap water. Takano and Iijima (1937) report that NaCl is fatal at a density above 0·7%, but development proceeds naturally below 0·6%.

The only direct observation of the animal breeding in salty water in the wild which we have come across is that of Waite (1901) in Bermuda, who reports the toad, referred to as '*Bufo agua*', breeding in brackish water and marshes. Straughan (1966), in Queensland, writes that preferred breeding sites are in the shallows and that the presence of aquatic vegetation, grasses or weeds, or whether the bottom is clear or covered with rocks, sand or vegetation has no effect on choice of breeding site.

Water, which is essential for breeding, may be removed from the toad's habitat, in several ways; e.g. on Barbados, many hundreds of estate ponds and low-lying areas where water may accumulate have been filled or drained for either aesthetic reasons or for mosquito control (Mungomery 1936*a*; Tucker 1940). Also, water may simply evaporate (requiring heat energy), or seep away through the soil. In the Barbados, Tucker (1940) reports that the animal is having difficulty in maintaining its populations, in part because of lack of suitable breeding water and oiling of water for mosquito control; thus, farmers are being encouraged to build artificial breeding ponds.

B. marinus may breed twice a year, laying between 10 000 and 21 000 eggs each time, according to Tyler (1976) but Straughan (1966) observed 8000–35 000 eggs being laid. Buzacott (1936) has recorded one female laying a clutch of 16 000 eggs and, on another occasion, nine females laying 125 000. When temperatures are sufficiently high and rainfall adequate, the toad will reproduce all year, but in marginal habitats, the breeding season usually coincides with the warmest and wettest times of the year (Oliver 1949). Wilhoft (1965) mentions that there are always some unfertilized eggs, and Tucker (1940) counted the number of toadlets surviving from an initial egg lay as ranging from 75 to 300, probably an underestimate, he reports, due to the difficulties of observation. Van Beurden (1980*b*) reports that at least in some populations females do not breed every year, but in tropical populations they will breed every year, sometimes more than once.

Zug and Zug (1979) report that eggs will hatch in 36 h–4 days. R. B. Floyd (personal communication 1981) finds that the development time of the eggs falls from 155 h at 18°C to about 1 day at 35°C.

Breeding success is aided by the animal's short development period – a larval (tadpole) life of between 25 days and 2 months, depending on water temperature (Tyler 1976; see also note 25). Rates of spermatogenetic activity in the adult male are correlated with the seasons, according to Saxena and Lal (1981), who ascribe the slow rate of spermatogenetic activity and the regressed condition of Leydig cells to declining daylength and ambient temperature during the winter.

Tyler (1975) remarks that some members of both sexes are found in breeding condition throughout the year, waiting for the right climate for breeding. Zug *et al.* (1975), in Papua New Guinea, report that there, in every month, at least some of the females have eggs ready for deposition. They suggest that the number of such females is partly dependent on the rainfall, since it appeared that heavy rain preceding the sampling date reduced the number of gravid females because they had bred during that rainy period. The year-round availability of eggs indicates that *B. marinus* is an opportunistic breeder. Wilhoft (1965) also found an inverse relationship between the observed number of gravid females and the amount of rain. Straughan (1966), in Queensland, writes that the breeding season starts with the first summer storms in September. Oviposition may occur throughout the day as well as night, although it was never observed to commence during the day. Floyd and Benbow (1984) found that breeding tends to occur when the water level rises above a certain level. They conclude that control measures are most efficient on wet nights.

In Australia, toads often attain adult length in their second summer (van Beurden 1978). Zug and Zug (1979) record that, in New Guinea, females reach sexual maturity at a snout-vent length of 70–80 mm; in the Canal Zone, Panama, the length is 90–100 mm and males mature at 85–95 mm. Zug *et al.* (1975), in Papua New Guinea, report no size difference between the (adult) sexes.

'Salt', by which is meant a specific quantity or 'chunk' of salt, considered as a particular object in one particular case, is entered on the egg envirogram as both resource and malentity; they must be different 'chunks' in the two cases. It is also a malentity of tadpoles.

On the adult envirogram, heat, water and light (tentatively) appear as modifiers of mates. Salt, rain and heat, in turn, modify water. The informal defining equations for the chain ending in salt for a female adult follow.

(male)Mat(subject female) $=_{\mathrm{df}}$ An offspring of both individuals will be produced
with probability greater than zero $\mid \xi$(male)(subject female).

By 'water' is meant a body of water, e.g. a lake or a pond.

(water)Mod^{+1}(subject female) $=_{\mathrm{df}}$ ($\exists$ male) such that
[(male)Mat(subject female) $\mid \xi$(water)(subject female) and
$\sim$(male)Mat(subject female) $\mid \sim\xi$(water)(subject female)].

The following defining equation refers to Ely's (1944) results on the most favourable medium. 'Salt' is, as usual, a particular 'chunk' of salt; it is not to be interpreted as salt in general. Attention is focussed on precisely that 'chunk' of salt which, when added to the water (0·5% salt) causes the water to be suitable for breeding.

(salt)Mod^{+2}(subject female) $=_{\mathrm{df}}$ ($\exists$ water) such that
[(water)Mod^{1}(subject female) $\mid \xi$(salt)(water) and $\sim$(water)Mod^{1}(subject female) $\mid$
$\sim\xi$(salt)(water)].

5. Many writers have noted the close association of *B. marinus* with humans. The following reasons have been suggested:

(i) lights (which attract insects);
(ii) food (refuse and pet food);
(iii) warmth;
(iv) water;
(v) shelter.

For example:

(i) Brattstrom (1962*b*), in studying homing, observed that, of 15 transported toads, 11 returned, all to the same light; he strongly suggests that the insects around the light were the main attraction. Dexter (1932) and many other concur. Oliver (1949) remarks that the animals characteristically return to good feeding sites.

(ii) Alexander (1964) observed toads eating (diurnally) canned dog-food remains and the following household refuse: raw lettuce, avocado, broccoli and carrot, cooked corn, rutabagas, black-eyed peas, and rice. No insects, which might have attracted the toads, were seen close by.

(iii) and (iv) R. B. Floyd (1981, pers. comm.) suggests that the greater warmth of urban areas (see note 12) and the greater availability of water for breeding (see note 4) attract toads.

(v) Several writers, including Krakauer (1968) and Alcala (1957), suggest that *B. marinus* prefers disturbed areas—around buildings, on farms, along canals, and in secondary growth. The continued expansion of Miami seems to be destroying the habitat of *B. terrestris*, while creating more disturbed areas for *B. marinus*. Such areas provide nooks and crannies for day shelter.

The informal defining equation for some human acting as a modifier by providing an object of food for a subject adult toad is:

$$\text{(human)Mod}^{+1}\text{(toad)} =_{\text{df}} (\exists\ \text{food}) \text{ such that } [\text{(food)Res(toad)} \mid \xi\text{(human)(food)} \text{ and } \sim\text{(food)Res(toad)} \mid \sim\xi\text{(human(food)}].$$

6. Adult toads are astonishingly catholic eaters (see envirogram).

In addition to insects etc., Krakauer (1968) found five toads in Florida with stomachs full of undigested grass (see also Zug *et al.* 1975 for New Guinea).

Mungomery (1938) reports that *B. marinus* can survive long periods without food. He kept several pairs of toads without food for one month and they showed no ill effects; one pair bred immediately upon release.

Oliver (1949) notes that if an abundant supply of insects is available, the toad will only stop eating when gorged to the point of distending its body.

Zug *et al.* (1975) find that forest-dwelling toads are better fed and bigger, with more animals in the diet. The greater abundance of plants found in the stomachs of savannah-dwelling toads shows deliberate rather than accidental ingestion by these toads, presumably to supplement meagre insect resources. Within its original range in Brazil, Strüssmann *et al.* (1984) found that medium-sized *B. marinus* eat most prey in proportion to their abundance, except spiders, which are eaten less and termites and ants which are eaten more than would be expected from their availability. Larger toads tend to eat more termites and less ants than medium-sized toads.

Once the mouth is formed, tadpoles eat the foam they were laid in. When this is finished, they eat organic matter in the water. *B. marinus* tadpoles show no preference in feeding from surface, midwater or substrate, in contrast to other species of toads. However, this may be because the high clutch numbers force this wide range in feeding behaviour (Tyler 1976). Zug and Zug (1979) remark that the ideal time for metamorphosis would seem to be at the beginning of the wet season (about May in the toad's native environment) when insects are abundant.

The informal defining equation for a specific 'chunk' of foam as a food resource for a subject tadpole is:

$$\text{(foam)Res(tadpole)} =_{\text{df}} \text{H(tadpole) is increased} \mid \xi\text{(foam)(tadpole)}.$$

Since 'foam' is not an animal, the second part of the defining equation is not used. 'Foam' is assumed to be nutritious, thus increasing H(tadpole).

7. Many writers agree that the toads are carnivorous and feed only on moving organisms. However, see notes 5(ii) and 8. Also, King (1969) comments that *B. marinus* can detect prey by smell alone. Clearly, movement is often a factor in arousing feeding responses, e.g. a toad has been recorded as pursuing and attempting to eat a ping-pong ball, and Grant (1948) reports a toad consuming a lighted cigarette butt. Movement is suggested as the operative factor in toads eating strychnine flowers (see note 8). F. A. Bianchi, in a personal communication to S. Easteal, mentions that when *B. marinus* was first introduced into Hawaii, it would eat nothing but flying or moving insects, although the descendents will eat solid and liquid food. Ingle and McKinley (1978) found that two moving objects close

together elicited more strikes than a single moving object. Fife (1973) comments that *B. marinus* never misses when it strikes, although frogs have error rates of 2–7%. Dean (1980*a*, *b*) has done a detailed study of the strike, in which the times taken to complete the movements 'start of lunge', 'start of tongue protrusion', . . ., 'end swallow' and 'toad still' were recorded. Dean observed that, in contrast to *B. americanus*, *B. marinus* strikes willingly when a second bombardier beetle is offered, even if the toad's behaviour on a previous occasion has shown discomfort. Camhi (1980) describes a similar study in which toads struck at cockroaches; in 55% of the strikes the cockroach escaped, apparently gaining prior information of the strike from the small but sharp puff of air made by the toad's lunge.

Most prey for large toads is in the 5·1–10 mm range (in length). The toads ignore anything less than 2 mm long (Zug and Zug 1979).

The informal defining equation for a particular 'chunk' of kinetic energy as a first-order modifier of a food object is:

> (kinetic energy)Mod^{+1}(toad $=_{\mathrm{df}}$ ($\exists$ food) such that [(food)Res(toad) |
> ξ(kinetic energy) (food) and $\sim$(food)Res(toad) | $\sim\xi$(kinetic energy)(food)].

8. In the Foster Gardens in Hawaii, a seasonally fatal epidemic occurs when blossoms fall from the strychnine trees. Toads, attracted by the movement, eat the blossoms and die of strychnine poisoning. Petals of the flowers contain 1·023% pure strychnine (Alexander 1964).

The informal defining equations for a particular strychnine blossom as a malentity and a specific 'chunk' of kinetic energy as a modifier are:

> (blossom)Mal(toad) $=_{\mathrm{df}}$ H(toad) is decreased | ξ(blossom)(toad)
>
> (kinetic energy)Mod^{+1}(toad) $=_{\mathrm{df}}$ ($\exists$ blossom) such that [(blossom)Mal(toad) |
> ξ(Kinetic energy)(blossom) and $\sim$(blossom)Mal(toad) |
> $\sim\xi$(kinetic energy)(blossom)].

9. Several authors, notably Boice and Boice (1971) have suggested that there is an hierarchical feeding order among toads which correlates positively with size. Sometimes, individuals will push others away from food in an extremely aggressive manner. Fellows (1969*a*) observed a number of toads sitting in a perfect circle around a straw-sized hole from which female termites were emerging. The toads struck at the emerging insects in a definite order and no two toads ever struck at the same time.

A toad which takes food which might otherwise have been food for the subject toad is modifying a resource. The informal defining equation is:

> (other toad)Mod^{-1}(subject toad) $=_{\mathrm{df}}$ ($\exists$ food) such that
> [(food)Res(subject toad) | $\sim\xi$(other toad)(food) and $\sim$(food)Res(subject toad) |
> ξ(other toad)(food)].

10. The mosquito *Mimomya elegans* (Taylor) was reported by van Beurden (1980*a*) to be feeding on the toad in Queensland. There is evidence to suggest that other species of mosquito are also predators. The informal defining equation is:

> (mosquito)Pred(toad) $=_{\mathrm{df}}$ H(toad) is decreased and H(mosquito) is increased |
> ξ(mosquito)(toad).

11. Cannibalism has been observed by Hinckley (1962), Bailey (1976) and Tyler (1976). The latter records that a newly metamorphosed toad is about 8 mm in length and at constant risk of being eaten by larger toads. This risk diminishes with size.

The envirogram shows the case that the subject animal is an older toad and the young toad is a resource. The informal defining equation is:

(young toad)Res(subject toad) $=_{df}$ H(subject toad) is increased and
H(young toad) is decreased | ξ(young toad)(subject toad).

12. There is a range of heat energy that can be considered beneficial or at least not harmful—this range will be a set of resources. Outside the beneficial range, both above and below, the animal will be increasingly disadvantaged to a point at which it will die—this range will be a set of malentities.

Brattstrom (1963) reports that, in South America, the average body temperature of the animal in the wild, calculated from all sources until 1963, was 25·2°C. Johnson (1972), in Australia, gives 21·3 ± 2·4°C as the body temperature. Van Beurden (1981), also in Australia, reports that when *B. marinus* is exposed to temperatures of 3°C, it takes from 1–2 h for the animal's deep body temperature to fall from 20 to 3°C. The raising of the deep body temperature occurs more quickly. He also found that toads from southerly (i.e. colder) areas recovered more quickly from exposure to very low temperatures of 0–2°C. Survival times of juveniles and tadpoles exposed to very low temperatures were short. However, all tadpoles survived at 8°C for 24 h.

Fifty per cent of newly metamorphosed toadlets die within 4 h when exposed to temperatures of either 4·5 or 40°C. 'On dry sunny days the activity of these toadlets is restricted to 10 m from the water edge—regular excusions are made every 15–20 min to the water for water uptake. Deprived of their "drink" and remaining exposed to the sun they died within 40 min. Similarly deprived but not exposed to the sun they died in 50 min.' (van Beurden 1978). A 12-h exposure of adults to 30° and 40°C was not lethal, but exposure for 28 and 48 h was. All adults survived at least 96 h at temperatures above 4°C. In an outdoor experiment with 52 adults in an enclosure, nine toads died during the first frost of the season (the temperature fell to −1°C for just over an hour). On the following day, 10 toads died (the temperature fell below 1°C for over 8 h). The position of the animals in the enclosure was thought to be important in this experiment, since the temperature beneath litter was about 2°C higher (van Beurden 1979). Warburg (1965) noted that *B. marinus* at a temperature of 37·5°C and very low humidity of 0–5% had a mean survival time of 4–6 h (maximum 8 h).

Krakauer (1968) argues that Miami (Florida), which experiences subzero temperatures about once every five years, is a marginal habitat for *B. marinus*. He comments that any nearby water will moderate the microclimate and that the most favourable habitat for *B. marinus* is the East Coast Rock Ridge, where the climate is mitigated by the Atlantic Ocean. He also indicates that nocturnal temperature inversions will cause ground frosts more frequently in open areas than in urban areas and hence that toads are attracted towards urban areas. Zug and Zug (1979) note that the limit of the range of *B. marinus* in Texas corresponds to the 15°C isopleth. Stuart (1951) found Guatemalan toads only below 1500 m, which is the isopleth for the 15°C mean minimum temperature.

It seems almost certain that all anurans use evaporation from the skin as a cooling device, both in stress situations and for normal thermoregulation. Other factors affecting body temperature will be the temperature of the surrounding air in the microenvironment and the temperature of the substrate; both of these involve conduction. A modifier of the substrate will be the amount of air it holds.

Duellman (1965) hypothesises that the low density of *B. marinus* in well-shaded forests might be because the thermal requirements of embryos are unsuited by shaded pools. He notes that the animals are abundant in nearby clear areas.

Oviposition can be interrupted by a fall in temperature. Delays of up to three days were observed by Straughan (1966) when the water temperature dropped below 72°F (22·2°C). Oviposition continued once the temperature returned to 78°F (25·6°C).

The informal defining equations for a particular 'chunk' of heat energy as a malentity modified by the subject animal itself (using evaporation) are:

(heat)Mal(subject toad) $=_{df}$ H(subject toad) is decreased | ξ(heat)(subject toad)

(subject toad)Mod^{-1}(subject toad) $=_{\mathrm{df}}$ ($\exists$ heat) such that
[(heat)Mal(subject toad) | $\sim\xi$(subject toad)(subject toad) and
$\sim$(heat)Mal(subject toad) | ξ(subject toad)(subject toad)].

In the latter definition, the interaction primitive ξ is used for the subject animal interacting with itself.

13. The frog, *Kaloula conjuncta* (Peters) of the family Microhylidae, shares the same breeding ponds as *B. marinus* in parts of the Philippines. *B. marinus* lays a much larger clutch of eggs, so that we might expect it to consume most available organic matter, particularly in adverse conditions. However, food is so abundant that the competition has little noticeable effect (Alcala 1957). Rabor (1952), also in the Philippines, observed *K. conjuncta* as a possible competitor.

The frog is entered on the tadpole envirogram as a first-order modifier of a class of food resources. For a particular food object, the informal defining equation is:

(*Kaloula*)Mod^{-1}(tadpole) $=_{\mathrm{df}}$ ($\exists$ food) such that [(food)Res(tadpole) |
$\sim\xi$(*Kaloula*)(food) and $\sim$(food)Res(tadpole) | ξ(*Kaloula*)(food)].

14. Alcala (1957) reports that some fish eat *B. marinus* larvae, but does not specify which ones (see note 1).

In this case, the fish is classified as a predator, it being understood that the larva, tadpole say, is nutritious and not poisonous to the fish.

(fish)Pred(tadpole) $=_{\mathrm{df}}$ H(tadpole) is decreased and H(fish) is increased |
ξ(fish)(tadpole)

15. Buzacott (1939) showed that domestic fowls could eat young toads (13/8–7/16″ i.e. 1·20–1·11 cm long) with impunity. He also records that the toad feeds on the cockroach which is an intermediate host for the fowl parasite, the eyeworm.

In this interesting modifier chain, a particular domestic fowl is classified as a predator of the subject toad; a particular eyeworm is a negative first-order modifier of the fowl, assuming here that the bird becomes ineffectual as a predator of toads when parasitised; a particular cockroach is a positive second-order modifier; any toad (it could be the subject animal) is a negative third-order modifier. The informal defining equations are:

(fowl)Pred(toad) $=_{\mathrm{df}}$ H(toad) is decreased and H(fowl) is increased |
ξ(fowl)(toad)

(eyeworm)Mod^{-1}(toad) $=_{\mathrm{df}}$ ($\exists$ fowl) such that [(fowl)Pred(toad) |
$\sim\xi$(eyeworm)(fowl) and $\sim$(fowl)Pred(toad) | ξ(eyeworm)(fowl)]

(cockroach)Mod^{+2}(toad) $=_{\mathrm{df}}$ ($\exists$ eyeworm) such that [(eyeworm)Mod^{1}(toad) |
ξ(cockroach)(eyeworm) and $\sim$(eyeworm)Mod^{1}(toad) | $\sim\xi$(cockroach)(eyeworm)]

(any toad)Mod^{-3}(toad) $=_{\mathrm{df}}$ ($\exists$ cockroach) such that [(cockroach)Mod^{2}(toad) |
$\sim\xi$(any toad)(cockroach) and $\sim$(cockroach)Mod^{2}(toad) |
ξ(any toad)(cockroach)].

16. In Puerto Rico, the ground lizard *Ameiva exsul* (Wolcott 1937) was useful in controlling the cane pests *Phyllophaga portoricencis* (the June beetle) and *Cnemarachis vandinei*. The lizard was practically exterminated by the introduced mongoose, and *B. marinus* was then introduced to control the cane pests. Any surviving lizards are competitors of *B. marinus* and their effectiveness is governed by the size of the mongoose population (Mettrick and Dunkley 1968).

Smyth (1917) also records the lizard as feeding on the beetles. He lists the following *Phyllophaga* spp. on Puerto Rico: *P. vandinei*, *P. portoricensis*, *P. guanicana* and *P. citri*, also *Phytalus insularis*. All these are eaten by the toad. The grubs are eaten by the Puerto Rican blackbird *Holoquiscalus brachypterus*, the bare-legged owl, 'mucaro' *Gymnasio nudipes nudipes*, the little blue heron, 'garza axul' *Glorida caerulea caerulescens*, and the mangrove cuckoo *Coccyzus minor nesiotes*. On St Kitts, *Phyllophaga patruel* is a resource of *B. marinus* and, at St Vincent, *P. patens*. Wasps of the family Scoliidae and the click beetle family, Elateridae, also attack the grubs, while flies on the family Tachinidae attack the adult beetles. The grubs are also susceptible to the fungus *Metarrhizium* and the bacterium *Micrococcus nigrofaciens* Nov. At the time of writing, humans were also a significant modifier of this resource; during seven months in 1914, 2 255 000 beetles were collected by paid workers on the sugarcane plantations. Other modifiers of the *Phyllophaga* spp. are mites, the humidity and texture of the soil, heat energy, and various fruits and plants (see note 43). Many authors have suggested that insects are seasonally abundant in *B. marinus'* environment; many species of insect emerge only when favourable conditions such as seasonal rains and appropriate temperatures occur. In some areas (Zug and Zug 1979; see note 34), this seasonal abundance results in greatly increasing activity among the toads.

The informal defining equations for a particular beetle as a resource, a particular lizard as a competitor of the subject toad for that resource and thus a negative first-order modifier, and a mongoose as a second-order modifier are:

(beetle)Res(toad) $=_{df}$ H(toad) is increased and H(beetle) is decreased |
ξ(beetle)(toad)

(lizard)Mod^{-1}(toad) $=_{df}$ ($\exists$ beetle) such that [(beetle)Res(toad) |
$\sim\xi$(lizard)(beetle) and $\sim$(beetle)Res(toad) | ξ(lizard)(beetle)]

(mongoose)Mod^{-2}(toad) $=_{df}$ ($\exists$ lizard) such that [(lizard)Mod^{1}(toad) |
$\sim\xi$(mongoose)(lizard) and $\sim$(lizard)Mod^{1}(toad) | ξ(mongoose)(lizard)].

17. The common keelback (a snake, *Amphiesma mairii*) thrives in captivity on a diet of *B. marinus* and is the only Australian species of animal known to utilise the toad regularly for food (Covacevich and Archer 1975).

The informal defining equation for a keelback as a predator is:

(keelback)Pred(toad) $=_{df}$ H(toad) is decreased and H(keelback) is increased |
ξ(keelback)(toad).

18. Both Tyler (1976) and Brattstrom (1962*b*) note that flash floods in drainage ditches and other confined waterways are dangerous to tadpoles, although Breder (1946) remarks that tadpoles can stem a considerable current.

In this case, a 'chunk' of kinetic energy acts as a malentity. The informal defining equation is:

(kinetic energy)Mal(tadpole) $=_{df}$ H(tadpole) is decreased |
ξ(kinetic energy)(tadpole).

19. At metamorphosis, young toads are at high risk of death by drowning if they are unable to climb from the water (Tyler 1976).

An object which is a particular 'chunk' of water is classified as a malentity of the young toad, which is the subject animal in this case; the water is modified by a steep-sided ditch. The informal defining equations are:

(water)Mal(young toad) $=_{df}$ H(young toad) is decreased | ξ(water)(young toad)

(ditch)Mod^{+1}(young toad) $=_{df}$ ($\exists$ water) such that [(water)Mal(young toad) |
ξ(ditch)(water) and $\sim$(water)Mal(young toad) | $\sim\xi$(ditch)(water)].

20. Tyler (1976) notes that the principal benefit of *B. marinus*' presence in Australia has been as an experimental animal for use in secondary schools, universities, and in medical research institutions, to the extent of 100 000 animals per year. These students and researchers as classed tentatively as malentities, with the understanding that 'student' is, for the purpose of this article only, classified as an animal and that 'H(student)' has some suitable interpretation. In North Queensland, the Innisfail Apex Club has made enough money from the sale of cane toads to build an old people's home, known locally as 'Toad Hall'.

The informal defining equation for a student as a malentity is:

$$(\text{student})\text{Mal}(\text{toad}) =_{\text{df}} \text{H(toad) is decreased and H(student) is unchanged} \mid \xi(\text{student})(\text{toad}).$$

21. Small tadpoles are 'eaten' by the aquatic insectivorous bladderwort plant *Utricularia* spp. The tadpoles are in danger particularly when water levels are low (Tyler 1976).

Since a bladderwort is not an animal, it is classified as a malentity. The informal defining equation is:

$$(\text{bladderwort})\text{Mal}(\text{tadpole}) =_{\text{df}} \text{H(tadpole) is decreased} \mid \xi(\text{bladderwort})(\text{tadpole}).$$

22. Mead (1961) gives the following complex interaction on Guam and Ponape Island between *B. marinus* and several other introduced and native species. The giant African snail (*Achatina fulica*) was accidentally introduced on boats with produce etc., and *B. marinus*, which was introduced effectively to control the black garden slug *Veronicella leydigi*, also predated the young of the snail. In addition, the toad consumed the native snails *Opeas* spp. Furthermore, examination of the toad's stomach contents revealed flesh and shell fragments from much larger snails, usually in the presence of dead fly maggots. Apparently, the toads were attracted by the movement of fly maggots to dead snails which had been crushed by cars. Cockroaches had thrived because of the large numbers of dead snails—and *B. marinus* thrives on cockroaches. Early traders had accidentally introduced rats; to control them, the monitor lizard (*Varanus* spp.) was brought in. Unfortunately, the lizard is diurnal and the rats nocturnal, so the lizard became a pest by consuming eggs and chickens. The monitor lizard also ate *B. marinus*, which poisoned it (see note 1). Cats and dogs were the best ratters on the Islands. However, they ate *B. marinus* and died. A beneficial consequence of the introduction of the monitor lizard was the predation of coconut pests: the coconut crab (*Birgus latro*) and grubs of the rhinoceros beetle; and the general agricultural pest, the giant African snail. The coconut crab also feeds on this snail.

Thus, the introduction of *B. marinus*:

(i) reduced the black slug population;
(ii) reduced the monitor lizard population;
(iii) reduced the cat and dog population;
(iv) aggravated the rat problem (by killing lizards, cats and dogs);
(v) reduced the natural control of coconut pests;
(vi) had some effect on the giant African snail population;
(vii) ameliorated the fly and cockroach problem (caused by the abundance of dead giant African snails).

Bailey (1976) and Tyler (1976) both comment on the extremely poor condition of many toads in New Britain (New Guinea). At that time, the toads had apparently eaten out almost the entire population of ground-dwelling insects. In consequence, they began eating the introduced giant African snail (*Achatina fulica*). This snail has a large and probably indigestible shell which has been known to puncture car tyres (see note 24). Insects are classified as first-order modifiers because, in their presence, the snail is less likely (unlikely) to be eaten but, in their absence, the probability of the snail being eaten increases markedly. Since other toads or other insectivores in general will eat insects, 'other toads, other insectivores' are second-order modifiers. Matsumoto *et al.* (1984) found that *B. marinus* eats *A. fulica* in the Bonin Islands, as well as ants, pill-bugs, Diptera larvae and other insect larvae.

The informal defining equations for the modifier chain ending with insectivore are:

(snail)Res(toad) $=_{df}$ H(toad) is increased and H(snail) is decreased | ξ(snail)(toad)

(insect)Mod^{-1}(toad) $=_{df}$ ($\exists$ snail) such that [(snail)Res(toad) | $\sim\xi$(insect)(toad) and $\sim$(snail)Res(toad) | ξ(insect)(toad)]

(insectivore)Mod^{-2}(toad) $=_{df}$ ($\exists$ insect) such that [(insect)Mod^{1}(toad) | $\sim\xi$(insectivore)(insect) and $\sim$(insect)Mod^{1}(toad) | ξ(insectivore)(insect)].

23. When faced with an enemy, *B. marinus* has a behaviour pattern which is apparently an attempt to convince the would-be predator that the toad is too large to eat. The toad drops the side of its body nearest the enemy and raises the other side, thus displaying the greatest possible surface area (Tyler 1976). The toad is thus acting as a modifier in its own environment. The informal defining equation is:

(toad)Mod^{-1}(toad) $=_{df}$ ($\exists$ enemy) such that [(enemy)Pred(toad) | $\sim\xi$(toad)(toad) and $\sim$(enemy)Pred(toad) | ξ(toad)(toad)].

The interaction primitive 'ξ' is used here for the case that the subject animal interacts with itself.

24. the Frenchi beetle *Lepidiota frenchi* feeds by preference on Moreton Bay ash, bloodwood and guava. Both the elimination of these trees, and soil fumigation using carbon bisulfide and paradichlorobenzene, were employed by farmers to help control this cane pest (in Queensland).

In 1941, it was apparent that *B. marinus* was playing only a minor role in controlling the grey-black and Frenchi beetles in Queensland (van Beurden 1978).

Fellows (1969*b*) reports that *B. marinus* will not eat large, hard-cased adult cane beetles, although they will readily eat softer, younger cane beetles. Presumably, the beetle in question is either the grey-backed beetle *Dermolepida albohirtum* or the Frenchi beetle *Lepidiota frenchi* (see note 22).

The informal defining equations for the chain 'subject toad, beetle, chemical human' are:

(beetle)Res(toad) $=_{df}$ H(toad) is increased and H(beetle) is decreased | ξ(beetle)(toad)

(chemical)Mod^{-1}(toad) $=_{df}$ ($\exists$ beetle) such that [(beetle)Res(toad) | $\sim\xi$(chemical)(beetle) and $\sim$(beetle)Res(toad) | ξ(chemical)(beetle)]

(human)Mod^{+2}(toad) $=_{df}$ ($\exists$ chemical) such that [(chemical)Mod^{1}(toad) | ξ(human)(chemical) and $\sim$(chemical)Mod^{1}(toad) | $\sim\xi$(human)(chemical)].

25. The tadpoles are very dark; this aids them in absorbing and maintaining high body temperature. It is to *B. marinus*' advantage to maximise growth and development rates to increase the probability of eggs surviving through the tadpole stage to metamorphosis before the pond dries up or flash floods sweep them away (Heatwole *et al.* 1968) (see also notes 12 and 18).

Tadpoles aggregate. Brattstrom (1962*a*) has done experiments which show that aggregated tadpoles absorb heat more readily than when dispersed and convey heat to the surrounding water, thus raising the temperature of their immediate surroundings.

Both R. B. Floyd (pers. comm.) and Mares (1972) remark that the tadpoles, often aggregated, vary their location in the pond in order to remain within their preferred temperature range.

Oliver (1949) lists the following as affecting tadpole development:

(i) water temperature;
(ii) amount and type of food;
(iii) amount of light;
(iv) number of tadpoles present.

R. B. Floyd (pers. comm.; 1983, 1984*a*, *b*) reports that egg survival rises from an average of 60% at 18°C to over 90% at 27°C, then falls to about 62% at 34°C. Outside these temperatures, survival is negligible. He believes that eggs are less tolerant than tadpoles of temperature extremes. At 14°C, eggs hatch after 155 h; the hatching time decreases approximately exponentially to about 25 h at 34°C. Floyd determined the temperature preference of larvae at six stages of development; he found that preferred temperature generally increased as larval development progressed. However, there was no significant correlation between temperature tolerance and temperature preference. Different acclimation temperatures at a median developmental stage had no effect on temperature preference. Critical thermal maxima and minima were studied for various acclimation temperatures for the tadpoles at ten stages of development.

Informal defining equations for a specific 'chunk' of heat energy as a resource of the subject tadpole and for another tadpole as a modifier are:

(heat)Res(tadpole) $=_{\mathrm{df}}$ H(tadpole) is increased $|$ ξ(heat)(tadpole).

(other tadpole)Mod^{+1}(tadpole) $=_{\mathrm{df}}$ ($\exists$ heat) such that [(heat)Res(tadpole) $|$ ξ(other tadpole)(tadpole) and $\sim$(heat)Res(tadpole) $|$ $\sim$$\xi$(other tadpole)(tadpole)].

26. Hinckley (1962), working in Fiji, reports that the animal eats dung beetles of the genera *Copris* and *Aphodius*. Cattle are included as second-order modifiers; almost any animal passing faeces could be included here.

The informal defining equations for a beetle as a resource, a particular dropping of dung as a modifier of that resource, and a particular cow as the provider of the dung and therefore a positive second-order modifier, are:

(beetle)Res(toad) $=_{\mathrm{df}}$ H(toad) is increased and H(beetle) is decreased $|$ ξ(beetle)(toad)

(dung)Mod^{+1}(toad) $=_{\mathrm{df}}$ ($\exists$ beetle) such that [(beetle)Res(toad) $|$ ξ(dung)(beetle) and $\sim$(beetle)Res(toad) $|$ $\sim$$\xi$(dung)(beetle)]

(cow)Mod^{+2}(toad) $=_{\mathrm{df}}$ ($\exists$ dung) such that [(dung)Mod^{1}(toad) $|$ $\sim$$\xi$(cow)(dung) and $\sim$(dung)Mod^{1}(toad) $|$ ξ(cow)(dung)].

27. Hinckley (1962), in Fiji, reports that adult toads occasionally choked to death when trying to swallow young mynahs and chickens.

A class of malentities '[oversized food]' is shown on the envirogram. The informal defining equation for a particular mynah as a malentity is:

(mynah)Mal(toad) $=_{\mathrm{df}}$ H(toad) is decreased and H(mynah) is decreased $|$ ξ(mynah)(toad).

28. Hutchinson and Kohl (1971) measured metabolic rate in terms of oxygen consumption and found that changes in metabolic rate were governed by the photoperiod (i.e. no internal rhythm was observed). Under various regimes of photoperiod, a pronounced decrease ion metabolic rate occurred in the two to three hours after onset of the photophase and a peak in metabolic rate in the corresponding two to three hours after darkness.

The informal defining equations for a particular 'chunk' of oxygen as a resource and a specific 'chunk' of light energy as a modifier are:

(oxygen)Res(toad) $=_{df}$ H(toad) is increased | ξ(oxygen)(toad)

(light)Mod^{-1}(toad) $=_{df}$ ($\exists$ oxygen) such that [(oxygen)Res(toad) | $\sim\xi$(light)(toad) and $\sim$(oxygen)Res(toad) | ξ(light)(toad)].

29. Illingworth (1941) reports that the ants *Pheidole megacephala* are eaten only on rainy nights, apparently giving away their position by throwing up mounds of soil. The informal defining equations are:

(ant)Res(toad) $=_{df}$ H(toad) is increased and H(ant) is decreased | ξ(ant)(toad)

(rain)Mod^{+1}(toad) $=_{df}$ ($\exists$ ant) such that [(ant)Res(toad) | ξ(rain)(ant) and $\sim$(ant)Res(toad) | $\sim\xi$(rain)(ant)].

30. Jakowska (1972), in the Dominican Republic, reports the tick *Amlyomma dissimile* as producing lesions on *B. marinus*. Female ticks will feed for five or six days on the toad, breed, then fall off. The young ticks may infest other toads so that infested toads, or the other known host, the iguana *Cyclura cornuta*, are first-order modifiers. The same tick was reported in Trinidad by Lever (1938).

The informal defining equations are:

(tick)Pred(toad) $=_{df}$ H(toad) is decreased and H(tick) is increased | ξ(tick)(toad)

(iguana)Mod^{-1}(toad) $=_{df}$ ($\exists$ tick) such that [(tick)Pred(toad) | $\sim\xi$(iguana)(tick) and $\sim$(tick)Pred(toad) | ξ(iguana)(tick)].

31. Johnson (1976) gives the following TL_{50} (50% tolerance limit) concentrations in ppm (μg/ml) for tadpoles:

TL_{50} values for herbicides with anurans in bioassays conducted at 21–22°C

Toxicant	24 h	48 h	96 h
Fenoprop	60	42	34
Sodium arsenate	195	150	123
2,4,5-T amine	425	382	340
2,4D amine	346	333	288

Chemical compositions of these toxicants may be found in Johnson's article.

These herbicides may enter the locality in at least two ways: by direct spraying and through run-off from spraying of the littoral area.

B. marinus tadpoles were more resistant than other anurans tested.

The informal defining equations for a particular 'chunk' of a particular herbicide as a malentity, for 'run-off' (an object consisting of a particular 'chunk' of water moving in the right direction) as a first-order modifier, and for a human (who puts the herbicide into the system) as a second-order modifier, are:

(herbicide)Mal(tadpole) $=_{df}$ H(tadpole) is decreased | ξ(herbicide)(tadpole)

(run-off)Mod^{+1}(tadpole) $=_{df}$ ($\exists$ herbicide) such that [(herbicide)Mal(tadpole) | ξ(run-off)(herbicide) and $\sim$(herbicide)Mal(tadpole) | $\sim\xi$(run-off)(herbicide)]

(human)Mod^{+2}(tadpole) $=_{df}$ ($\exists$ run-off) such that [(run-off)Mod^{1}(tadpole) | ξ(human)(run-off) and $\sim$(run-off)Mod^{1}(tadpole) | $\sim\xi$(human)(run-off)].

32. Kloss (1974) reports the following four nematodes (Rhabditoidae) infesting *B. marinus*: *Rhabdias sphaerocephala* Goodey 1924; *R. fuelleborni* Travassos 1927; *R elegans* Gutierrez 1945; *R. hermaphrodita* Kloss 1971. All species have a complex two-generation life cycle: a free-living generation in the excrement of the host which will penetrate the skin of almost any animal; and an hermaphroditic generation within the host, usually in the lungs.

The informal defining equation is:

> (nematode)Pred(toad) $=_{\mathrm{df}}$ H(toad) is decreased and H(nematode) is increased | ξ(nematode)(toad).

33. Except for a few instances of diurnal feeding (e.g. see note 5; Alexander 1964), the usual adult cycle is one of nocturnal activity and diurnal disappearance. Zug and Zug (1979) found that not all individuals are active in feeding, even during optimum conditions and abundance, which suggests that toads feed maximally when active and then retire for several days to assimilate their food. In the wet season in Papua, at least 31% of the population were active on any one night, with a maximum of 50% on one particular night. Most toads reached a peak of activity about two hours after dusk.

A detailed study by Jaeger and Hailman (1981), in which they made illumination measures, showed that the toad is active at night in bright, open places such as mud flats or grassy lawns and is usually inactive during the day. Feeding appeared to be confined to dim illumination at night; they never observed foraging during the day. Two individuals became active shortly before dark when general illumination was 20 and 60 lux, while the others waited until the illumination was less than 0·01 lux.

The informal defining equation for a 'chunk' of light energy as a first-order modifier of some specific food object is:

> (light)Mod^{-1}(toad) $=_{\mathrm{df}}$ ($\exists$ food) such that [(food)Res(toad) | $\sim\xi$(light)(food) and $\sim$(food)Res(toad) | ξ(light)(food)].

34. It is not known whether *B. marinus* drinks. However, M. J. Tyler (pers. comm.) writes, 'To the best of my knowledge there is no record of any species of frog drinking'. Like all amphibians, water is absorbed through the skin. Krakauer (1970) reports that *B. marinus* survived 140 d (i.e. to termination of experiment) immersed in distilled water. Heatwole and Newby (1972) determined that activity greatly influences evaporative water loss. In plotting activity against hydrated weight, they found that *B. marinus* was most active between 50 and 59% of its fully hydrated weight and that it still remained active when its percentage weight was as low as 30–39%. They concluded that the animal was well adapted to relatively dry conditions.

Krakauer (1970) tested the toad's dehydration tolerance. The following figures are from Table 1 of his article (the values in parentheses are for *Rana pipiens*):

Weight (g)	84·4	(10·4)
Body water (%)	77·2	(83·5)
Tolerance (%)	52·6	(52·2)
Essential water (%)	60·9	(70·8)

'Body water' is the difference between wet weight (empty bladder) and oven-dried weight as a percentage of body weight. 'Tolerance' is the lethal limit of desiccation, i.e. the difference between wet weight and weight at death as a percentage of (wet weight − dry weight). 'Essential water' is the difference between weight at death and dry weight as a percentage of weight at death.

Machin (1969), in laboratory experiments, showed that low humidity and high air flow over the toad are important factors in evaporative water loss. He comments that toad skin acts as a diffusion barrier and that it becomes less permeable as the humidity drops. For tadpoles, heat energy can be a malentity in another way; Gomoll (1968) in Guam, and others comment that occasionally *B. marinus* lays eggs in small puddles that are in danger of drying up.

Zug and Zug (1979) suggest that the ideal time for metamorphosis would be the beginning of the wet season when high humidity permits rapid and distant dispersal. Takana and Iijima (1939) find that toadlets die quickly if the relative humidity is below 70–80%.

Of several species of tadpole tested, Valerio (1971) reports *B. marinus* as being the second least resistant to being removed from water (he used tadpoles which had reached a late stage). Of ten *B. marinus* tadpoles, all survived up to seven hours and all were dead by ten hours.

In Papua, Zug and Zug (1979) noticed greatly reduced activity among the toads in the dry season. As the number of consecutive dry days increases, the activity of the population decreases. They suggest two causes of this decrease: *1* during the dry season, there are less prey available, and *2* there is a high water loss from the animal. They suggest that the toad uses a crouched posture to lessen the skin area through which water can evaporate (see also note 3). They report also that hydration occurs faster in water than in saturated soil. The rate of water loss is size-dependent. Large toads lose more water at a faster rate but, because they have much more water to lose, they survive better.

We have assumed above that we are discussing healthy animals. However, in the case reported in note 22, near-starving toads that ranged too far from cover in search of food during the night died of dehydration in the morning sun, being too weak to return (Bailey 1976; Tyler 1976).

The informal defining equations for a 'chunk' of water as a resource and the subject toad itself as a modifier of that resource (by reducing its activity) are:

$$\text{(water)Res(subject toad)} =_{\text{df}} \text{H(subject toad) is increased} \mid \xi\text{(water)(subject toad)}$$

$$\begin{aligned}&\text{(subject toad)Mod}^{+1}\text{(subject toad)} =_{\text{df}} (\exists \text{ water) such that}\\&[\text{(water)Res(subject toad)} \mid \xi\text{(subject toad)(subject toad) and}\\&\sim\text{(water)Res(subject toad)} \mid \sim\xi\text{(subject toad)(subject toad)}].\end{aligned}$$

35. Krakauer (1970) reports that toads placed in seawater (15% NaCl) 'thrashed around' immediately and all died within hours. At 10% NaCl, there was 100% survival after 96 h.

Curiously, Wingate (1965), in Bermuda, writes, 'adults occasionally swim across salt waters to the smaller islets and I once intercepted a large adult specimen swimming ashore on Nonsuch Island from the mainland 1500 ft (457·2 m) distant'.

Here it is assumed that salt is a malentity. The informal defining equation is:

$$\text{(salt)Mal(toad)} =_{\text{df}} \text{H(toad) is decreased} \mid \xi\text{(salt)(toad)}.$$

36. Mares (1972) comments that in experiments with tadpoles, crowding inhibits growth. This has not been observed in the wild. We have tentatively classified 'other tadpoles' as malentities because inhibited growth may reduce 'H'. The informal defining equation for another tadpole as a malentity is:

$$\begin{aligned}&\text{(other tadpole)Mal(tadpole)} =_{\text{df}} \text{H(tadpole) is decreased and H(other tadpole)}\\&\text{is decreased} \mid \xi\text{(other tadpole)(tadpole)}.\end{aligned}$$

37. Mares (1972) reports a tadpole captured by a dragonfly larva (Odonata) but released after a struggle. The informal defining equation for a dragonfly as a predator is:

$$\begin{aligned}&\text{(dragonfly)Pred(tadpole)} =_{\text{df}} \text{H(tadpole) is decreased and H(dragonfly) is}\\&\text{increased} \mid \xi\text{(dragonfly)(tadpole)}.\end{aligned}$$

38. There is an unknown but significant predator of *B. marinus* in northern Australia. This predator disembowels the toad and consumes the viscera. Cassels (1970) reports a koel

(*Eudynamys scolopacea*) killing and eating two toads in this way. Several ecologists support the theory that the predator is the white-tailed water rat (*Hydromys chrysogaster*). Frauca (1974) often observed the Australian crow (*Corvus orru*) eating dead toads from the road in similar fashion.

The informal defining equation for a koel as a predator is:

> (koel)Pred(toad) $=_{\text{df}}$ H(toad) is decreased and H(koel) is increased | ξ(koel)(toad).

39. *B. marinus* in Hawaii eats the adults of the oriental beetle *Ardoretus sinicus* Burm., which feed at night on many plants including rose, grape, cycad, okra, bean, soya bean, pigeon pea, sweet potato, asparagus, taro, banana, cotton, canna, acalypha, Mexican creeper. Many larvae and pupae of the beetle are killed by the green muscadine fungus *Metarrhizium anisopliae*. Larvae are also parasitised by the Scolia wasp *Campsomeris marginella modesta* Smith and the rolling wasp *Tiphia segregata* Crawf. Lights discourage the beetle (contrast with note 5). Arsenate of lead is effectively used by gardeners (Fullaway and Krauss 1945).

In Queensland, Mungomery (1936*a*) reports that the scarabaeid beetle population emerges in full force only during the wetter period of the year.

The informal defining equations for the beetle as a resource, a specific 'chunk' of light as a first-order modifier, and a particular human who acts as a second-order modifier by providing a light, are:

> (beetle)Res(toad) $=_{\text{df}}$ H(toad) is increased and H(beetle) is decreased | ξ(beetle)(toad)
>
> (light)Mod^{-1}(toad) $=_{\text{df}}$ ($\exists$ beetle) such that [(beetle)Res(toad) | $\sim\xi$(light)(beetle) and $\sim$(beetle)Res(toad) | ξ(light)(beetle)]
>
> (human)Mod^{+2}(toad) $=_{\text{df}}$ ($\exists$ light) such that [(light)Mod^{1}(toad) | ξ(human)(light) and $\sim$(light)Mod^{1}(toad) | $\sim\xi$(human)(light)].

40. *B. marinus* eats the adults of this beetle (*Pantomorus* sp.) which feeds on at least the following: geranium, hibiscus, bean, alfalfa, citrus, boa (*Acacia koa*), ti (*Cordyline terminalis*), sugarcane. Larvae are eaten by the click beetle (*Monocrepidus exsul*) and adults are also eaten by mynah birds and mongooses. This beetle, like the scarab, is also controlled by arsenate of lead (Fullaway and Krauss 1945).

The informal defining equations for the beetle as a resource and a mynah bird as a first-order modifier are:

> (beetle)Res(toad) $=_{\text{df}}$ H(toad) is increased and H(beetle) is decreased | ξ(beetle)(toad)
>
> (mynah)Mod^{-1}(toad) $=_{\text{df}}$ ($\exists$ beetle) such that [(beetle)Res(toad) | $\sim\xi$(mynah)(beetle) and $\sim$(beetle)Res(toad) | ξ(mynah)(beetle)].

41. *B. marinus* is known to eat domestic bees. Goodacre (1947) reports finding 300 bees in the stomach contents of one toad. Apiarists have adopted the practice of raising their hives on stakes two feet in height to prevent this predation. The toads seem to suffer no ill effects from being stung.

The informal defining equations for a bee as a resource, a raised hive as a modifier, and a human as a second-order modifier, are:

> (bee)Res(toad) $=_{\text{df}}$ H(toad) is increased and H(bee) is decreased | ξ(bee)(toad)
>
> (hive)Mod^{-1}(toad) $=_{\text{df}}$ ($\exists$ bee) such that [(bee)Res(toad) | $\sim\xi$(hive)(bee) and $\sim$(bee)Res(toad) | ξ(hive)(bee)]

$$(\text{human})\text{Mod}^{+2}(\text{toad}) =_{\text{df}} (\exists \text{ hive}) \text{ such that } [(\text{hive})\text{Mod}^{1}(\text{toad}) \mid \xi(\text{human})(\text{hive}) \text{ and } \sim(\text{hive})\text{Mod}^{1}(\text{toad}) \mid \sim\xi(\text{human})(\text{hive})].$$

42. Zug and Zug (1979) observed an instance of *B. marinus* following the calls of male frogs of the species *Physalaemus pustulosus* to their pool and later eating two of them. Other observations suggest that *B. marinus* recognises the various sounds made by prey. However, vision appears to be the toad's primary sense (see also note 54 on cricket song).

The informal defining equations for a frog as a resource and a 'chunk' of 'sound energy' (strictly, kinetic energy) as a modifier is:

$$(\text{frog})\text{Res}(\text{toad}) =_{\text{df}} H(\text{toad}) \text{ is increased and } H(\text{frog}) \text{ is decreased} \mid \xi(\text{frog})(\text{toad})$$

$$(\text{sound})\text{Mod}^{+1}(\text{toad}) =_{\text{df}} (\exists \text{ frog}) \text{ such that } [(\text{frog})\text{Res}(\text{toad}) \mid \xi(\text{sound})(\text{toad}) \text{ and } \sim(\text{frog})\text{Res}(\text{toad}) \mid \sim\xi(\text{sound})(\text{toad})].$$

43. The *Phylophaga* spp. listed in note 16, often called the 'May' or 'June' beetles are attracted by at least the following fruit trees (Dexter 1932): banana (*Musa* sp.); casuarina (*Casuarina equisetifolia*); flamboyant (*Delonix regia*); almendro (*Terminalia catappa*); guava (*Inga laurina*); coconut (*Cocos nucifera*); breadfruit (*Artocarpus communis*); trumpet (*Cecropia peltata*).

Smyth (1917) lists many other plants 'greatly relished' by *Phyllophaga*, including: salcilla (*Schrankia portoricensis*), quenepa (*Melia azedarach*), tamarind (*Tamarindus indicus*), jobo (*Spondias lutea*), cecropia (*Cecropia palmata*), pigweed, or bledo (*Amaranthus* spp.), mallow (*Malachra rotundifolia*), and *Petiveria alliacea*. He also mentions that adult *Phylophaga vandinei* are strongly attracted to light.

Diaspore dispersal can be categorised by the operative energy source(s). The major division is between parent plant energy and external energy sources. The latter will include various agencies such as humans, animals, wind, water etc. (M. J. Liddle and A. Bulow-Olson, pers. comm.), all of which appear in the environment of the toad as second-order modifiers. Some of these modifiers may work in combination, modifying each other and thus entering the environment as third-order modifiers in the formal sense.

The informal defining equations for a particular plant as a first-order modifier and a particular human as a second-order modifier are:

$$(\text{plant})\text{Mod}^{+1}(\text{toad}) =_{\text{df}} (\exists \text{ beetle}) \text{ such that } [(\text{beetle})\text{Res}(\text{toad}) \mid \xi(\text{plant})(\text{beetle}) \text{ and } \sim(\text{beetle})\text{Res}(\text{toad}) \mid \sim\xi(\text{plant})(\text{beetle})]$$

$$(\text{human})\text{Mod}^{+2}(\text{toad}) =_{\text{df}} (\exists \text{ plant}) \text{ such that } [(\text{plant})\text{Mod}^{1}(\text{toad}) \mid \xi(\text{human})(\text{plant}) \text{ and } \sim(\text{plant})\text{Mod}^{1}(\text{toad}) \mid \sim\xi(\text{human})(\text{plant})].$$

44. Zug and Zug (1979) suggest, from a study of fat body weight, that in some areas the females require a period of intense feeding to replenish their lipid stores before vitellogenesis can begin. In this sense, therefore, an item of food modifies the female mate of a male adult subject toad. The informal defining equation for a specific item of food is:

$$(\text{food})\text{Mod}^{+1}(\text{toad}) =_{\text{df}} (\exists \text{ female toad}) \text{ such that } [(\text{female toad})\text{Mat}(\text{toad}) \mid \xi(\text{food})(\text{female toad}) \text{ and } \sim(\text{female toad})\text{Mat}(\text{toad}) \mid \sim\xi(\text{food})(\text{female toad})].$$

45. Mungomery (1936*b*) observes that male toads can change their sex, although the conditions (if any) which induce such a change are not known. The mechanism is as follows: a rudimentary ovary, the Bidders organ, is present in all young toads. Subsequently, it degenerates in females but persists in males. Internal secretions may bring about a slow change from male to female, with the Bidders organ functioning as an ovary. Eggs are normal but markedly fewer.

Zug and Zug (1979) report that in field data on *B. marinus*, there is a marked tendency towards one sex only being observed—either male or female—and that there is no known explanation of this. However, R. B. Floyd (pers. comm., 1981) suggests that collection time, site and method of collection, all have a big influence on which sex is actually collected. Van Beurden (1978), in Queensland, reports a 1 : 1 sex ratio.

Lucas (1969) reports that, at Stuttgart zoo, a toad hybrid, *B. blombergi* × *B. marinus*, was raised.

If Mungomery is correct in the observation that a male toad can change its sex, there is presumably a time after which such an animal is available as a mate, in the formal sense, of a subject male. In this case, at that particular time, one might argue that the new female has interacted with itself in order to enter the environment of the subject male; the mutated toad is thus a modifier of itself. This has not been entered on the envirogram, since the whole argument is tenuous. However, the informal defining equation is given here:

$$\begin{aligned}&(\text{mutated toad})\text{Mod}^{+1}(\text{toad}) =_{\text{df}} (\exists \text{ mutated toad}) \text{ such that}\\&[(\text{mutated toad})\text{Mat}(\text{toad}) \mid \xi(\text{mutated toad})(\text{mutated toad}) \text{ and}\\&\sim(\text{mutated toad})\text{Mat}(\text{toad}) \mid \sim\xi(\text{mutated toad})(\text{mutated toad})].\end{aligned}$$

46. Takano and Iijima (1937) find that the presence of calcium chloride ($CaCl_2$) is essential for tadpole development. The informal defining equation is:

$$(CaCl_2)\text{Res}(\text{tadpole}) =_{\text{df}} \text{H}(\text{tadpole}) \text{ is increased} \mid \xi(CaCl_2)(\text{tadpole}).$$

47. Takano and Iijima (1939) note that, in crowded conditions, large tadpoles eat smaller ones. The informal defining equation is:

$$\begin{aligned}&(\text{larger tadpole})\text{Pred}(\text{tadpole}) =_{\text{df}} \text{H}(\text{tadpole}) \text{ is decreased and H}(\text{larger tadpole})\\&\text{is increased} \mid \xi(\text{larger tadpole})(\text{tadpole}).\end{aligned}$$

48. The giant water beetles (Dytiscidae) *Hydrophilus ater* and *Megadytes giganteus* are reported by Tucker (1940) as attacking *B. marinus* tadpoles in Barbados. The informal defining equation is:

$$\begin{aligned}&(\text{water beetle})\text{Pred}(\text{tadpole}) =_{\text{df}} \text{H}(\text{tadpole}) \text{ is decreased and H}(\text{water beetle})\\&\text{increased} \mid \xi(\text{water beetle}) (\text{tadpole}).\end{aligned}$$

49. Young tadpoles use their gills to obtain oxygen. Older tadpoles have lungs and can rise to the surface to breathe. This is an advantage in warm waters which have a lower oxygen content. Even with lungs, tadpoles can still use their gills (Tyler 1975; M. J. Tyler, pers. comm.).

The informal defining equation for a specific 'chunk' of oxygen as a resource is:

$$(\text{oxygen})\text{Res}(\text{tadpole}) =_{\text{df}} \text{H}(\text{tadpole}) \text{ is increased} \mid \xi(\text{oxygen})(\text{tadpole}).$$

50. Tyler (1975) reports that (in Australia) the fork-tailed kite and ibis and (in Bermuda) herons eat both juvenile and adult toads (see also note 38).

The informal defining equation for a heron as a predator is:

$$\begin{aligned}&(\text{heron})\text{Pred}(\text{toad}) =_{\text{df}} \text{H}(\text{toad}) \text{ is decreased and H}(\text{heron}) \text{ is increased} \mid\\&\xi(\text{heron})(\text{toad}).\end{aligned}$$

51. Van Beurden (1978) showed that there was high dietary overlap of *Lymnodynastes terraereginae* and other frogs with *B. marinus* at Lake Ainsworth in Queensland. He remarks that the observed declining populations of the toad may be due to this competition.

A particular frog which competes with the subject toad for a particular item of food is a modifier of that particular resource. The informal defining equation is:

$$(\text{frog})\text{Mod}^{-1}(\text{toad}) =_{\text{df}} (\exists\ \text{food})\ \text{such that}\ [(\text{food})\text{Res}(\text{toad}) \mid {\sim}\xi(\text{frog})(\text{food})\ \text{and}\ {\sim}(\text{food})\text{Res}(\text{toad}) \mid \xi(\text{frog})(\text{food})].$$

52. Takano and Iijima (1937) observe that tadpoles will develop in pH range 4–9. If they mean by this that the tadpole will not develop outside this range, then pH, like heat energy (see note 12), will have a range that constitutes resources and another that constitutes malentities.

The informal defining equation for a 'chunk' of water with too low a pH for the tadpole to develop follows. In order to make it clear, the object is referred to as 'hydrogen ions' on the envirogram.

$$(\text{acid})\text{Mal}(\text{tadpole}) =_{\text{df}} \text{H}(\text{tadpole})\ \text{is decreased} \mid \xi(\text{acid})(\text{tadpole}).$$

53. Breder (1946) reports tadpoles of *Rana palmipes* eating *B. marinus* eggs. The informal defining equation for an *R. palmipes* tadpole as a predator of a subject egg is:

$$(\text{tadpole})\text{Pred}(\text{egg}) =_{\text{df}} \text{H}(\text{egg})\ \text{is decreased and H}(\text{tadpole})\ \text{is increased} \mid \xi(\text{tadpole})(\text{egg}).$$

54. Cade and Rice (1960) show that the field cricket *Teleogryllus oceanicus* (Le Guillou) is eaten by the toad in Hawaii. In their observations of 116 toad droppings, 68 contained cricket remains. 'All atempts to lure *B. marinus* to taped *T. oceanicus* song were unsuccessful. Even when song was broadcast close to the toads, they showed no apparent response. When crickets were placed in front of the toads, however, they were often eaten.' (see note 7 on moving organisms and note 42 on Zug and Zug's observation on calls of frogs).

The informal defining equation for a cricket as a resource is:

$$(\text{cricket})\text{Res}(\text{toad}) =_{\text{df}} \text{H}(\text{toad})\ \text{is increased and H}(\text{cricket})\ \text{is decreased} \mid \xi(\text{cricket})(\text{toad}).$$

55. Hutchings (1979) reports that the crayfish *Cherox* will eat *B. marinus* tadpoles with no ill effects, also that three species of *Euastacus*, a freshwater crayfish, will prey on adult toads, tear them apart and eat the limbs and the viscera.

The informal defining equation for a crayfish as a predator of a subject tadpole is:

$$(\text{crayfish})\text{Pred}(\text{tadpole}) =_{\text{df}} \text{H}(\text{tadpole})\ \text{is decreased and H}(\text{crayfish})\ \text{is increased} \mid \xi(\text{crayfish})(\text{tadpole}).$$

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References

Abel, J. J., and Macht, M. I. (1911). The poisons of the tropical toad, *Bufo agua*. *J. Am. Med. Assoc.* **56**, 1531–6.

Abel, J. J., and Macht, D. I. (1912). Two crystalline pharmacological agents obtained from the tropical toad, *Bufo agua*. *J. Pharmacol. and Exp. Ther.* **3**, 319–77.

Adams, N. G. K. (1967). *Bufo marinus* eaten by *Rattus rattus*. *N. Qld Nat.* **34**, 5.

Alcala, A. C. (1957). Philippine notes on the ecology of the Giant Marine Toad. *Silliman J.* **4**, 90–6.

Alexander, T. R. (1964). Observations on the feeding behavior of *Bufo marinus* (Linne). *Herpetologica* **20**, 225–9.

Allen, E. R., and Neill, W. T. (1956). Effect of marine toad toxins on man. *Herpetologica* **12**, 150–1.

Bailey, P. (1976). Food of the marine toad, *Bufo marinus*, and six species of skink in a cacao plantation in New Britain, Papua New Guinea. *Aust. Wildl. Res.* **3**, 185–8.

Baldwin, P. H., Schwartz, C. W., and Schwartz, E. R. (1952). Life history and economic status of the mongoose in Hawaii. *J. Mammal.* **33**, 335–6.

Bianchi, F. A., and Easteal, S. (1981). Eating habits of *Bufo marinus*. Unpublished.

Blair, A. P. (1947). Defensive use of parotoid secretion by *Bufo marinus*. *Copeia* **1947**, 137.

Boice, R., and Boice, C. (1971). Interspecific competition in captive *Bufo marinus* and *Bufo americanus* toads. *J. Biol. Psychol.* **21**, 32–6.

Boughton, W. C., and Sabath, M. D. (1980). The distribution records of the marine toad *Bufo marinus*. Part 1: Australia. AES Working Paper 2/80. (School of Australian Environmental Studies, Griffith University: Nathan, Aust. 4111.)

Brattstrom, B. H. (1960). Thermoregulation in tropical amphibians. *Yearb. Am. Phil. Soc. (1960)* 284–7.

Brattstrom, B. H. (1962*a*). Thermal control of aggregation behavior in tadpoles. *Herpetologica* **18**, 38–46.

Brattstrom, B. H. (1962*b*). Homing in the giant toad *Bufo marinus*. *Herpetologica* **18**, 176–80.

Brattstrom, B. H. (1963). A preliminary review of the thermal requirements of amphibians. *Ecology* **44**, 238–55.

Brattstrom, B. H. (1968). Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol.* **23**, 93–111.

Brattstrom, B. H., and Adis, N. B. (1952). Notes on a collection of reptiles and amphibians from Oaxaca, Mexico. *Herpetologica* **8**, 59–60.

Brattstrom, B. H., and Howell, T. A. (1954). Notes on some collections of reptiles and amphibians from Nicaragua. *Herpetologica* **10**, 114–23.

Breder, C. M. (1946). Amphibians and reptiles of the R W Chucunaque Drainage, Darien, Panama, with notes on their life histories and habits. *Bull. Am. Mus. Nat. Hist.* **86**, 375–436.

Buzacott, J. H. (1936). How frequently do giant toads produce eggs? *Cane Gr. Quart. Bull.* **25**, 1–5.

Buzacott, J. H. (1939). Toads and fowls. *Proc. Cane Pests Board Conference, Mackay 1939*, 28–9.

Cade, W. H., and Rice, R. (1980). Field crickets (Orthoptera : Gryllidae) as prey of the toad *Bufo marinus*. *Can. Entomol.* **112**, 335–6.

Camhi, J. M. (1980). The escape system of the cockroach. *Sci. Am.* **243**, 144–56.

Cassels, A. J. (1966). Disembowelled toads near water. *N. Qld Nat.* **34**, 6.

Cassels, M. (1920). As told by Dr Watsford (1970). Another predator on the Cane Toad (*Bufo marinus*). *N. Qld Nat.* **37**, 6.

Chen, K. K., and Chen, A. L. (1933). Notes on the poisonous secretions of twelve species of toads. *J. Pharmacol. and Exp. Ther.* **47**, 281–93.

Covacevich, J., and Archer, M. (1975). The distribution of the cane toad, *Bufo marinus*, in Australia and its effects on indigenous vertebrates. *Mem. Queensl. Mus.* **17**, 305–10.

Dean, J. (1980*a*). Encounters between Bombardier beetles and two species of toads (*Bufo americanus*, *B. marinus*): speed of prey-capture does not determine success. *J. Comp. Physiol.* **135**, 41–50.

Dean, J. (1980*b*). Effect of thermal and chemical components of Bombardier beetle chemical defense: glosopharyngeal response in two species of toads (*Bufo americanus*, *B. marinus*). *J. Comp. Physiol.* **135**, 51–9.

Dexter, R. R. (1932). The food habits of the imported toad, *Bufo marinus*, in the sugar cane sections of Puerto Rico. Bulletin No. 74, Proc. Fourth Cong. International Society of Sugar Cane Technologists, San Juan, Puerto Rico, 2–6.

Duellman, W. E. (1965). A biogeographic account of the herpetofauna of Michoacan, Mexico. *Univ. Kans. Publ. Mus. Nat. Hist.* **15**, 627–709.

Easteal, S. (1981). The history of introductions of *Bufo marinus* (Amphibia : Anura); a natural experiment in evolution. *Biol. J. Linn. Soc.* **16**, 93–113.

Easteal, S. (1982). The genetics of introduced populations of the marine toad, *Bufo marinus* (Linneaus) (Amphibia : Anura); a natural experiment in evolution. Ph.D. Thesis, School of Australian Environmental Studies, Griffith University, Brisbane.)

Ely, C. A. (1944). Development of *Bufo marinus* larvae in dilute sea water. *Copeia* 1944, 256.

Fellows, A. G. (1969*a*). Toads and termites. *Victorian Nat.* **86**, 136.

Fellows, A. G. (1969*b*). Cane beetles and toads. *Victorian Nat.* **86**, 165.

Fife, K. V. (1973). The visual fields of the frog and toad: a comparative study. *Behav. Biol.* **9**, 707–18.

Floyd, R. B. (1983). Ontogenetic change in the temperature tolerance of larval *Bufo marinus* (Anura : Bufonidae). *Comp. Biochem. Physiol.* **75A**, 267–71.

Floyd, R. B. (1984*a*). Variation in temperature preference with stage of development of *Bufo marinus* larvae. *J. Herpetol.* **18**, 153–8.

Floyd, R. B. (1984*b*). Thermal physiology of *Bufo marinus* embryos in larvae: the ecological significance of laboratory observations. Ph.D. Thesis, School of Australian Environmental Studies, Griffith University, Brisbane.)

Floyd, R. B., and Benbow, K. F. (1984). Nocturnal activity of a population of cane toads. *Koolewong* 12–14.

Frauca, H. (1974). Crows. Channel-bill Cuckoos and Cane Toads. *Aust. Birdl.* **1**, 112–14.

Freeland, W. J. (1984). Cane toads: a review of their biology and impact on Australia. (Conservation Commission of the Northern Territory: Winnellie, N.T.)

Fullaway, D. T., and Krauss, N. L. H. (1945). Common Insects of Hawaii. (Tougg Publishing: Honolulu.)

Gomoll, L. (1968). Terrestrial animals. Chapter 3. In 'A Naturalist's Guide to Guam'. (Ed. R. E. Key.) (Agana: Guam.)

Goodacre, W. A. (1947). The giant toad (*Bufo marinus*), an enemy of bees. *N.S.W. Agric. Gaz.* **58**, 374–5.

Grant, C. (1948). Selection between armed and unarmed arthropods as food by various animals. *J. Ent. Zool. Clarmont Cal.* **40**, 66.

Harding, R., and Catterall, C. P. (1983). Small-scale patterns of variation at the Sorbitol Dehydrogenase locus in an introduced toad, *Bufo marinus* (Amphibia : Anura). *Aust. J. Zool.* **31**, 913–23.

Heatwole, H., and Newby, R. C. (1972). Interaction of internal rhythm and loss of body water in influencing activity levels of amphibians. *Herpetologica* **28**, 156–62.

Heatwole, H., de Austin, S. B., and Herrero, R. (1968). Heat tolerances of two species of tropical anurans. *Comp. Biochem. Physiol.* **27**, 807–15.

Hinckley, A. D. (1962). Diet of the Giant Toad *Bufo marinus* (L.) in Fiji. *Herpetologica* **18**, 253–9.

Hutchings, R. W. (1979). A native predator of the cane toad (*Bufo marinus*). *N. Qld Nat.* **45(124)**, 4–5.

Hutchinson, V. H., and Kohl, M. A. (1971). The effect of photoperiod on daily rhythms of oxygen consumption in the tropical toad, *Bufo marinus*. *Z. Vergl. Physiol.* **75**, 367–82.

Illingworth, J. F. (1941). Feeding habits of *Bufo marinus*. *Proc. Hawaii. Entomol. Soc.* **11**, 51.

Ingle, D., and McKinley, D. (1978). Effects of stimulus configuration on elicited prey catching by the marine toad (*Bufo marinus*). *Anim. Behav.* **26**, 885–91.

Jaeger, R. G., and Hailman, J. P. (1981). Activity of neotropical frogs in relation to ambient light. *Biotropica* **13**, 59–65.

Jakowska, S. (1972). Lesions produced by ticks *Amblyomma dissimile* in *Bufo marinus* toads from the Dominican Republic. *Am. Zool.* **12**, 731.

Johnson, C. R. (1972). Thermal relations and daily variation in the thermal tolerance of *Bufo marinus*. *J. Herpetol.* **6**, 35–8.

Johnson, C. R. (1976). Herbicide toxicities in some Australian anurans and the effect of subacute dosages on temperature tolerance. *Zool. J. Linn. Soc.* **59**, 79–83.

King, W. (1969). Adaptions for nocturnal survival. *Anim. Kingdom* **72**, 29–32.

Kloss, G. R. (1974). *Rhabdias* (Nematoda, Rhabditoidae) from the *marinus* group of *Bufo*: a study of sibling species. *Arq. Zool.* **25**, 61–120.

Knowles, R. P., and Levin, J. (1964). The poison toad and the canine. *Small Animal Clinician* **59**, 39 42.

Krakauer, T. (1968). The ecology of the neotropical toad, *Bufo marinus* in South Florida. *Herpetologica* **24**, 214–21.

Krakauer, T. (1970). Tolerance limits of the toad *Bufo marinus* in South Florida. *Comp. Biochem. Physiol.* **33**, 15–26.

La Rivers, I. (1948). Some Hawaiian ecological notes. *Wassman Collector* **7**, 85–110.

Lawson, W. J. (1987). The Cane toad *Bufo marinus*: a bibliography. Griffith University, School of Australian Environmental Studies Working Paper 1/87.

Lehmann, D. L. (1966). Two blood parasites of Peruvian amphibia. *J. Parasitol.* **52**, 613.

Lever, R. J. A. W. (1937). The giant toad. *Fiji Agric. J.* **8**, 36.

Lever, R. J. A. W. (1938). The giant toad—distribution, diet and development. *Fiji Agric. J.* **9**, 28.

Lever, R. J. A. W. (1944). Food of the giant toad. *Fiji Agric. J.* **15**, 28.

Lever, R. J. A. W. (1945). The giant toad in the Solomon Islands. *Fiji Agric. J.* **16**, 88.

Licht, L. E. (1967). Death following possible ingestion of toad eggs. *Toxicon* **5**, 141–2.

Licht, L. E., and Low, B. (1968). Cardiac responses of snakes after ingestion of toad parotoid venom. *Copeia* 1968; 547–51.

Lucas, J. (ed) (1969). 'International Zoo Yearbook.' Vol. 19. (Zoological Society of London: London.)

Machin, J. (1969). Passive water movements through skin of the toad *Bufo marinus* in air and in water. *Am. J. Physiol.* **216**, 1562–8.

Mares, M. A. (1972). Notes on *Bufo marinus* tadpole aggregations. *Tex. J. Sci.* **23**, 433–5.

Matsumoto, Y., Matsumoto, T., and Miyashita, K. (1984). Feeding habits of the marine toad, *Bufo marinus* in the Bonin Islands, Japan. *Jap. J. Ecol.* **34**, 289–97.

Mead, A. R. (1961). The Giant African Snail: a problem in economic malacology. (University of Chicago Press: Chicago.)

Mettrick, D. F., and Dunkley, L. C. (1968). Observations on the occurrence, growth and morphological variation of the trematode, *Mesocoelium danforthi* Hoffman 1935, in Jamaica. *Carib. J. Sci.* **8**, 71–5.

Mungomery, R. W. (1935). The Giant American Toad (*Bufo marinus*). Cane Growers Quarterly Bulletin (Qld), July 1935, pp. 21–7.

Mungomery, R. W. (1936*a*). A survery of the feeding habits of the Giant Toad (*Bufo marinus* L.), and notes on its progress since its introduction into Queensland. Proceedings of the Queensland Society of Sugar Cane Technologists 1936, pp. 63–74.

Mungomery, R. W. (1936*b*). Sex reversal in the Giant Toad. Cane Growers Quarterly Bulletin (Qld), July 1936, p. 7.

Mungomery, R. W. (1938). Toad protection. Minutes Cane Pests Board Conference, Meninger, pp. 36–7.

Mungomery, R. W. (1940). Frenchi grub depredations and suggestions for control. Cane Growers Quarterly Bulletin, April 1940, pp. 171–4.

Mungomery, R. W., and Buzacott, J. H. (1935). Control of the 'Greyback Cane Beetle' (*Lepidoderma albohirtum* Waterh.) in north Queensland. Proc. 5th Cong. Int. Soc. Sugar Cane Technologists, Brisbane. pp. 456–64.

Niven, B. S. (1987). Logical synthesis of an animal's environment: sponges to non-human primates. I. Primitive terms and definitions. *Aust. J. Zool.* **35**, 597–606.

Oliver, J. A. (1949). The peripatetic toad. *Nat. History* **58**, 30–3.

Pearse, B. W. (1980*a*). The effect of toad poison on vertebrates. Unpublished paper available Griffith University Library, Nathan, Aust. 4111.

Pearse, B. W. (1980*b*). The effects of feeding on *Bufo marinus* by native and exotic fishes. Unpublished paper available Griffith University Library.

Pemberton, C. E. (1934). Local investigations on the introduced tropical American toad, *Bufo marinus*. *Hawaii Plant. Rec.* **38**, 186–92.

Pemberton, C. E. (1949). Longevity of the tropical American toad, *Bufo marinus* L. *Science (Wash. D.C.)* **110**, 512.

Pippet, J. R. (1975). The marine toad, *Bufo marinus*, in Papua New Guinea. *Papua New Guinea Agric. J.* **26**, 23–30.

Rabor, D. S. (1952). Preliminary notes on the giant toad, *Bufo marinus* (Linn.), in the Philippine Islands. *Copeia* 1952, 281–2.

Sabath, M. D., Boughton, W. C., and Easteal, S. (1981). Expansion of the range of the introduced toad *Bufo marinus* in Australia from 1935 to 1974. *Copeia* 1981, 676–80.

Saxena, P. K., and Lal, S. R. (1981). Seasonal changes in testes and thumb pads of the toad *Bufo marinus* (Linn.) and the correlation with fluctuations in the environmental factors. *Anat. Anz. Jena.* **149**, 337–44.

Simmonds, H. W. (1937). The giant toad. *Fiji Agric. J.* **8**, 45–6.

Simmonds, H. W. (1957). The giant toad—*Bufo marinus*—in Fiji. *Fiji Agric. J.* **28**, 77–8.

Smyth, E. G. (1917). The white-grubs injuring sugar cane in Puerto Rico. *Puerto Rico Univ. J. Agric.* **1**, 141–69.

Straughan, I. R. (1966). The natural history of the 'Cane Toad' in Queensland. *Aust. Nat. Hist.* **15**, 230–2.

Strüssmann, C., Ribeiro do Vale, M. B., Meneghini, M. H., and Magnusson, W. E. (1984). Diet and foraging mode of *Bufo marinus* and *Leptodactylus ocellatus*. *J. Herpetol.* **18**, 138–46.

Stuart, L. C. (1951). The distributional implications of temperature tolerances and haemoglobin values in the toads *Bufo marinus* (Linnaeus) and *Bufo bocourti* Brocchi. *Copeia* 1951, 220–9.

Takano, S., and Iijima, K. (1937). Studies on the life history and habits of *Bufo marinus* L. in Formosa. Part I. The relation between the growth of the tadpole and the quality of the breeding water. *Taiwan Govt Sug. Expt. Stat. Report Jap. No.* **9**, pp. 212–13.

Takano, S., and Iijima, K. (1939). Studies on the life history and habits of *Bufo marinus* L. in Formosa. Part II. Ecology of the tadpole and the toadlet. *Taiwan Govt Sug. Expt. Stat. Report. Jap. No.* **4**, p. 51.

Tucker, R. W. E. (1940). *Bufo marinus* L. in Barbados. *Agric. J. Barbados* **8**, 145–50.

Tyler, M. J. (1975). 'The Cane Toad *Bufo marinus*. An Historical Account and Modern Assessment.' A report to the Vermin and Noxious Weeds Destruction Board, Victoria and the Agricultural Protection Board, Western Australia.

Tyler, M. J. (1976). 'Frogs.' (Collins: Sydney.)

Valerio, C. E. (1971). Ability of some tropical tadpoles to survive without water. *Copeia* 1971, 364–75.

van Beurden, E. K. (1978). Report on the results of stage 1 of an ecological and physiological study of the Queensland cane toad *Bufo marinus*. Report to the Australian National Parks and Wildlife Service, Canberra.

van Beurden, E. K. (1979). Report on the results of stage 2 of an ecological and physiological study of the Queensland cane toad *Bufo marinus*. Report to the Australian National Parks and Wildlife Service, Canberra.

van Beurden, E. K. (1980*a*). Mosquitoes [*Mimomya elegans* (Taylor)] feeding on the introduced toad *Bufo marinus* (Linnaeus): implications for control of a toad pest. *Aust. Zool.* **20**, 501–4.

van Beurden, E. K. (1980*b*). Report on the results of stage 3 of an ecological and physiological study of the Queensland cane toad *Bufo marinus*. Report to the Australian National Parks and Wildlife Service, Canberra.

van Beurden, E. K. (1981). Tolerance of Australian *Bufo marinus* to low temperature. Unpublished.

van Beurden, E. K., and Grigg, G. C. (1980). An isolated and expanding population of the introduced toad *Bufo marinus* in New South Wales, Australia. *Aust. Wildl. Res.* **7**, 305–10.

van Volkenberg, H. L. (1935). Biological control of an insect pest by a toad. *Science* **82(2125)**, 278–9.

Waite, F. C. (1901). *Bufo agua* in the Bermudas. *Science* **13**, 342–3.

Warburg, M. R. (1965). Studies on the water economy of some Australian frogs. *Aust. J. Zool.* **13**, 317–30.

Watson, J. M. (1960). Notes on the wildlife of Fiji and its conservation. *Fiji Agric. J.* **30**, 67–70.

Weber, N. A. (1938). The food of the giant toad, *Bufo marinus* (L.), in Trinidad and British Guiana with special reference to the ants. *Ann. Entomol. Soc. Am.* **31**, 499–503.

Wilhoft, D. C. (1965). The annual reproductive cycle of *Bufo marinus* in Australia. *Am. Zool.* **5**, 259.

Wingate, D. B. (1965). Terrestrial herpetofauna of Bermuda. *Herpetologica* **21**, 202–18.

Wolcott, G. N. (1937). What the giant Surinam toad *Bufo marinus* L. is eating now in Puerto Rico. *Univ. Puerto Rico J. Agric.* **21**, 79–84.

Zug, G. R., Lindgren, E., and Pippet, J. R. (1975). Distribution and ecology of the marine toad, *Bufo marinus*, in Papua New Guinea. *Pac. Sci.* **29**, 31–50.

Zug, G. R., and Zug, P. B. (1979). The marine toad, *Bufo marinus*, a natural history resume of native populations. Smithsonian contributions to Zoology No. 284. (Smithsonian Institution Press: Washington.)

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Logical Synthesis of an Animal's Environment: Sponges to Non-human Primates.
VI.* The Chimpanzee, *Pan troglodytes*

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Abstract

The environment of the chimpanzee, *Pan troglodytes*, is classified according to the defining equations in the first paper of this series. An envirogram displaying objects in the environment in their correct place is presented. Notes on the envirogram include informal versions of the appropriate defining equations which are used for the classification.

Introduction

Chimpanzees (*Pan troglodytes*) '... are found in a wide belt that extends across equatorial Africa from the west coast to within a few hundred kilometres of the east coast ... living in habitats that range from rain and montane forests to dry woodlands, and sometimes even savanna with widely scattered trees' (Goodall 1986). Early observations of wild chimpanzees were carried out in the Gombe National Park in Tanzania from 1960 by Goodall and many others. More recently studies have been done in Senegal (Tutin *et al.* 1983), Kasoge (McGrew and Tutin 1978; Nishida and Uehara 1980), Liberia (Anderson *et al.* 1983) and Mahale (Takasaki 1983; Takahata *et al.* 1984). The diversity of habitats has enabled cross-cultural studies to be done, such as differences in the use of twigs for capturing termites (McGrew *et al.* 1979; McGrew and Collins 1985) and differences in social behaviour, for instance according to McGrew and Tutin (1978), the aspect of social grooming referred to as the 'grooming-hand-clasp' occurs among animals in Kasoge but not at Gombe. (Both areas are in Tanzania.) Such studies across a range of habitats has led to the suggestion that we are observing the beginning of speciation; however, the evidence for speciation in the sense of Paterson (1985) is still rather nebulous. A useful bibliography of early literature on the chimpanzee is that of Baldwin and Teleki (1973).

I aimed to show that the mathematical definition of environment given in paper 1 of the series (Niven 1987) may be used to classify the environment of a wild chimpanzee. Of the five species dealt with in the series the chimpanzee is by far the most similar to our own, not only anatomically, biochemically and physiologically, but also in its social relationships. Much work done on captive chimpanzees relates to observations in the wild and is referred to where appropriate in the notes on the envirogram given below.

Female chimpanzees have menstrual cycles similar to humans (see note 9). The young animal reaches puberty at the age of 7 years and a male enters the adult male hierarchy when it is about 13–15. Details of developmental stages are given by van Lawick-Goodall (1971), Goodall (1986) and others. Life expectancy in the wild is unknown, but is probably 40–50 years (Riss and Goodall 1977). Graham (1979) reported on a captive female of 48 years and de Waal (1982) reports a maximum age of 50. A captive chimpanzee may weigh as much as 60 lbs (27 kg) at 11 (Smith *et al.* 1975).

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Because of the many similarities between the chimpanzee and our own species, behavioural and medical studies of the animal are many and seem to be increasing. Thus, 'the chimpanzee has an adrenarche like that of man (whereas macaques and baboons do not . . . the chimpanzee is the only known model of membranous dysmenorrhea . . .'; also the sex steroid and chorionic gonadotropin profiles are almost identical (Graham and Hodgen 1979). These authors also urge the expansion of captive breeding as 'the only certain method of preserving the chimpanzee'. They estimate that, at the time, 'upwards of 1000 chimpanzees' were held captive in the USA. Doering *et al.* (1980) worked on the effect of gonadotropin-releasing hormone (GnRH) on male chimpanzees in the Stanford Outdoor Primate Facility as a parallel to clinical trials conducted with GnRH as a possible therapeutic agent in human sexual impotence. (They found that the effect was not statistically significant.)

Among the many studies relating chimpanzee behaviour to human psychology Gaillard *et al.* (1979) compared sleep stages in humans with chimpanzees, baboons and Rhesus monkeys. They found 'remarkable similarities'. de Waal (1982) remarked of the chimpanzees in a large breeding colony at the Arnhem Zoo in Holland 'Their interest in power is not greater than that of humanity; it is just more obvious.'

While well aware of the dangers of drawing inferences both about wild chimpanzees and humans from observations on captive chimpanzees, behaviourists and others continue with detailed and suggestive studies. King *et al.* (1980) make a plea for 'the ideal captive enclosure (which) would provide opportunities for the expression of . . . behaviors and their preservation and propagation in future generations of chimpanzees'. They point out that 'the importance of behavioral studies of primates born in captivity is steadily increasing as the natural populations of many species continue to dwindle' (because of the interaction with humans). King and her colleagues studied 'grooming', 'play' and other behaviour, as did Merrick (1977) and others. van Wulfften Palthe and van Hooff (1975) record the successful adoption by a female of a five-week-old infant which had been reared by humans from the day of its birth (successful adoption is not known among wild chimpanzees). Buirski *et al.* (1978) have rated wild chimpanzees at Gombe for 'personality' using methods applied previously to humans, baboons and dolphins. Other workers have concentrated on 'aggression' among wild or captive chimpanzees (e.g. de Waal and Hoekstra 1980). The work of Woodruff and Premack (1981) seems to suggest that captive adult chimpanzees have at least some concept of simple proportions and numbers. Many workers (e.g. Asano *et al.* 1982) have trained captive animals to recognise symbols or solve problems (Premack and Woodruff 1978). The studies of Premack (1983), also on captive chimpanzees, may relate to the use of language as a tool for problem-solving by humans (however, see comments following his paper). Reynolds (1980) draws inferences about human behaviour on the basis of observations by himself and others on chimpanzees. Goodall (1986) gives a summary of various attempts to teach captive chimpanzees to communicate by using the sign language of deaf-and-dumb people. Goodall remarks that chimpanzees probably perceive objects in much the same way as a human child; they are capable of learning and have some sense of time. In Australia, Green (1987) has initiated a ten-year study into chimpanzee play behaviour among free-range chimpanzees at Taronga Zoo in Sydney.

Many and detailed studies of chimpanzee society do not at present foster much hope that enlightenment regarding the structure of human society will follow. For instance Goodall (1986) writes 'In chimpanzee society some individuals meet on a fairly regular basis, others but seldom. There is always uncertainty; it is never possible for a chimpanzee, upon wakening in the morning, to be quite sure whom he will encounter during the day.' So in this sense chimpanzee society differs markedly from both village and industrialised society among humans. Also workers among wild chimpanzees are encountering major difficulties in interpreting chimpanzee behaviour, for example Tutin *et al.* (1983) believe that social organisation seems unlikely to be related to the availability of food in any simple way, but rather that there are complex adaptations of whole groups of the animals to threats from predators, or the patchy distribution of food and nesting sites.

The mathematical definition of environment which is used in this series of papers is a 'complete' definition in the sense that all permutations of H(subject animal) and H(object animal) are included. Thus we have:

	H(subject): Increases	Decreases
H(object):		
Increases	(Mate)	Predator
Decreases or is unaffected	Resource	Malentity

Interactions during which H(subject animal) is unchanged do not give us a class belonging to the centrum. The definition of mate is stochastic and uses part of 'H' only. For certain social interactions among chimpanzees (and humans) 'H' is irrelevant. For instance 'social grooming' which apparently gives pleasure (de Waal 1982; Goodall 1986) cannot be represented by the definition. Grooming for salt, dry skin particles or fleas is totally different; in this case the subject animal is relieved of a malentity or a predator by the groomer, so the groomer is a first-order modifier in the environment of the subject animal. So while many behavioural aspects of the chimpanzee, such as its use of twigs to collect termites (see note 1), are catered for by the mathematical definition, other aspects, such as 'grooming' and 'play' are not. There seems to be a good case for treating the ecology of the chimpanzee, at least partially, in a fashion similar to the ecology of humans, which necessarily includes a cultural component (Stewart 1983). There are phenomena in a chimpanzee's environment which seem likely to be relevant not so much to the individual but rather to the social group, as is clearly the case with humans. Unfortunately the science of human ecology has not yet reached the stage at which we may make a precise comparison with chimpanzee ecology (Stewart 1982). A mathematical definition of the human environment is presently under construction by myself and F. J. Willett, using as a basis studies of small group interactions among humans, e.g. Patterson and Willett (1951). It will be of great interest to reclassify the chimpanzee environment with reference to the new human environment definition. When this is done, social grooming will come into its own.

The Envirogram

The envirogram for the chimpanzee displays objects in their correct logical place in the environment. This type of diagram enables workers on the animal to relate their own results to those of others and may be used as a guide to further experimentation or observation.

The subject animal for the envirogram is either a female or male adult or an infant; the notes make it clear in each case. Many reports on chimpanzees have been combined. Thus, the envirogram presented here is a concatenation of many individual envirograms for animals observed in different places at different times. The numbers on the envirogram refer to the notes which follow. They appear in no particular order. The various parts of the envirogram were constructed in an entirely haphazard order as the literature became available. The square brackets indicate a set of objects. Thus '[food]' refers to a set of food objects. The parentheses are used for explanatory purposes, e.g. 'kinetic energy (gravitation)' and also for doubtful or very rare cases, e.g. '(other female in same group)' (see note 5, case ii).

A semiformal version of the appropriate defining equations (see Niven 1987) is given at the end of each note. The following symbols are used:

(i) $=_{df}$: 'is equal by definition to', or, more strictly, the form '$x =_{df} y$' means 'x' is to be interchangeable with 'y'.

(ii) ∃: the existential operator of formal logic. Read '∃ bushbuck' as 'there exists a bushbuck' or 'there is at least one bushbuck' or, more informally, 'we can find a bushbuck'. In this paper, expressions such as '∃ bushbuck' are always followed by the words 'such that'.

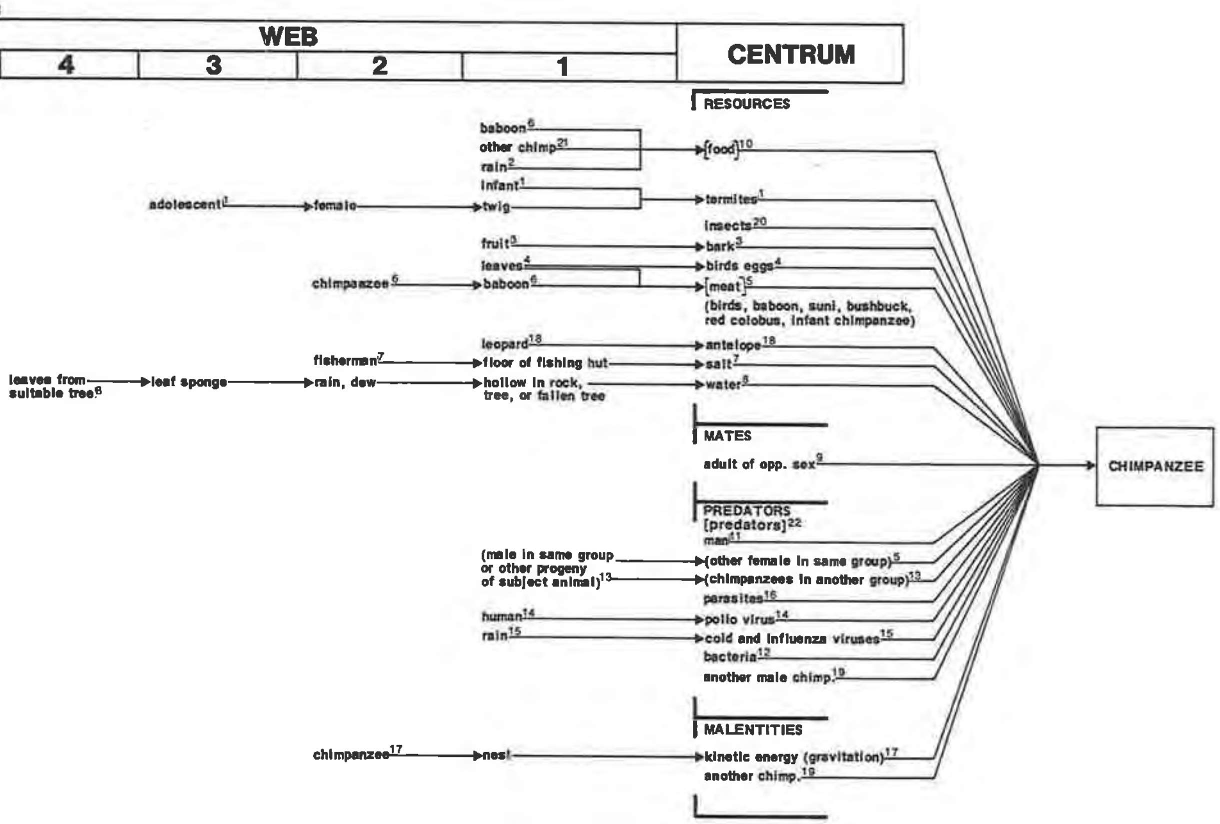

Fig. 1. Envirogram for chimpanzee.

(iii) $|$: ‘$x \mid y$’ means ‘x’ occurs (will occur), assuming ‘y’. This is the symbol used for conditional events (and conditional probabilities). The expression ‘$A \mid B$’ may be read ‘Event A occurs, given that event B occurs’; it refers to ‘event A under the condition that B’, or ‘event A under the hypothesis that B’. The use of the conditional in the definitions implies that the environment of the subject animal is independent of its habitat. Thus an object which is reported in Gombe, say, as being a food object and hence classified as a resource of that particular subject chimpanzee is also classified as a resource of a subject chimpanzee at Mahale; in ordinary English it is a *potential* resource. Similarly mates, predators, malentities and modifiers are all *potential* mates, etc.

Notes on the Envirogram

1. Termites are eaten from October to January. The soldier termites are readily available after rain, when they are near the surface. The female adult chimpanzee will choose a grass stem or a twig of a suitable shape from one of a number of different species of tree, vine or bush. She strips the leaves from it, thus acting as a modifier of the tool which she then pokes into the hole to collect the termies, which are then eaten. They may be given to her infant to eat. The infant cannot use the tool, but her adolescent offspring may make use of it, although unable to manufacture it (van Lawick-Goodall 1971).

A detailed study of ant-gathering behaviour was undertaken by Nishida (1972), who observed three kinds of tools used, the most common being the ‘poking rod’; Nishida divides the last type into five categories which differentiate between the materials used and the way and the degree to which these materials are modified. Further studies are described in Nishida and Uehara (1980, 1983), Nishida and Hiraiwa (1982) and McGrew (1974). Uehara (1982) observed a group of wild chimpanzees employing several techniques to feed on one particular species of termite, apparently according to phenological changes in the prey's activities. Jones and Sabater-Pi (1969) and Sabater-Pi (1974) have also studied the use of twigs for collecting termites, and Buirski *et al.* (1978) record driver ants being eaten using the same methods of collection. McGrew *et al.* (1979) compare termite-collecting among chimpanzees in western, central and eastern Africa; they found that differences exist and suggest that some of these may be cultural. McBeath and McGrew (1982) working at Mt Assirak in Senegal concluded that the habitat relates strongly to tool use; there is a strong preference for *Grewia* as the raw material. Some groups of chimpanzees at Kasoge do not seem to use tools at all but destroy the termite mound, or scrape the rotten bark with their hands (Nishida and Uehara 1980).

In the case that the subject chimpanzee is an adult female, a particular termite is a resource modified by a twig, which is in turn modified by the subject female. If an adolescent offspring received the twig from its mother, then the mother (the subject female) can no longer act as a modifier in her own environment by poking the twig into the hole to collect the termites; the adolescent is thus a third-order modifier of the subject female. The subject female's infant is acting as a first-order modifier when it ‘competes’ for the termite. The informal defining equations follow.

$$\text{(termite)Res(female)} =_{\text{df}} \text{H(female) is increased and H(termite) is decreased} \mid \xi\text{(termite)(female)}$$

$$\text{(twig)Mod}^{+1}\text{(female)} =_{\text{df}} (\exists\ \text{termite) such that [(termite)Res(female)} \mid \xi\text{(twig)(termite) and } {\sim}\text{(termite)Res(female)} \mid \xi\text{(twig)(termite)]}$$

$$\text{(female)Mod}^{+2}\text{(female)} =_{\text{df}} (\exists\ \text{twig) such that [(twig)Mod}^{1}\text{(female)} \mid \xi\text{(female)(twig) and } {\sim}\text{(twig)Mod}^{1}\text{(female)} \mid {\sim}\xi\text{(female)(twig)]}$$

$$\text{(adolescent)Mod}^{-3}\text{(female)} =_{\text{df}} (\exists\ \text{female) such that [(female)Mod}^{2}\text{(female)} \mid {\sim}\xi\text{(adolescent)(female) and } {\sim}\text{(female)Mod}^{2}\text{(female)} \mid \xi\text{(adolescent)(female)]}$$

$$(\text{infant})\text{Mod}^{-1}(\text{female}) =_{\text{df}} (\exists \text{ termite}) \text{ such that } [(\text{termite})\text{Res}(\text{female}) \mid {\sim}\,\xi(\text{infant})(\text{termite}) \text{ and } {\sim}(\text{termite})\text{Res}(\text{female}) \mid \xi(\text{infant})(\text{termite}).$$

2. Rain acts as a modifier for all food resources, since chimpanzees very rarely eat when it is raining. Males sometimes perform a 'ritual dance' in the rain (van Lawick-Goodall 1971). Nishida (1980*a*) reports that heavy rain inhibits all chimpanzee activities. Uehara and Nishida (1987) note that body weights tend to decrease in the later part of the wet season presumably because of food shortage in the middle of the wet season.

The informal defining equation for a specific amount of rain acting as a modifier of a particular item of food is:

$$(\text{rain})\text{Mod}^{-1}(\text{chimpanzee}) =_{\text{df}} (\exists \text{ food}) \text{ such that } [(\text{food})\text{Res}(\text{chimpanzee}) \mid {\sim}\,\xi(\text{rain})(\text{chimpanzee}) \text{ and } {\sim}(\text{food})\text{Res}(\text{chimpanzee}) \mid \xi(\text{rain})(\text{chimpanzee})].$$

3. Bark is eaten when fruit is least abundant (Nishida 1976). The nutritious part is the phloem. The animal pulls off strips of bark, holds them in both hands, and scrapes the inner surface with its incisors. The informal defining equations are:

$$(\text{bark})\text{Res}(\text{chimpanzee}) =_{\text{df}} H(\text{chimpanzee}) \text{ is increased} \mid \xi(\text{bark})(\text{chimpanzee})$$

$$(\text{fruit})\text{Mod}^{-1}(\text{chimpanzee}) =_{\text{df}} (\exists \text{ bark}) \text{ such that } [(\text{bark})\text{Res}(\text{Chimpanzee}) \mid {\sim}\,\xi(\text{fruit})(\text{chimpanzee}) \text{ and } {\sim}(\text{bark})\text{Res}(\text{chimpanzee}) \mid \xi(\text{fruit})(\text{chimpanzee})].$$

4. A wad of leaves is always seen to be eaten with eggs. However, it is not known whether a chimpanzee would sometimes eat an egg without leaves. Leaves are also sometimes eaten with meat. In both cases, these need not be the kind of leaves normally eaten for food (van Lawick-Goodall 1971). The informal defining equations are:

$$(\text{egg})\text{Res}(\text{chimpanzee}) =_{\text{df}} H(\text{chimpanzee}) \text{ is increased and } H(\text{egg}) \text{ is decreased} \mid \xi(\text{egg})(\text{chimpanzee})$$

$$(\text{wad})\text{Mod}^{+1}(\text{chimpanzee}) =_{\text{df}} (\exists \text{ egg}) \text{ such that } [(\text{egg})\text{Res}(\text{chimpanzee}) \mid \xi(\text{wad})(\text{egg}) \text{ and } {\sim}(\text{egg})\text{Res}(\text{chimpanzee}) \mid {\sim}\,\xi(\text{wad})(\text{egg})].$$

5. The hunting of bushbuck and other animals tends to occur in cycles; the chimpanzee, mainly the male, will hunt for two months, say, and then not at all for the following month. Hunts are usually more successful when the chimpanzees cooperate. All chimpanzees, adolescent or adult, female or male, occasionally beg meat from successful hunters. There is one recorded case of a chimpanzee building a tree-nest and eating his meat in it.

Teleki (1973*a*) observed interactions and attacks among chimpanzees, baboons, serval cats, domestic cats, and genets.

Nishida *et al.* (1979) remark that, although in the Gombe National Park, baboons are often attacked, this does not occur in the Mahale Mountains 40 miles (64 km) away; they suggest that the artificial feeding at Gombe brings chimpanzees into contact with baboons more often. In the Mahale area, much less meat is eaten and hunting is invariably opportunistic rather than cooperative. Takahata *et al.* (1984) working in the Mahale area, recorded 54 episodes of predatory behaviour, involving juvenile blue duiker, bushbuck, bushpig, warthog, red colobus, savanna monkey, red-tailed monkey, francolin and crowned hawk eagle. Chimpanzees may not be able to kill larger animals; they were not observed to attack adult bushpigs or bushbucks. In Mahale females hunt more frequently than in Gombe. Females tend to hunt juvenile adults by seizure while males tend to hunt monkeys by chasing.

There are two varieties of cannibalism:

(i) Intergroup. When a mother with an infant is attacked, the mother often escapes, but the infant is captured and eaten, often with accompanying ritual. The suggestion has been made that such infant killings are related to tensions arising because of overlapping ranges. A female who has lost her infant changes her status within the group from 'mother' to 'female' and may be expected to go into oestrus within two months. One female who lost her infant was groomed for a long period by three males without, however, reciprocating.

(ii) Intragroup. A higher ranking female will (very seldom) steal and eat another female's infant. Also, males have been observed to kill and eat infants of immigrant females (Goodall 1977; Nishida 1980*b*). Human infants have also been eaten (Goodall 1986).

The informal defining equation for some particular item, a bird, say, as a resource is:

$$\begin{gathered}\text{(bird)Res(chimpanzee)} =_{\text{df}} \text{H(chimpanzee) is increased and H(bird) is decreased} \mid \\ \xi\text{(bird)(chimpanzee)}.\end{gathered}$$

6. Chimpanzees often steal meat from a baboon; in this case, the baboon 'supplies' the resource and so is acting as a first-order modifier. The chimpanzee acts as a second-order modifier in its own environment by catching the baboon (see note 5).

Morris and Goodall (1977) record five instances when chimpanzees took meat from baboons, and five further instances when this probably occurred. Nevertheless, baboons and chimpanzees often feed peacefully together on vegetable foods.

The informal defining equations for a baboon as a first-order modifier and the subject chimpanzee as a second-order modifier follow. A particular item of meat is envisaged as the resource.

$$\begin{gathered}\text{(baboon)Mod}^{+1}\text{(chimpanzee)} =_{\text{df}} (\exists\ \text{meat) such that [(meat)Res(chimpanzee)} \mid \\ \xi\text{(baboon)(chimpanzee) and} \sim\text{(meat)Res(chimpanzee)} \mid \sim\xi\text{(baboon)(chimpanzee)]}\end{gathered}$$

$$\begin{gathered}\text{(chimpanzee)Mod}^{+2}\text{(chimpanzee)} =_{\text{df}} (\exists\ \text{baboon) such that} \\ \text{[(baboon)Mod}^{1}\text{(chimpanzee)} \mid \xi\text{(chimpanzee)(baboon) and} \\ \sim\text{(baboon)Mod}^{1}\text{(chimpanzee)} \mid \sim\xi\text{(chimpanzee)(baboon)]}.\end{gathered}$$

7. Van Lawick-Goodall (1971) records the animal eating soil from the floor of fishing huts, presumably in order to obtain salt. The informal defining equations are:

$$\text{(salt)Res(chimpanzee)} =_{\text{df}} \text{H(chimpanzee) is increased} \mid \xi\text{(salt)(chimpanzee)}$$

$$\begin{gathered}\text{(hut)Mod}^{+1}\text{(chimpanzee)} =_{\text{df}} (\exists\ \text{salt) such that [(salt)Res(chimpanzee)} \mid \\ \xi\text{(hut)(chimpanzee) and} \sim\text{(salt)Res(chimpanzee)} \mid \sim\xi\text{(hut)(chimpanzee)]}\end{gathered}$$

$$\begin{gathered}\text{(fisherman)Mod}^{+2}\text{(chimpanzee)} =_{\text{df}} (\exists\ \text{hut) such that [(hut)Mod}^{1}\text{(chimpanzee)} \mid \\ \xi\text{(fisherman)(hut) and} \sim\text{(hut)Mod}^{1}\text{(chimpanzee)} \mid \sim\xi\text{(fisherman)(hut)]}.\end{gathered}$$

8. Chimpanzees in the Gombe National Park may obtain their water directly from nearby streams or lakes pausing to drink when they cross a stream (Goodall 1986). However, they have also been observed drinking from water-filled tree- or rock-holes. The envirogram shows the case in which the rock-hole is out of lip-reach. The chimpanzee chews a wad of leaves into a 'sponge'; the sponge is then used to sop up water. Thus, the animal acts as a fifth-order modifier in its own environment (not shown on envirogram) (van Lawick-Goodall 1971). The informal defining equations are:

$$\text{(water)Res(chimpanzee)} =_{\text{df}} \text{H(chimpanzee) is increased} \mid \xi\text{(water(chimpanzee)}$$

$$\begin{gathered}\text{(hollow rock)Mod}^{+1}\text{(chimpanzee)} =_{\text{df}} (\exists\ \text{water) such that} \\ \text{[(water)Res(chimpanzee)} \mid \xi\text{(hollow rock)(water) and} \sim\text{(water)Res(chimpanzee)} \mid \\ \sim\xi\text{(hollow rock)(water)]}\end{gathered}$$

(rain)Mod^{+2}(chimpanzee) $=_{\text{df}}$ ($\exists$ hollow rock) such that
[(hollow rock)Mod^1(chimpanzee) | ξ(rain)(hollow rock) and
$\sim$(hollow rock)Mod^1(chimpanzee) | $\sim\xi$(rain)(hollow rock)]

(leaf sponge)Mod^{+3}(chimpanzee) $=_{\text{df}}$ ($\exists$ rain) such that
[(rain)Mod^2(chimpanzee) | ξ(leaf sponge)(rain) and $\sim$(rain)Mod^2(chimpanzee) |
$\sim\xi$(leaf sponge)(rain)]

(leaves)Mod^{+4}(chimpanzee) $=_{\text{df}}$ ($\exists$ leaf sponge) such that
[(leaf sponge)Mod^3(chimpanzee) | ξ(leaves)(chimpanzee) and
$\sim$(leaf sponge)Mod^3(chimpanzee) | $\sim\xi$(leaves)(chimpanzee)].

Animals in the Mahale Mountains, Tanzania have been observed to drink water from streams and from Lake Tanganyika by Nishida (1980*a*). The use of a sponge was not observed here.

9. A female will copulate with almost all mature males, but copulation between siblings is rare, and mother–son true copulation is very rare (Goodall 1986). In any one period of sexual activity, the males present will copulate in sequence according to their social rank. Occasionally, a female will have a consort (a male who accompanies her; these associations are relatively brief, never more than six months). The consort is not preferred for copulation, but simply because of his proximity, he is likely to copulate with her more often than other males. Thus, the so-called 'α-male' and the consort are most likely to sire any offspring. In the course of the usual social training, she will also 'copulate' (in a non-adult sense) with juveniles and infants, including her own if sufficiently young. Females are receptive to copulation at all times, although most often during maximum tumescence. The pale pink swelling of the sex skin of the female's genital area is larger and more attractive to males in some females than others (van Lawick-Goodall 1971; Riss and Busse 1977; Lemmon and Allen 1978). Allen (1981), reporting on a group of captive chimpanzees, suggests that male chimpanzees sometimes form an individual mating preference regardless of the hormonal status of his available partners.

The normal sexual cycle of a mature female is 37 d, with a range of 29–42 d. Menstrual bleeding occurs between oestrous phases (Tutin and McGrew 1973). Graham (1979) found no equivalence to human menopause; animals aged 35–48 y continued to menstruate.

The informal defining equation for an adult male as a mate of an adult subject female in oestrous is:

(male)Mat(female) $=_{\text{df}}$ An offspring of both individuals will be produced with
probability greater than zero | ξ(male)(female).

10. Food eaten by the wild chimpanzee includes fruit, seeds, leaves, flowers, pith, termites, ants, larvae of moths, beetles, wasps, gallflies etc., bee larvae and honey, fledglings, birds' eggs, monkeys, rats, mongooses, suni, baboon, bush pig, squirrel and buck. Lists of food are given by many authors, including van Lawick-Goodall (1971), Silk (1978), Nishida *et al.* (1979), Sabater-Pi (1979). Riss and Busse (1977) looked at the time spent on feeding by a free-ranging male, as well as type of food; they found that the time was very variable, depending on the difficulty of access. Sabater-Pi reported on relative importance of plants and also on feeding behaviour. Nishida and Uehara (1983) noted that the wild chimpanzees of Kasoge in the Mahale Mountains between 1965 and 1981 utilised 328 food items from 198 species of plant and also consumed 12 species of mammals, 5 species of birds or their eggs, and more than 15 genera of insects, including at least 25 species. Females at Gombe are more insectivorous than males (Goodall 1986). Wild chimpanzees seem to be conservative in their dietary habits; at Kosoge in the Mahale Mountains, Takasaki (1983) reported on mangoes being eaten, apparently for the first time and remarked that other cultivated foods

were not yet eaten. Some evidence that chimpanzees in Sapo, Liberia use stones as 'hammers' to break open nuts is given by Anderson *et al.* (1983). This behaviour seems to be rare and has not been entered on the envirogram.

The informal defining equation for a particular item of food as a resource is:

(food)Res(chimpanzee) $=_{\mathrm{df}}$ H(chimpanzee) is increased | ξ(food)(chimpanzee).

If the item of food is a live animal, then the phrase 'and H(food) is decreased' should be inserted immediately after the word 'increased'.

11. Some African people consider that chimpanzee flesh is a delicacy. The young animals are captured, fattened and slaughtered (van Lawick-Goodall 1971). The informal defining equation is:

(human)Pred(chimpanzee) $=_{\mathrm{df}}$ H(chimpanzee) is decreased and H(human) is increased | ξ(human)(chimpanzee).

12. Cole *et al.* (1970) found several species of the bacterium *Mycoplasma* in captive chimpanzees. They remark that considerable controversy exists concerning the role of mycoplasma in various diseases of humans, and suggest the experimental use of chimpanzees and other non-human primates in this regard. Gastric enteritis, chronic diarrhoea and other gastrointestinal disorders have been observed (Goodall 1986).

In the informal defining equation below, the bacterium is assumed to induce a disease in the subject animal. The bacterium is treated as an animal.

(bacterium)Pred(chimpanzee) $=_{\mathrm{df}}$ H(chimpanzee) is decreased and H(bacterium) is increased | ξ(bacterium)(chimpanzee).

13. This refers to the case of infant cannibalism (see note 5 case ii). A male in the same group, or other offspring of the mother may act as protector (Goodall 1977). The subject animal here is an infant chimpanzee. The informal defining equations are:

(other female)Pred(infant) $=_{\mathrm{df}}$ H(infant) is decreased and H(other female) is increased | ξ(other female)(infant)

(male)Mod^{-1}(infant) $=_{\mathrm{df}}$ ($\exists$ other female) such that [(other female)Pred(infant) | $\sim\xi$(male)(infant) and $\sim$(other female)Pred(infant) | ξ(male)(infant)].

14. Fifteen chimpanzees were affected and six of them died at Gombe in one epidemic which followed an outbreak of poliomyelitis in neighbouring villages. The suggestion has been made that many diseases of humans also affect chimpanzees (van Lawick-Goodall 1971; Walsh *et al.* 1981). For convenience, the poliomyelitis virus is classified here as a predator, although it is usually thought of as a protist rather than an animal. The informal defining equations are:

(virus)Pred(chimpanzee) $=_{\mathrm{df}}$ H(chimpanzee) is decreased and H(virus) is increased | ξ(virus)(chimpanzee)

(human)Mod^{+1}(chimpanzee) $=_{\mathrm{df}}$ ($\exists$ virus) such that [(virus)Pred(chimpanzee) | ξ(human)(chimpanzee) and $\sim$(virus)Pred(chimpanzee) | $\sim\xi$(human)(chimpanzee)].

It was decided in 1967 to adminster oral polio vaccine in bananas to the Gombe chimpanzees (Goodall 1983).

15. Every rainy season, at least some chimpanzees catch cold (van Lawick-Goodall 1971). For convenience, a virus is classified here as a predator, although it is usually thought of as a protist rather than an animal. The informal defining equations are:

(virus)Pred(chimpanzee) $=_{df}$ H(chimpanzee) is decreased and H(virus) is increased | ξ(virus)(chimpanzee)

(rain)Mod^{+1}(chimpanzee) $=_{df}$ ($\exists$ virus) such that [(virus)Pred(chimpanzee) | ξ(rain)(chimpanzee) and $\sim$(virus)Pred(chimpanzee) | $\sim\xi$(rain)(chimpanzee)].

16. File (1976) and File *et al.* (1976) give details of intestinal parasitic infections detected in wild chimpanzees. Lists of parasites are given by Myers and Kuntz (1972) and Myers *et al.* (1973). Included are protozoa, aganthocephala, cestodes, nematodes, platyhelminths and arthropods. Some malaria parasites have been observed in chimpanzee blood in the first stage of their development cycle (Goodall 1983).

The informal defining equation for a particular nematode as a predator is:

(nematode)Pred(chimpanzee) $=_{df}$ H(chimpanzee) is decreased and H(nematode) is increased | ξ(nematode)(chimpanzee).

17. Chimpanzees, like all the Pongidae beyond infancy, build nests in the wild for sleeping at night and occasionally for sleeping during the day. Variation in the building technique seems to depend on local conditions. Nevertheless, a cultural element in the behaviour cannot be completely ruled out. It is nearly always the case that a new night-nest is constructed each night. The nests are usually in trees, in which case they help to prevent falls. Ground-nests are also constructed sometimes. Chimpanzees occasionally fall or are pushed out of trees without damage. However, in one recorded instance, the animal fell partially on to a rock, broke his neck and died. The nest is made by weaving branches together, some of which are broken off in the process. Several different species of tree are used. Day-nests are often built during rain (van Lawick-Goodall 1971; Teleki 1973*b*; Baldwin *et al.* 1981). Goodall (1983, 1986) lists several observations of falls which resulted in injury.

A particular chunk of kinetic energy is classified as a malentity which is modified by the nest of the subject animal, which in turn modifies its own environment by constructing the nest. The informal defining equations are:

(kinetic energy)Mal(chimpanzee) $=_{df}$ H(chimpanzee) is decreased | ξ(kinetic energy)(chimpanzee)

(nest)Mod^{-1}(chimpanzee) $=_{df}$ ($\exists$ kinetic energy) such that [(kinetic energy)Mal(chimpanzee) | $\sim\xi$(nest)(chimpanzee) and $\sim$(kinetic energy)Mal(chimpanzee) | ξ(nest)(chimpanzee)]

(chimpanzee)Mod^{+2}(chimpanzee) $=_{df}$ ($\exists$ nest) such that [(nest)Mod^{1}(chimpanzee) | ξ(chimpanzee)(nest) and $\sim$(nest)Mod^{1}(chimpanzee) | $\sim\xi$(chimpanzee)(nest)].

18. Hasegawa *et al.* (1983) have evidence of chimpanzees in the Mahale Mountains eating small antelopes (bushbuck and duiker) that have been killed by leopards or other predators or have died of disease. The authors saw several chimpanzees one morning searching for and then eating a dead bushbuck which had been killed and left in a tree by a leopard the night before. The authors believe that this behaviour lends support to the theory that our hominid ancestors in Africa also ate animals that they had not killed.

The informal defining equations for a bushbuck as a resource (after its death) and a leopard as a first-order modifier are:

(bushbuck)Res(chimpanzee) $=_{df}$ H(chimpanzee) is increased | ξ(bushbuck)(chimpanzee)

$$\text{(leopard)Mod}^{+1}\text{(chimpanzee)} =_{\text{df}} (\exists\ \text{bushbuck}) \text{ such that } [\text{(bushbuck)Res(chimpanzee)} \mid \xi\text{(leopard)(bushbuck) and } \sim\text{(bushbuck)Res(chimpanzee)} \mid \sim\xi\text{(leopard)(bushbuck)}].$$

19. According to Riss and Busse (1977), a dominant male with relatively great copulatory success occupies its position in the hierarchy because of age, size, physical fitness, dominance status of its mother, personality, and the formation of cooperating coalitions with others. Van Lawick-Goodall (1971) records occasional violence among the animals; handfuls of hair may be pulled out, blows may result in wounding or an animal being dislodged from a tree. An attacking male would be classified as a predator if the subject male is harmed by the encounter, and the attacker increases its status and thus its H, via an increased probability of reproduction. If the subject male is damaged and the H of the other chimpanzee is decreased by a reduction in status, then the other animal is classified as a malentity. The informal defining equation in the latter case is:

$$\text{(other chimp)Mal(subject male)} =_{\text{df}} \text{H(subject male) is decreased and H(other chimp) is decreased} \mid \xi\text{(other chimp)(subject chimp)}.$$

Other aggressive acts among chimpanzees may be directed towards strange chimpanzees, or local chimpanzees who act in an abnormal manner (because of disease or accident, for instance). An entire community was exterminated in 1975 (Goodall 1986).

20. Nishida and Uehara (1983) list the following insects: ten genera of Hymenoptera, including the honeybee *Apis mellifera* and several species of ant; two genera of Isoptera; one genus of Hemiptera; one of Coleoptera; one of Orthoptera; and one of Lepidoptera. Chimpanzees eat soldier and worker ants and termites, eggs, pupae, larvae, and workers of bees, also the honey and mainly the larvae of the other insects.

The informal defining equation for a particular bee as a resource is:

$$\text{(bee)Res(chimpanzee)} =_{\text{df}} \text{H(chimpanzee) is increased and H(bee) is decreased} \mid \xi\text{(bee)(chimpanzee)}.$$

21. Wild chimpanzees request food from one another by vocalisations and gestures (Savage-Rumbaugh *et al.* 1978).

An animal which provides a specific item of food for the subject animal is acting as a positive first-order modifer. The informal defining equation is:

$$\text{(other chimp)Mod}^{+1}\text{(subject chimp)} =_{\text{df}} (\exists\ \text{food}) \text{ such that } [\text{(food)Res(subject chimp)} \mid \xi\text{(other chimp)(food) and } \sim\text{(food)Res(subject chimp)} \mid \sim\xi\text{(other chimp)(food)}].$$

In the case that the subject animal is an infant chimpanzee, the mother provides food (Silk 1978). Silk also observed adolescents soliciting food from their mothers, and gives percentages of success of such solicitation and of the mothers' resistance, from weaning until the age of four years.

22. Tutin *et al.* (1983), working at Mt Assirik, in Senegal, consider that four species of Carnivora 'can be considered as potential predators of chimpanzees, namely lion (*Panthera leo*); leopard (*Panthera pardus*); wild dog (*Lycaon pictus*); and spotted hyaena (*Crocuta crocuta*)'. However, no examples of actual attacks are given, so I have not included any of these carnivores on the envirogram.

References

Allen, M. (1981). Individual copulatory preference and the 'strange female effect' in a captive group-living male chimpanzee (*Pan troglodytes*). *Primates* **22**, 221–36.

Anderson, J. R., Williamson, E. A., and Carter, J. (1983). Chimpanzees of Sapo Forest, Liberia: density, nests, tools and meat-eating. *Primates* **24**, 594–601.

Asano, T., Kojima, T., Matsuzawa, T., Kubota, K., and Murofushi, K. (1982). Object and color naming in chimpanzees (*Pan troglodytes*). *Proc. Japan Acad.* **58**, *Ser. B*, 118–22.

Baldwin, L. A., and Teleki, G. (1973). Field research on chimpanzees and gorillas: an historical, geographical and bibliographical listing. *Primates* **14**, 315–30.

Baldwin, P. J., Sabater-Pi, J., McGrew, W. C., and Tutin, C. E. G. (1981). Comparison of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates* **22**, 474–86.

Buirski, P., Plutchik, R., and Kellerman, H. (1978). Sex differences, dominance and personality in the chimpanzee. *Anim. Behav.* **26**, 123–9.

Cole, B. C., Graham, C. E., and Ward, J. R. (1970). The isolation of mycoplasmas from chimpanzees. In 'The Chimpanzee'. Vol. 2. (Ed. G. H. Bourne.) pp. 390–409. (Karger: Basel.)

de Waal, F. (1982). 'Chimpanzee Politics: Power and Sex among Apes.' (Jonathon Cape: London.)

de Waal, F. B. M., and Hoekstra, J. A. (1980). Contexts and predictability of aggression in chimpanzees. *Anim. Behav.* **28**, 929–37.

Doering, C. H., McGinnis, P. R., Kraemer, H. C., and Hamberg, D. A. (1980). Hormonal and behavioral response of male chimpanzees to a long-acting analogue of gonadotropin-releasing hormone. *Arch. Sex. Behav.* **9**, 441–50.

File, S. K. (1976). *Probstmayria gombensis* from the chimpanzee. *J. Parasitol.* **62**, 256–8.

File, S. K., McGrew, W. C., and Tutin, C. E. G. (1976). The intestinal parasites of a community of feral chimpanzees. *J. Parasitol.* **62**, 259–61.

Gaillard, J.-M., Bert, J., and Klein, M. (1979). Temporal organization of sleep stages in man and in three monkey species: an interspecific comparison. *Phys. and Behav.* **23**, 639–43.

Goodall, J. (1977). Infant killing and cannibalism in free living chimpanzees. *Folia Primatol.* **28**, 259–82.

Goodall, J. (1983). Population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. *Z. Tierpsychol.* **61**, 1–60.

Goodall, J. (1986). 'The Chimpanzees of Gombe. Patterns of Behavior.' (The Bellknap Press: Cambridge, Massachusetts.)

Graham, C. E. (1979). Reproductive function in aged female chimpanzees. *Am. J. Phys. Anthropol.* **50**, 291–300.

Graham, C. E., and Hodgen, G. D. (1979). The use of chimpanzees in reproductive biology. *J. Med. Primatol.* **8**, 265–72.

Green, R. J. (1988). How does the play of chimpanzees (*Pan troglodytes*) vary with age and sex? Int. Ethol. Conference, 20th, August 7–16, 1987, University of Wisconsin, Madison. (Ed. I. R. Inglis.) pp. 74–75. (ADAS: London.)

Hasegawa, S., Hiraiwa, M., Nishida, T., and Takasaki, H. (1983). Evidence on scavenging behavior in chimpanzees. *Curr. Anthropol.* **24**, 231–2.

Jones, C., and Sabater-Pi, J. (1969). Sticks used by chimpanzees in Rio Mundi, West Africa. *Nature (Lond.)* **223**, 100–1.

King, N. E., Stevens, V. J., and Mellen, J. D. (1980). Social behavior in a captive chimpanzee (*Pan troglodytes*) group. *Primates* **21**, 198–210.

Lemmon, W. B., and Allen, M. L. (1978). Continual sexual receptivity in the female chimpanzee (*Pan troglodytes*). *Folia Primatol.* **30**, 80–8.

McBeath, N. M., and McGrew, W. C. (1982). Tools used by wild chimpanzees to obtain termites at Mt Assirik, Senegal: the influence of habitat. *J. Hum. Evol.* **11**, 65–72.

McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *J. Hum. Evol.* **3**, 501–8.

McGrew, W. C., and Collins, D. A. (1985). Tool use by wild chimpanzees *Pan troglodytes* to obtain termites *Macrotermes herus* in the Mahale Mountains, Tanzania. *Am. J. Primatol.* **9**, 47–62.

McGrew, W. C., and Tutin, C. E. G. (1978). Evidence for a social custom in wild chimpanzees? *Man (N.S.)* **13**, 234–51.

McGrew, W. C., Tutin, C. E. G., and Baldwin, P. J. (1979). Chimpanzees, tools, and termites: cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man (N.S.)* **14**, 185–214.

Merrick, N. J. (1977). Social grooming and play behavior of a captive group of chimpanzees. *Primates* **18**, 215–24.

Morris, K., and Goodall, J. (1977). Competition for meat between chimpanzees and baboons of the Gombe National Park. *Folia Primatol.* **28**, 109–121.

Myers, B. J., and Kuntz, R. E. (1972). A checklist of parasites and commensals reported for the chimpanzee. *Primates* **13**, 433–71.

Myers, B. J., Kuntz, R. E., and Kamara, J. A. (1973). Parasites and commensals of chimpanzees captured in Sierra Leone, West Africa. *Proc. Helminthol. Soc. Wash.* **40**, 298–9.

Nishida, T. (1972). The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. *J. Hum. Evol.* **2**, 357–70.

Nishida, T. (1976). The bark-eating habits in primates, with special reference to their status in the diet of wild chimpanzees. *Folia Primatol.* **25**, 277–87.

Nishida, T. (1980*a*). Local differences in responses to water among wild chimpanzees. *Folia Primatol.* **33**, 189–209.

Nishida, T. (1980*b*). On inter-unit-group aggression and intra-group cannibalism among wild chimpanzees. *Hum. Ethol. Newsl.* **31**, 21–4.

Nishida, T., and Hiraiwa, M. (1982). Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *J. Hum. Evol.* **11**, 73–99.

Nishida, T., and Uehara, S. (1980). Chimpanzees, tools and termites: another example from Tanzania. *Curr. Anthropol.* **21**, 671–2.

Nishida, T., and Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. *Afr. Stud. Monogr.* **3**, 109–30.

Nishida, T., Uehara, S., and Nyundo, R. (1979). Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates* **20**, 1–20.

Niven, B. S. (1987). Logical synthesis of an animal's environment: sponges to non-human primates. I. Primative terms and definitions. *Aust. J. Zool.* **35**, 597–606.

Paterson, H. E. H. (1985).The recognition concept of species. In 'Species and Speciation'. (Ed. E. S. Vrba.) Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria, 1–29.

Patterson, T. T., and Willett, F. J. (1951). Unofficial strike. *Sociol. Rev.* **43**, 57–94.

Premack, D. (1983). The codes of man and beasts. *Behav. and Brain Sc.* **6**, 125–67.

Premack, D., and Woodruff, G. (1978). Chimpanzee problem-solving: a test for comprehension. *Science (Wash. D.C.)* **202**, 532–5.

Reynolds, V. (1980). 'The Biology of Human Action.' 2nd Edn. (W. H. Freemand: Oxford.)

Riss, D. C., and Busse, C. C. (1977). Fifty-day observation of a free-ranging adult male chimpanzee (*Pan troglodytes schweinfurthii*). *Folia Primatol.* **28**, 283–7.

Riss, D. C., and Goodall, J. (1977). The recent rise to the alpha-rank in a population of free-living chimpanzees. *Folia Primatol.* **27**, 134–51.

Sabater-Pi, J. (1974). An elementary industry of the chimpanzees in the Okorobiko Mountains, Rio Muni (Republic of Equatorial Guinea), West Africa. *Primates* **15**, 351–64.

Sabater-Pi, J. (1979). Feeding behaviour and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains in Rio Muni (West Africa). *Z. Tierpsychol.* **50**, 265–81.

Savage-Rumbaugh, E. S., Rumbaugh, D. M., and Boysen, S. (1978). Symboli communication between two chimpanzees (*Pan troglodytes*). *Science (Wash. D.C.)* **201** *(4356)*, 641–4.

Silk, J. B. (1978). Patterns of food sharing among mother and infant chimpanzees (*Pan troglodytes schweinfurthii*) at Gombe National Park, Tanzania. *Folia Primatol.* **29**, 129–41.

Smith, A. H., Butler, T. M., and Pace, N. (1975). Weight growth of colony-reared chimpanzees. *Folia Primatol.* **24**, 29–59.

Stewart, P. J. (1982). Human ecology. The peculiar science of a peculiar mammal. *Bull. Br. Ecol. Soc.* **13**, 159–63.

Stewart, P. (1983). Culture in the evolution of evolution. *Co-Evol. Quart.* **37**, 46–8.

Takahata, Y., Hasegawa, T., and Nishida, T. (1984). Chimpanzee predation in the Mahale mountains from August, 1979 to May, 1982. *Int. J. Primatol.* **5**, 213–33.

Takasaki, H. (1983). Mahale chimpanzees taste mangoes-toward acquisition of a new food item? *Primates* **24**, 273–5.

Teleki, G. (1973*a*). Notes on chimpanzee interactions with small carnivores in Gombe National Park, Tanzania. *Primates* **14**, 407–11.

Teleki, G. (1973*b*). Group response to the accidental death of a chimpanzee in Gombe National Park, Tanzania. *Folia Primatol.* **20**, 81–94.

Tutin, C. E. G., and McGrew, W. C. (1973). Chimpanzee copulatory behavior. *Folia Primatol.* **19**, 237–56.

Tutin, C. E. G., McGrew, W. C., and Baldwin, P. J. (1983). Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus* at Mt Assirik, Senegal. *Primates* **24**, 154–73.

Uehara, S. (1982). Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). *Folia Primatol.* **37**, 44–76.

Uehara, S., and Nishida, T. (1987). Body weights of wild chimpanzees *Pan trogolodytes schweinfurthii* of the Mahale Mountains National Park, Tanzania. *Am. J. Phys. Anthropol.* **72**, 315–22.

van Lawick-Goodall, J. (1971). 'In the Shadow of Man.' (Houghton Mifflin: Boston.)

van Wulfften Palthe, T., and van Hooff, J. A. R. A. M. (1975). A case of the adoption of an infant chimpanzee by a suckling foster chimpanzee. *Primates* **16**, 231–4.

Walsh, G. P., Meyers, W. M., Binford, C. H., Gerone, P. J., Wolf, R. H., and Leininger, J. R. (1981). Symp. Epidemiology of Leprosy, Geillo, Norway, 1981. *Lepr. Rev.* **52** (Suppl. 1), 77–83.

Woodruff, G., and Premack, D. (1981). Primitive mathematical concepts in the chimpanzee: proportionality and numerosity. *Nature (Lond.)* **293** *(5833)*, 568–70.

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THE ECOSYSTEM AS AN ALGEBRAIC CATEGORY: A MATHEMATICAL BASIS FOR THEORY OF COMMUNITY AND ECOSYSTEM IN ANIMAL ECOLOGY

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Keywords: Ecosystem, Community, Algebra, Theory, Animal, Treehole

Abstract: A formal definition of 'ecosystem' is shown to obey the axioms of category theory. The definition makes use of a previously published symbolic definition of an animal's environment and includes also the formalized notion of an animal community. A product of the category is a food web in the ecosystem. Methods of classification and comparison of real-life communities and ecosystems result from the definitions. Non-overlapping communities within the same habitat may be differentiated precisely. Illustrative examples of communities and ecosystems are given using the ecology of the Common Octopus *(Octopus vulgaris)*. An analysis of R.L. Kitching's water-filled treehole communities is also given.

Introduction

Rosen (1958) showed how the algebra of categories might be useful in general in theoretical biology. In the present paper it is shown that the 'ecosystem' of animal ecology obeys the three axioms of category theory (see for example Manes 1976). The ecosystem will be defined by using a formal symbolic definition of the environment of an animal which has been found useful in field ecology. The definition of ecosystem given here incorporates a definition of community. Both definitions lend themselves to simple classifications of observed communities and ecosystems which accord well with present practices of field ecologists. A product in the category is a food web in the ecosystem.

An animal's environment

A symbolic definition of an animal's environment was published by Niven (1980). This was used by Andrewartha and Birch (1984) as a basis for their own approach to animal ecology. These authors also used the definition to classify the environments of a number of animal species including limpets, insects, a moose and a buffalo. They introduce a diagram called an 'envirogram' which displays objects in the environment in their correct place according to the formal definition. The environment is defined as a structured set of objects. There are two subsets, called the 'centrum' and the 'web'.

The *centrum* includes those objects which affect the subject animal directly; it is subdivided into four subsets called 'Resources', 'Mates', 'Predators' and 'Malentities'. Resources are objects such as items of food, packages of energy (heat, light etc.) and places such as suitably-placed rocky shelves for breeding purposes. The definition of 'Mate' requires that an offspring will probably result from the union, thus a sterile animal of the opposite sex would not be classified as a mate. Self-matings are allowed. The subset 'Predators' includes also the parasites of the subject animal; these objects benefit from the encounter with the subject animal. A 'Malentity' is an object which adversely affects the subject animal without itself benefitting by the encounter. A typical malentity is the person who steps on an ant; the human probably does not even notice the encounter whereas the subject animal (the ant) is damaged or destroyed.

The *web* includes those objects which affect the subject animal indirectly. It is subdivided into various orders of 'modifiers'. First-order modifiers are objects which modify elements of the centrum. Thus a person acting as a malentity in the environment of an ant may be 'modified' by being stung by a wasp and hence removed from the scene so that the ant does not encounter the person at all; the wasp is classified as a first-order modifier in the environment of the ant. Second-order modifiers modify first-order modifiers, and so on. The web is formally defined as an infinite set of modifiers. In practice animal ecologists rarely use modifiers of order greater than two, nevertheless these do sometimes form part of an ecological study, for example Andrewartha and Birch (1984) give some third-order modifiers for the limpet *Cellana tramoserica* and Kitching (1983) gives an envirogram for the aquatic snail *Lymnaea peregra* which includes some third-order modifiers. It is often convenient in theoretical work to refer to objects in the *centrum* as 'zero-order modifiers'.

The definition of environment incorporates four primitive terms special to the theory of animal ecology. The interpretation of one of these includes stochastic variables. In addition the definition of a mate is a probabilistic sentence. Thus the proposed mathematical basis is probabilistic in two different ways both of which are at a foundational level. Since the definitions of community and ecosystem given in this paper are dependent on the environment definition they too are fundamentally stochastic. Also since the environment definition is a functional one it follows that the definitions of 'community' and 'ecosystem' are likewise functional. Each subset of the environment is defined for a specific animal at some specific time. In practice this is no obstacle to the use of the resulting classification in a practical case, since results observed from studies of many animals of the same species during intervals of time are concatenated to yield an envirogram. More formally we may replace the sub-index 't' in the definitions by 'τ' representing an interval of time.

Community

There are at least three notions of community in current ecology literature:

(i) In human ecology 'community' is used to mean a set of humans usually in a specific place. This set would be called a 'population' by animal ecologists.

(ii) In plant ecology 'community' is often used to mean the set of all plants in a particular area, which may or may not interact in an obvious way.

(iii) In animal ecology 'community' is often used to mean a set of interacting populations in which the interactions are fairly obvious and easily measured.

In the present article the third meaning is used, except that the interactions are formally among individuals instead of populations.

The idea of 'habitat' is required in order to define an animal community. Unfortunately the word has been used in at least two quite different ways in animal ecology. In this article 'habitat' is used to mean "... a place that might be habitable for the animal whose ecology is being studied. The boundaries of the habitat and the qualities that determine the boundaries are fixed arbitrarily by the ecologist". This is the meaning accepted by Andrewartha and Birch (1984). The quotation is from Elton (1949). So a habitat is a specific place, not a class of places. 'Habitat' will now be used as the fifth primitive term special to animal ecology.

In lieu of "animal 'a' is a kth-order modifier of animal 'b' " we now write "Mod^k: a $\rightarrow$b", *i.e.* "a kth-order modifier sends animal 'a' to animal 'b' ". The idea of modifiers in an environment is thus transformed into the mathematical notion of a morphism. Then an nth-order animal community C_n within a habitat is a structured set of animals a, b, ... such that for every ordered pair (a, b) we have Mod^k: a $\rightarrow$b, $k = 0, 1, 2, \ldots, n$, where k is the smallest integer for every pair.

If n is small then C_n will be a set of animals which are closely knit together and several different communities may occur. Animal ecologists usually work with such communities. If for the moment we imagine that the elements of C_n are plants and their connecting morphisms are known then the plant ecologists' notion of community would be satisfied when n is large. For this definition to be helpful certain universal modifiers must be excluded. Oxygen and thermal energy are examples of universal modifiers. In any group of animals units of oxygen or heat are resources for all the animals, thus an animal 'a' which uses some particular unit of energy, say, is removing this resource from animal 'b' and is thus formally a first-order modifier in b' s environment. So all animals in a habitat are sent to each other by the morphism Mod^1 (first order modifier). For this reason we exclude the universal modifiers when classifying a community.

Ecosystem

The nth-order ecosystem $\mathcal{E}_n$ associated with the animal community C_n is a category. The morphisms of $\mathcal{E}_n$ are the modifiers in the environments of the animals $a \in C_n$ of order not greater than n. The objects of $\mathcal{E}_n$ are the elements of C_n. The universal modifiers which were excluded when classifying C_n we now include in $\mathcal{E}_n$.

The ecosystem obeys the three axioms of category theory (see *e.g.* Manes 1976) as follows:

I. The associative law. For example if animal 'a' is a mate of (a third-order modifier of a predator) of animal 'b' then animal 'a' is (a mate of a third-order modifier) of a predator of animal 'b'.

II. Identity morphism. An identity morphism in $\mathcal{E}_n$ may be obtained as follows. We have, for animals 'a' and 'b', that a = b iff Ea = Eb, where Ea and Eb are the two environments (Niven 1983). If now we write E^{-1} X for the animal whose environment is X then E^{-1} Ea = a thus E^{-1} E: a $\rightarrow$ a and 'E^{-1} E' is identity morphism in $\mathcal{E}_n$.

III. If for animals a, b, a', b', (a, b) $\neq$ (a', b') then Hom (a, b) $\cap$ Hom (a', b') = 0 i.e. the set of morphisms connecting one pair of animals is disjunct from the set of morphisms connecting any different pair of animals. This must be so if we include the end animals.

Notice that Hom (a, b) may well include non-animal objects such as plants, viruses, particles of soil or mineral matter, quantities of water, units of energy and so on. In most field studies many hundreds of animals of scores of different species are likely to form the community and the non-animal objects in the ecosystem may be extremely numerous. It may sometimes, in a specific case in the field, seem sensible to add some extra non-animal objects, which would not normally be included in $\mathcal{E}_n$ because, although they are modifiers of some animal in the community, they do not enter into a connecting link between some pair of animals. We shall call these 'external modifiers'. An example is given in the ecosystem of the following section.

An interesting mathematical object within the category $\mathcal{E}_n$ is the product X^{Pred} Y where X and Y are sets included in C_n and for all $x \in X$ and all $y \in Y$ we have that Pred: x $\rightarrow$ y, 'Pred' standing for 'predator'. The product may be extended to more than two sets. It may also be defined in terms of 'resource' instead of 'predator'. This mathematical object is the analogue of an interesting object in field ecology called a 'food web'. Food webs are well explained by Cohen (1978), who gives an example in which a species of snake eats a certain species of frog which in turn eats two species of insect. If we refer to the four sets of these animals in the habitat as S, F, I_1 and I_2 then the two products are:

$S^{\text{Pred}}\ F^{\text{Pred}}\ I_1$
and $S^{\text{Pred}}\ F^{\text{Pred}}\ I_2$

Cohen also includes three species of the willow, *Salix*, in his example; for the purposes of this paper, however, we omit the sets of plants.

Illustrative examples of communities and ecosystems

The Common Octopus, *Octopus vulgaris*, is particularly well-known in the Mediterranean. Its food consists mainly of crabs, lobsters, bivalves and gastropods (Mangold 1983; Ambrose and Nelson 1983). R.F. Ambrose (pers. comm. 1984) remarks "Crabs seem to be the favourite food everywhere. Octopuses often hunt 'speculatively' by feeling under rocks and in cracks; all the hunting I have observed in the field has been of this sort." However if the anemone *Calliactis parasitica* is present on the crab *Dardanus arroser*, the octopus will not eat that crab (Ross 1971; Ross and von Boletzky 1979). Thus a crab of this species is a resource of a subject octopus and an anemone of the right species is a first-order modifier. An octopus constructs a lair which affords a certain amount of protection from its predators, the most important of which are large eels, in particular the Common Moray, *Gymnothorax mordax* (Grzimek 1974, Lane 1960). Thus the lair is a first-order modifier of an eel of this species in the environment of a subject octopus.

As an illustrative example consider a small habitat in the Mediterranean containing an octopus lair. The animals present are:

1 *Octopus vulgaris*;
2 crabs *(Dardanus arroser)* of opposite sex;
1 anemone *(Calliactis parasitica)*;
1 eel *(Gymnothorax mordax)*;
2 passing fish.

We have the following morphisms:

Pred: octopus → crab_1
Res: crab_1 → octopus
Pred: octopus → crab_2
Res: crab_2 → octopus
Mat: crab_1 → crab_2
Mat: crab_2 → crab_1

All these morphisms are zero-order modifiers, so a zero-order community C_0 in the habitat is the set {octopus, crab_1, crab_2}.

If now we add the eel to C_0 we may write down the following morphisms:

Pred: eel → octopus
Res: octopus → eel
Mod^1: crab_1 → eel
Mod^1: eel → crab_1
Mod^1: crab_2 → eel
Mod^1: eel → crab_2

The crabs are resources of a resource of the eel and are thus first-order modifiers in the environment of the eel. The eel is a predator of a predator of the crabs and is thus a first-order modifier in the environments of both crabs. Thus the set {octopus, crab_1, crab_2, eel} is a first-order community C_1 in the habitat.

If now to the zero-order community of {octopus, crab_1, crab_2} we add the anemone, we may add the following morphisms:

Mod^1: anemone → octopus
Mod^2: octopus → anemone
Mod^1: anemone → crab_1
Mod^1: crab_1 → anemone
Mod^1: anemone → crab_2
Mod^1: crab_2 → anemone

As explained above the anemone is a first-order modifier in the environment of the octopus. When we consider the anemone as the subject animal we find that a crab enters its environment as a first-order modifier by conveying the anemone to its food; we can find an item of food which is such that it does not become a resource of the anemone without the intervention of the crab. Thus the octopus, as a predator of the crab, is a second-order modifier in the environment of the anemone. Notice that the crab is not a resource, mate, predator or malentity of the anemone, *i.e.* it is not a zero-order modifier in the anemone's environment. So there is a basic asymmetry in the morphisms between anemone and octopus. When we examine the functional relations between crab and anemone, however, we find symmetry; a crab is a first-order modifier of the anemone and the anemone is a first-order modifier of the crab. These arguments lead, then, to the conclusion that the set {octopus, crab_1, crab_2, anemone} is a second-order community, C_2, in the habitat.

Now consider the set {octopus, crab_1, crab_2, eel, anemone}. The morphisms to be added are:

Mod^3: eel → anemone
Mod^2: anemone → eel.

The first of these comes about because in the environment of the anemone the octopus is a second-order modifier so the eel acts as a third-order modifier if it eats the octopus. The second morphism is true because the octopus is classified as a resource in the eel's environment; the crab is a resource of the octopus and the anemone a modifier of that resource. Thus the given set is C_3, a third-order community in the habitat. The two passing (anonymous) fish may possibly enter into the scheme if high order morphisms are considered, or if they happen to be suitable octopus prey. However two large fish of suitable species are unlikely to be elements of an animal community of low order which contains the octopus.

The ecosystems associated with C_0, C_1, C_2 and C_3 will include such objects as oxygen and thermal energy, both of which are resources of all the animals. The octopus lair, which is a first-order modifier, may be added to $\mathcal{E}_1$, $\mathcal{E}_2$ and $\mathcal{E}_3$ as an external object, since it does not link any pair of animals. The lair protects the octopus from the eel and so is a first-order modifier in the eel's environment by modifying a resource. It is also a first-order modifier in the octopus' environment by modifying a predator. However we cannot write Mod^k: eel $\rightarrow$ octopus for some small k via a path which includes the lair. So the lair is an 'external modifier'. In a real-life habitat in the Mediterranean containing large numbers of many species of animals the lair would almost certainly be incorporated in the ecosystem via chains of modifiers connecting pairs of animals and it would be unnecessary to add any external modifiers.

An analysis of a water-filled treehole community

R.L. Kitching has studied communities of animals, mainly insects, in water-filled treeholes in England, Australia and Indonesia (Kitching 1986, pres. comm.). In this analysis only the first of these studies is used (Kitching 1971). It was undertaken in the beech forests of Wytham Woods, Berkshire, England. The following animals were found:

(i) Two species of mosquito, *Aedes geniculatus* (Olivier) and *Anopheles plumbus* Stephens, referred to here as 'A_1' and 'A_2'.

(ii) Two species of midges, *Metriocnemus martinii* Thienemann and *Dasyhelea dufouri* Laboulbéne, referred to as 'M' and 'D'.

(iii) The hoverfly *Myiatropa florea* (Linnaeus), referred to as 'Y'.

(iv) A small detritus-eating beetle *Prionocyphon serricornis* Müller, referred to as 'P'.

The mosquitoes require sugar secretions to provide flight energy and the females require a blood meal to ensure maturation of eggs. Herbs provide the sugar and vertebrates the blood. Midge D requires plant juices for food and the females probably feed on the blood of other adult insects. The hoverfly requires pollen meals provided in Wytham Woods by flowers of teasel and ivy. All the insects in the water-filled treeholes are preyed upon by birds, spiders, other insects and a variety of other insectivorous animals. They may be blown away and be unable to find further treeholes in which to lay eggs. Heavy rain or extreme temperatures will cause considerable mortality. The larvae of A_1, A_2, M, D, Y and P are all saprophages *i.e.* they eat rotten compostlike particles present in the water.

In order to deal with the insects throughout a lifecycle we choose a suitable interval of time during which the modifiers in the insects' environments may act. Since all the larvae in one particular treehole have as resources the rotting particles in the water they are first-order modifiers of each other. Thus if we choose just one water-filled treehole as the habitat the community is a first-order one which includes all members of all six species. If now we use a larger habitat then the predators of the adult insects should be included in a higher order community, such as web-spinning spiders (there may perhaps be a dozen of these), seven or eight species of insectivorous birds, a few species of entophagous insects and possibly a bat (Kitching, pers. comm. 1986). The corresponding first-order ecosystems include the compost-like particles in the water, the water itself and the universal modifiers oxygen and thermal energy. To include the vertebrates which supply the blood meals for the mosquitoes we need to consider higher-order modifiers.

Discussion

The definitions of community and ecosystem provide a simple method for differentiating communities and ecosystems in the field even when in the same habitat. It will often be possible for a field ecologist to observe two nonoverlapping nth-order communities in one habitat providing n is small. The method of classification also provides a means of comparison across the boundaries of habitats and animal species.

The point that the system described here is a stochastic one at a fundamental level accords well with the view of many ecologists that stochastic systems have validity in ecology (See *e.g.* Wiens 1984). It is also widely accepted that population ecology is a basis for community ecology (Southwood 1980, Strong *et al.* 1984), an attitude with which the definitions of this article are in accord.

The environment definition has been used by Andrewartha and Birch (1984) for classifying the environment of our own species. However I myself believe that psychological and cultural matters are of such importance in human ecology that a separate definition should be constructed for our species. Work on this definition is in progress. It may well be that analogues of the community and ecosystem definitions will hold also for humans; for the moment it seem preferable to exclude humans from the system. Future work also is planned for an extension to plant ecology. The morphisms connecting plants and modular organisms have not yet been studied. A more complete definition of ecosystem should be possible once these morphisms are written down.

The use of such a general algebra as the theory of categories lends itself to the construction of a further axiom once the work on plants, modular organisms and humans has been completed. Only with a complete axiomatic system will it be possible to derive theorems which relate directly to ecology and enable us to do the necessary arithmetic to manipulate and predict ecological systems in much the same way as we manipulate and predict physical systems.

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REFERENCES

Ambrose, R.F. and B.V. Nelson. 1983. Predation by Octopus vulgaris in Mediterranean. PSZNI: Marine Ecology 4: 251-261.

Andrewartha, H.G. and L.C. Birch. 1984. *The Ecological Web. More on the Distribution and Abundance of Animals*. University of Chicago Press, Chicago.

Cohen, J.E. 1978. *Food Webs and Niche Space*. Princeton University Press, Princeton, New Jersey.

Elton, C. 1949. Population interspersion. An essay on animal community patterns. J. Ecol. 37: 1-23.

Grzimek, B. (ed). 1974. *Grzimek's Animal Life Encyclopedia*, Vol. 3. Van Nostrand Reinhold, New York.

Kitching, R.L. 1971. An ecological study of water-filled treeholes and their position in the woodland ecosystem. J. Anim. Ecol. 40: 281-302.

Kitching, R.L. 1983. *Systems Ecology*. University of Queensland Press, Brisbane.

Lane, F.W. 1960. *Kingdom of the Octopus*. Sheridan House, New York.

Manes, E. 1976. *Algebraic Theories*. Springer, New York.

Mangold, K. 1983. Food, feeding and growth in cephalopods. Mem. Nat. Mus. Victoria 44: 81-93.

Niven, B.S. 1980. The formal definition of the environment of an animal. Aust. J. Ecol. 5: 37-46.

Niven, B.S. 1983. Two different animals may not have the same environment. J. theor. Biol. 105: 369-370.

Niven, B.S. 1986. The logical synthesis of an animal's environment: sponges to non-human vertebrates. Aust. J. Zool. (In press).

Rosen, R. 1958. The representation of biological systems from the standpoint of the theory of categories. Bull. Math. Biophysics 20: 317-341.

Ross, D.M. 1971. Protection of hermit crabs (*Dardnus* spp.) from octopus by commensal sea anemones (*Calliactis* spp.). Nature 230: 401-402.

Ross, D.M. and S. von Boletzky. 1979. The association between the Pagurid *Dardanus arroser* and the Actinian *Calliactis parasitica*: recovery of activity in inactive *D. arroser* in the presence of cephalopods. Mar. Behav. Physiol. 6: 175-184.

Southwood, T.R.E. 1980. Ecology - a mixture of pattern and probabilism. In: E. Saarinen (ed), *Conceptual Issues in Ecology*. D. Reidel Publishing Company, Dordrecht, Holland.

Strong, D.R., J.H. Lawton and Sir Richard Southwood. 1984. *Insects on Plants*. Harvard University Press, Cambridge, Massachusetts.

Strong, D.R., D. Simberloff, L.G. Abele and A.B. Thistle (eds). 1984. Preface to *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, New Jersey.

Wiens, J.A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In: D.R. Strong, *et al.* (eds.), pp. 439-457.

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Formalization of the Paterson concept of an animal species

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Formalization of the Paterson concept of an animal species

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ABSTRACT: A symbolic definition of 'species' based on Paterson's recognition concept is given. It contains four of the five primitive terms used by the author to define 'environment' and 'animal community'. The definition of 'species' contains the author's symbolic definition of a potential mate of an animal as used by ANDREWARTHA and BIRCH (1984) *as part of 'environment' thus the Paterson concept is closely linked at a foundational level both with the Andrewartha and Birch notion of an animal's environment and 'animal community' defined as a set of animals which are functionally related* (NIVEN, 1987).

I. INTRODUCTION

J. H. WOODGER (1952) wrote

> In considering the relation of mathematics to biology we must distinguish between the process of applying existing mathematics to biology and the less familiar process of letting biological statements suggest new mathematical ones.

In the present article I shall use the 'less familiar' method of formalization to show that the recognition concept of species (PATERSON, 1985) is closely linked *via* the primitive terms used in the mathematical definitions with both the Andrewartha and Birch idea of an animals envi-

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ronment (ANDREWARTHA and BIRCH, 1984) and the notion of an animal community as a set of animals which are connected by their functional relations (NIVEN, 1987b). The general approach taken by WOODGER (1937 ; 1939) was derived directly from WHITEHEAD and RUSSELL (1925) in that Woodger used their notation and followed their methods of translating natural language sentences into formalized sentences written in a rigorously circumscribed symbolic language. Woodger's work was difficult for biologists to read and understand ; its inaccessibility has resulted in its being less widely known than one might expect. A formalized system for evolutionary theory was constructed by WILLIAMS (1970) following Woodger's ideas but using more modern notation which is much easier to read ; even so, Williams' work has had little impact on the day–to–day work of biologists. In my present work on formalized theory of ecology of which this paper forms a part I have complied with the following conditions : (i) close contact is kept with field workers, (ii) intermediate theoretical results are checked immediately against data from a wide range of appropriate biological organisms, (iii) the difficult and cumbersome notation of Whitehead and Russell is replaced by more modern notation interspersed with enough natural language to convey meaning without losing too much rigour. The result has been that the formalization is readily accessible to ecologists who are able to make use of the results in practice, for example the mathematical definition of 'environment' to classify objects within the environment of an animal (ANDREWARTHA and BIRCH, 1984).

The formalization method should be contrasted with the method of mathematical modelling also used by ecologists. Models are often poor predictors at least partly because the mathematics we use has foundations derived from physical not biological science. Thus the theory of differential equations used in animal population dynamics (e.g. MAY, 1974) was developed initially to deal with Newtonian physics and the n–dimensional Euclidean geometry used by HUTCHINSON (1957) as a model for the concept of 'niche' has at the foundational level primitive terms like 'point' which is derived from ideas about physical space.

In this paper first I present an interpretation of the four primitive terms 'An', 'Off', 'Hab' and 'ξ'. I shall then repeat the definition of 'mate' given in NIVEN (1987a) and use it to define 'species', illustrating both definitions with examples. Finally I shall comment on some aspects of the 'species' definition and discuss the foundational connections with other concepts of animal ecology. A list of symbols is given in an Appendix.

2. THE PRIMITIVE TERMS AN, OFF, HAB AND ξ

In any formalized system such as a branch of mathematics it is necessary to include certain undefined words or phrases called 'primitive terms'. It is not possible to construct a branch of mathematics in which all terms are defined. The primitive terms are then used in definitions. Axioms are assumed sentences containing the primitive terms and the definitions. The rules of deduction of the system enable us to evolve theorems from the axioms.

In addition to the four primitive terms which are used in the definition of 'species' there is a fifth within my system, called 'H' and known as 'the survival and reproduction primitive'. This is used in the definition of 'environment' (NIVEN, 1980), 'animal community' (NIVEN, 1987b) and 'niche' (to be published) and will not be referred to again in this article except briefly in the discussion. However it should be noted that the inclusion of 'H' implies that the overall formalized system is stochastic at a foundamental level.

'An' stands for 'animal', meaning individuals of the Kingdom Animalia of MARGULIS and SCHWARTZ (1982). By 'An(x)' I mean that x is an animal.

'Off' stands for 'offspring'. This primitive term is sometimes sub-indexed by 't' or 'δt' which indicates the time of birth or the time interval during which the offspring is born. So 'x $\mathrm{Off}_{\delta t}$ y' means that x is born to y during the interval δt.

'Hab' stands for 'habitat'. The term is derived from ELTON (1966) and refers to the place in which the ecologist confidently expects to find the animal of interest. It may also be sub-indexed by 't' or 'δt'. By 'B Hab a' I mean that the place 'B' is a habitat of 'a', where 'a' is specified to be an animal i.e. An(a). B may be a specific pond, paddock, field, forest, continent, ocean or small region of ocean and so on. It may even be an entire planet. When necessary a region of the atmosphere is included, or a certain depth of soil. In this paper B is always a specific place, not a class of places.

'ξ' is the interaction primitive of the system. By 'ξxy' I mean that an interaction occurs between x and y evoking immediately in y some physical, physiological or behavioural response or a change of position and no other object (other than x) reduces or enhances this effect of x on y i.e. x affects y directly. Judgement as to whether the response is significant is to be made by the ecologist. For instance if an animal 'y' gazes at some object 'x', a tree say, this is a response of 'y' to the tree and doubtless some sort of physiological process is evoked. A response of this type would often be regarded by the ecologist as trivial, and ignored. Like 'Off' and 'Hab' the interaction primitive may be sub-indexed by 't' or 'δt'.

The inclusion of ξ as a primitive term and the time-dependence of 'Off', 'Hab' and 'ξ' imply that the system is interactive and dynamic at a foundational level.

3. THE FORMAL DEFINITION OF MATE

By a 'mate' in the environment of a subject animal I mean much the same as the ordinary English phrase 'potential mate'. The definition is appropriate for all animals including those which are hermaphroditic or self-mating. It is necessary that offspring are possible, so a sterile animal of opposite sex cannot be a mate even if copulation occurs.

Finally, in view of modern developments in genetic engineering the possibility is allowed that the defined 'mate' is not even necessarily an animal, but may be an artefact.

It is essential that the time be specified ; this is easily seen when we consider as an example the mating habits of the chimpanzee (*Pan troglodytes*). The normal sexual cycle of a mature female chimpanzee is thirty-seven days, with a range of twenty-nine to forty-two days. Menstrual bleeding occurs between oestrous phases. Although female chimpanzees are receptive to copulation at all times they are more likely to mate during maximum tumescence. Copulation with brothers is very rare and mother-son true copulation has never been observed (LEMMON and ALLEN, 1978 ; TUTIN and MCGREW, 1975 ; VAN LAWICK-GOODALL, 1971). Thus if we fix our attention on a particular female chimpanzee as subject animal we observe that at certain times it is not possible for the subject animal to conceive offspring. During such periods an adult male, even in the close vicinity, is excluded from being a 'mate' by the formalization given here.

These considerations lead to the following definition of an object 'm' to be a mate of subject animal 'a' at time 't' :

$$\text{Prob}\ [(\exists x)\ \ (x\ \text{Off}_{t+\beta}\text{a}\ \ \&\ \ x\ \text{Off}_{t+\beta}\text{m})\ \ |\xi_t\ \text{ma}] > 0$$

i.e. the probability is greater than zero that there is at least one object 'x' which at time t$+\beta$ is an offspring of both 'a' and 'm', given that a significant interaction in the sense of ξ occurs at time t. β is the gestation time. Neither 'x' nor 'm' are necessarily animals.

In the case of chimpanzees, with the subject animal a female chimpanzee in oestrous at time t, 'm' would be a suitable adult male chimpanzee. The use of the conditional '|' (given that) implies that we would classify a suitable male chimpanzee as a mate even in the case that the male is a long way removed from the subject female ; in ordinary English words we are defining a potential mate. In the case of an hermaphrodite, like the earthworm *Lumbricus terrestris* for instance (EDWARDS and LOFTY, 1972) the mate 'm' would simply be another fertile adult. The definition also holds good for self-mating animals such as the rat tapeworm *Hymenolepsis diminuta* (BURT, 1980). If we replace 'm' in the definition by the subject animal 'a' we obtain :

$$\text{Prob}\ [(\exists x)\ \ (x\ \text{Off}_{t+\beta}\text{a}|\xi\text{aa}] > 0$$

Here we interpret 'ξ_{aa}' as that the interaction occurs within the subject animal 'a' ; the animal interacts with itself.

4. THE FORMAL DEFINITION OF SPECIES

Paterson's recognition concept of species is described in a number of articles (PATERSON, 1980 ; 1981 ; 1984 ; 1985 ; PATERSON and MACNAMARA, 1984 ; LAMBERT and PATERSON, 1985). He arrived at his (non–mathematical) definition *via* a careful consideration of evolutionary concepts. His specific–mate–recognition notion is dependent on the idea that the recognition response of a potential mating partner is of supreme importance ; without such a response the probability of mating is negligibly small. The use of a specific habitat is a necessary feature of the recognition response and this is catered for in the mathematical definition by the use of the conditional '|' (given that). Thus we have, for subject animal 'a', that the species S_a is the set of animals 'x' of which 'a' is an element such that :

$$x\ \text{Mat a or}\ x\ \text{Mat Mat a}\ |\ \text{B Hab}\ (x\ \text{and a}),$$

i.e. animal 'x' is either a (potential) mate of 'a' or a mate of a mate of 'a' given that 'B' is a habitat of both 'x' and 'a'. More formally we define an animal species S_a at time 't' as follows :

$$\mathrm{S_a} =_{\mathrm{Df}} \{x{:}x = \mathrm{a}\ \mathrm{V}x\ \mathrm{Mat_t a}\ \mathrm{V}x\ \mathrm{Mat_t Mat_t a} \mid \mathrm{An(a)}\ \&\ \mathrm{An}(x)\ \&\ \mathrm{B}\ \mathrm{Hab_t}(x\ \&\ \mathrm{a})\}$$

For hermaphroditic animals the term 'x $\mathrm{Mat_t}$ $\mathrm{Mat_t}$ a' is redundant. The sub–index 't' may be replaced by 'δt' if, for example, we wish to include juvenile animals which will become (potential) mates of 'a' during the interval of time δt.

5. COMMENTS ON THE FORMAL DEFINITION

1) It does not follow from the formal definition that either the parents or offspring of the animal 'a' are elements of the set $\mathrm{S_a}$. Thus mutations resulting in some change of mate recognition in at least one pair of offspring may well result in a different species.
2) Paterson deals with animals in the wild state. If the biologist should so desire the habitat 'B' in the mathematical definition could be some artificial place, such as a cage in a zoo, thus leading to the classification of animals such as lions and tigers, dogs and jackals, or mallard and pintail ducks, being defined as being of the same species. However these are very peculiar cases and, although they are logically valid, they seem unlikely to be of any practical use.
3) Another peculiar and artificial case is that of artificial insemination. The mathematical definition can be 'forced' to cover this case by making both the habitat 'B' and the time interval 'δt' large enough to include both parents.
4) In the case of a perpetually self–mating animal the definition reduces to just the animal 'a' which is in habitat 'B'; thus the definition is not suitable for animals which reproduce parthenogenetically. In the case of an animal which has only daughters for several generations, followed by normal bisexual reproduction for one or two generations the mathematical definition covers only the latter case.
5) In the overall formalized system human beings are excluded because of cultural and psychological factors (NIVEN, 1987a). However both the mate and species definitions given in this paper are valid for humans.
6) The inclusion of the probabilistic sentence used to define 'mate' implies that the definition of 'species' given in this paper is stochastic.

6. DISCUSSION

An advantage of the formalization method is that the relations among concepts are clarified. The definition of species involves four primitive terms ; the definition of environment as used by ANDREWARTHA and BIRCH (1984) involves an overlapping set of four primitive terms. The following table makes the situation clear :

Definition	*Primitive Terms*
Resource	An H ξ
Mate	Off ξ
Predator	An H ξ
Malentity	An H ξ
Total Centrum	An Off H ξ
Web	An Off H ξ
Total Environment	An Off H ξ
Species	An Off ξ Hab

All five primitive terms are used in the mathematical definition of 'animal community' (NIVEN, 1987b). The use of Elton's notion of habitat as a particular place where an animal lives links the present definition of species to Elton's ideas also.

Thus the formalization method provides a rational basis for an integrated theory of ecology ; concepts which apparently are quite independent of one another such as 'resource of an animal', 'predator', 'species' and 'animal community' are found to be linked together at the foundational level.

The mathematical definitions of 'environment' and 'community' have resulted in practical classifications of objects in an animal's environment and for kinds of community. In particular, ANDREWARTHA and BIRCH (1984) have developed a useful diagram, called an 'envirogram' on which the objects in the environment are displayed in their logically correct order. The mathematical definition of environment refers to the environment of an individual animal (NIVEN, 1980) ; the derived envirogram is for many animals over a stretch of time. In contrast the mathematical definition of 'species' does not yield a practical method of classification. However it will be shown in a future publication that a mathematical definition of 'niche' which includes that of 'species' yields a practical method of classifying niches. Thus while the primary aim of formalization is to construct theorems which will aid in prediction the definitions themselves are of some practical use to ecologists.

In any mathematically–based scientific theory primitive terms which remain undefined in the system are essential. It is simply not possible to do without them. Nevertheless people may find it unsatisfactory in particular that the habitat referred to in the species definition is dependent on choice and not laid down in some objective manner. The onus is on scientists who feel strongly about this to suggest an alternative, stating specifically what the new primitive terms are. Certainly there must be many alternatives. I do not know if the number of possible formalizations of theory of ecology is infinite but it must be very large. Now that it has been shown to be possible to construct one such system it should not be too difficult to construct alternatives and I invite interested theoreticians to do so.

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Nathan, January 1988

APPENDIX: SYMBOLS

t	An instant of time.
δt	An interval of time.
∃	There is at least one ... such that.
|	Given that.
>	Greater than.
&	And.
V	Or.
=	Is the same object as.
{*x* : ...}	The set of *x*'s such that.

REFERENCES

ANDREWARTHA H. G., BIRCH L. C., 1984 — *The Ecological Web : more on the distribution and abundance of animals*. The University of Chicago Press, Chicago.

BURT M. D. B., 1980 — Aspects of the life history and systematics of *Hymenolepis diminuta*. In Arai Hisao P. (ed.), *Biology of the Tapeworm* Hymenolepis diminuta. Academic Press, New York.

EDWARDS C. A., LOFTY J. R., 1972 — *Biology of Earthworms*. Chapman and Hall, London.

ELTON C., 1966 — *The Pattern of Animal Communities*. Methuen, London.

HUTCHINSON G. E., 1957 — Concluding remarks. *Cold Spring Harbor Symp. on Quant. Biol.*, **22**, 415–427.

LAMBERT D. M., PATERSON H. E. H., 1984 — On 'Bridging the Gap between Race and Species' : The isolation concept and and alternative. *Proc. Linn. Soc. N.S.W.* **107**, 501–514.

LEMMON W. B., ALLEN M. L., 1978 — Continual sexual receptivity in the female chimpanzee (*Pan troglodytes*). *Folia Primatol.*, **30**, 80–88.

MARGULIS L., SCHWARTZ K. V., 1982 — *Five Kingdoms : an illustrated guide to the phyla of life on earth*. Freeman, San Francisco.

MAY R. M., 1974 — *Model Ecosystems 2nd Edn*. Princeton University Press, Princeton, New Jersey.

NIVEN B. S., 1980 — The formal definition of the environment of an animal. *Australian Journal of Ecology*, **5**, 37–46.

NIVEN B. S., 1987a — The Logical Synthesis of an Animal's Environment. I. Primitive terms and definitions. *Australian Journal of Zoology*, in press.

NIVEN B. S., 1987b — The ecosystem as an algebraic category : a mathematical basis for theory of community and ecosystem in animal ecology with examples from the ecology of the cephalopod *Octopus vulgaris* and R. L. Kitching's water-filled treehole communities. *Coenosis*, in press.

PATERSON H. E. H., 1980 — A comment on 'mate recognition systems'. *Evolution*, **34**, 330–331.

PATERSON H. E. H., 1981 — The continuing search for the unknown and unknowable : a critique of contemporary ideas on speciation. *South African Journal of Science*, **77**, 113–119.

PATERSON H. E. H., 1985 — The recognition concept of species. In Vrba E. S. (ed.), *Species and speciation*. Transvaal Museum Monograph No. 4, Transvaal Museum Pretoria, pp. 21–29.

PATERSON H. E. H., MACNAMARA M., 1984 — The recognition concept of species. *South African Journal of Science*, **80**, 312–318.

TUTIN C. E. G., MCGREW W. C., 1973 — Chimpanzee copulatory behaviour. *Folia Primatol*, **19**, 237–256.

VAN LAWICK-GOODALL J., 1971 — *In the Shadow of Man–Houghton Miffin*, Boston.

WHITEHEAD A. N., RUSSELL B., 1925 — *Principia Mathematika 2nd Edn.* The University Press, Cambridge, England.

WILLIAMS M. B., 1970 — Deducing the consequences of evolution : a mathematical model. *J. Theor. Biol.*, **29**, 343–385.

WOODGER J. H., 1937 — *The Axiomatic Method in Biology*. Cambridge University Press, Cambridge, England.

WOODGER J. H., 1939 — The technique of theory construction. In *International Encyclopedia of Unified Science*, Vol. II, No. 5. The University of Chicago Press, Chicago.

WOODGER J. G., 1952 — From biology to mathematics. *Brit. J. Philos. Science* **3**, 1–21.

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THE ANIMAL NICHE: A FORMALIZED FUNCTIONAL DEFINITION AND ITS USE IN CLASSIFYING NICHES

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Abstract. A formalized functional definition of niche is given using an extension of the standard definition of a mathematical relation. The niche is conceived as a relation between species and environment; previously published mathematical definitions of both these concepts are incorporated and described briefly, together with examples. The new definition of niche may be used to classify animal niches. It is unlikely, because of the lack of an associated identity operator, to be of use in further mathematical development, however, because of its simple form it lends itself to use by field ecologists.

Introduction

In a thoughtful and interesting article Alley (1982) discusses the concept of niche in ecology and stresses the necessity for a functional definition. The concept of an ‘empty’ niche is severely criticised. Alley suggests that a variety of levels of analysis are necessary, ranging from ‘‘Elton’s goal of partitioning organisms into ‘professional’ classes (such as scavengers and parasites) - to - a detailed examination of ecological relations -’’.

In the present article I give a formalized functional definition of the concept of niche in animal ecology, using the formalization technique introduced by Woodger (1937, 1939, 1952) who wrote ‘‘In considering the relation of mathematics to biology we must distinguish between the process of applying existing mathematics to biology and the less familiar process of letting biological statements suggest new mathematical ones’’. Woodger’s work was difficult for biologists to read and understand; its inaccessibility has resulted in the method being less widely known among biologists and biomathematicians than one might expect. An exception is a formalized system for evolutionary theory which was constructed by Williams (1970) following Woodger’s ideas but using more modern notation. In my work on formalized theory of ecology of which this paper forms a part I have complied with the following: (i) close contact is kept with field workers, (ii) the difficult and cumbersome notation of Whitehead and Russell (1925) which was used by Woodger is replaced by more modern notation interspersed with enough natural language to convey meaning without losing too much rigour, (iii) intermediate theoretical results are checked immediately against data from a wide range of appropriate biological organisms.

The *modus operandi* for the total study is to construct a new branch of pure mathematics specifically for ecology. Thus mathematics is conceived to be a formalized language, containing sentences. Russell (1953) wrote ‘‘Pure mathematics consists entirely of assertions to the effect that, if such and such a proposition is true of *anything*, then such and such another proposition is true of that thing’’. The techniques for the construction are derived from standard works in mathematical logic such as Church (1956). In this article the niche is treated as a relation between an animal species and the objects in the environment of the members of that species. The niche definition uses an extension of the Wiener-Kuratowski definition of relation (Kuratowski and Mostowski, 1976). The mathematical definitions of environment and species are dealt with in Niven (1987a, 1988e). The niche definition was foreshadowed in Niven (1982).

The formalization method in biomathematics should be contrasted with the method of mathematical modelling familiar to many ecologists. Models are often poor predictors, at least partly because the mathematics we use has foundations derived from the physical, not biological, sciences. Thus the theory of differential equations used in animal population dynamics by for example May (1974) was developed initially to deal with Newtonian physics and the n-dimensional Euclidean geometry used by Hutchinson (1957) as a model for the concept of niche has at the foundational level primitive terms like ‘point’ which is derived from ideas about physical space.

In this paper first I present an interpretation of the five primitive (undefined) terms ‘An’, ‘Off’, ‘Hab’, ‘H’ and ‘ξ’, all of which are derived from ideas within the biological sciences. I shall then briefly repeat the mathematical definitions of environment and species given in full elsewhere and use them to define the animal niche, illustrating all three definitions with examples. I shall show how the niche definition may be used for the classification of a niche in some practical cases. I then comment on some consequences of using the definition, in particular its relevance to the principle of competitive exclusion. A list of symbols is given in the Appendix.

The primitive terms AN, OFF, HAB, H and ξ

In any formalized system such as a branch of mathematics it is necessary to include certain undefined words or phrases called 'primitive terms'. It is not possible to construct a branch of mathematics in which all terms are defined. The primitive terms are then used in definitions. Axioms are assumed sentences containing the primitive terms and the definitions and the rules of deduction of the system enable us to evolve theorems from the axioms. The following interpretations apply:

'An' stands for 'animal', meaning individuals of the Kindom Animalia of Margulis and Schwartz (1982). By 'An (χ)' I mean that χ is an animal.

'Off' stands for 'offspring'. This primitive term is sometimes sub-indexed by 't' or 'δt' which indicates the time of birth or the time interval during which the offspring is born. So 'χ Off$_{\delta t}$ y' means that χ is born to y during the interval δt.

'Hab' stands for 'habitat'. The term is derived from Elton (1966) and refers to the place in which the ecologist confidently expects to find the animal of interest. It may also be sub-indexed by 't' or 'δt'. By 'B Hab a' I mean that the place 'B' is a habitat of 'a', where 'a' is specified to be an animal i.e. An (a). B may be a specific pond, paddock, field, forest, continent, ocean or small region of ocean and so on. It may even be an entire planet. When necessary a region of the atmosphere is included, or a certain depth of soil. In this paper B is always a specific place, not a class of places.

'H' is the survival and reproduction primitive of the system. It is derived from 'an animal's chance to survive and multiply' in Andrewartha and Birch (1954). H (χ) is a positive real number which is a non-decreasing function of:

(i) the expectation of life of χ at birth or on entering its present stage of the life cycle, and

(ii) the probability that χ will have an offspring.

'H' may be sub-indexed by 't' or 'δt'. Unlike the notion of 'fitness' in evolutionary theory, 'H' refers to the present generation only, not a sequence of generations.

'ξ' is the interaction primitive of the system. By '$\xi \chi$y' I mean that an interaction occurs between χ and y evoking immediately in y some physical, physiological or behavioural response or a change of position and no other object (other than χ) reduces or enhances this effect of χ on y, i.e. χ affects y directly. Judgement as to whether the response is significant is to be made by the ecologist. For instance if an animal 'y' gazes at some object 'χ', a tree say, this is a response of 'y' to the tree and doubtless some sort of physiological process is evoked. A response of this type would often be regarded by the ecologist as trivial, and ignored. Like 'Off', 'Hab' and 'H' the interaction primitive may be sub-indexed by 't' or 'δt'.

The inclusion of 'H' as a primitive term implies that the formalized system is stochastic at a foundational level 'ξ', which is incorporated in all definitions, ensures that the system is totally interactive. The time-dependence of 'Off', 'Hab', 'H' and 'ξ' implies that the system is dynamic.

Environment

A symbolic definition of an animal's environment was published by Niven in 1980. The environment was defined as a structured set of objects which were functionally related to the subject animal. An improved formulation was published by Niven (1982) and used by Andrewartha and Birch (1984) to classify objects in the environment; these authors derived, from the mathematical definition, a useful diagram called an 'envirogram' which displays objects in the environment in their correct logical place. The definition is for one animal at a particular time; the envirogram is for many animals at different times and is used as a practical tool for the field ecologist. The formulation of the definition which was used by Andrewartha and Birch is not easy to manipulate; for this reason I have since developed a simpler formulation which is suitable for teaching undergraduates and facilitates very precise classification of objects in the environment by non-mathematicians (Niven, 1987a).

The structured set of objects which constitute the environment of an individual animal at some particular time is divided into two subsets called the 'centrum' and the 'web'. The centrum is further subdivided into 'resources', 'mates', 'predators' and 'malentities'. Each of these four subsets is defined by a mathematical sentence containing a conditional; in ordinary English the centrum contains *potential* resources, mates etc; this device means that an object which is not at that time in the animal's immediate vicinity may still be defined as a resource or other element of the animal's environment. The web consists of an infinite structured set of 'modifiers'. Zero-order modifiers are elements of the centrum and first-order modifiers modify these elements. Second-order modifiers modify objects which are first-order modifiers and so on. The conditional form of defining sentence is used throughout.

For subject animal 'a' the definitions of a resource, mate, predator and malentity are:

$$\text{r Res}_t\ \text{a} =_{df} [\{H_t(a) > H_{t-}(a)\} \mid \xi_t\ \text{ra}]\ \&$$

$$[\text{An}(r) \supset \{H_t(r) \leq H_{t-}(r)\} \mid \xi_t\ \text{ra}]$$

$$\text{m Mat}_t\ \text{a} =_{df} \text{Prob}\ [(\exists x)(x\ \text{Off}_{t+\beta}\ \text{a}\ \&$$

$$x\ \text{Off}_{t+\beta}\ \text{m}) \mid \xi_t\ \text{ma}] > 0$$

$$\text{p Pred}_t\ \text{a} =_{df} [\{H_t(a) < H_{t-}(a)\{\ \&$$

$$\{H_t(p) > H_{t-}(p)\} \mid \xi_t\, pa]$$

$$c\ \mathrm{Mal}_t\, a =_{df} [\{H_t(a) < H_{t-}(a)\} \mid \xi_t\, ca]\ \&$$

$$[\mathrm{An}(c) \supset \{H_t(c) \leq H_{t-}(c)\} \mid \xi_t\, ca]$$

The interval of time 'β' in the definition of a mate is the gestation time. A predator must be an animal.

The centrum is the set of objects which are resources, mates, predators or malentities. Formally:

$$C_t\, a =_{df} \{x\colon x\ \mathrm{Res}_t\, a \vee x\ \mathrm{Mat}_t\, a \vee x\ \mathrm{Pred}_t\, a \vee x\ \mathrm{Mal}_t\, a\}.$$

In the web the modifiers of order greater than zero are divided into two sets called 'positive' and 'negative' modifiers, depending on whether their presence or absence causes the lower order modifier to appear in the system. Formally:

$$w\ \mathrm{Mod}_t^{+\,(n+1)} a =_{df} (\exists x)\ [\{x\ \mathrm{Mod}_t^n\, a \mid (\xi_t\, wx \vee \xi_t\, wy)\}\ \&$$

$$\{\sim x\ \mathrm{Mod}_t^n a \mid (\xi_t\, wx \vee \xi_t\, wy)\}]$$

$$w\ \mathrm{Mod}_t^{-(n+1)} a =_{df} (\exists x)\ [\{x\ \mathrm{Mod}_t^n a \mid \sim(\xi_t\, wx \vee \xi_t\, wy)\}\ \&$$

$$\{\sim x\ \mathrm{Mod}_t^n a \mid (\xi_t\, wx \vee \xi_t\, wy)\}$$

$n = 0, 1, 2\ldots$; y is either 'a' or a modifier of order $<n$; $\mathrm{Mod}_t^n a =_{df} \mathrm{Mod}_t^{+n} a \vee \mathrm{Mod}_t^{-n} a$.

The total environment of the subject animal is the union of the centrum and the web in which the structure of the four subsets of the centrum and their attached modifier chains is preserved.

The following examples from the ecology of the Atlantic fulmar *(Fulmarus glacialis)* are taken from Fisher (1952). Large numbers of these fulmars used to attend whale flensing, in the days when whales were hunted. They disregarded the men and gorged whale blubber and oil. Thus blubber is classified as a resource of a subject adult fulmar:

H (fulmar) is increased $|\xi$ (blubber) (fulmar).

Fulmars are attracted to glacier run-off streams in order to feed on planktonic creatures. Occasionally, Fisher records, some are killed by ice-falls. We classify a particular (loose) block of ice as a malentity:

H (fulmar) is decreased $|\xi$ (ice) (fulmar).

A different kind of resource is observed when we consider the breeding habits of the bird. A female fulmar prospects for and chooses a nesting site, usually a ledge on a high cliff, when still a non-breeding juvenile. The bird may occupy the site for over four years before laying eggs there. A suitable ledge is clearly a necessity for a subject female fulmar to breed and thus a resource:

H (fulmar) is increased | ξ (ledge) (fulmar).

An adult male fulmar is classified as a mate of the subject female:

An offspring of both individuals will be produced with probability greater than zero | ξ (male fulmar) (subject female).

The ledge, as a nesting site, is also a positive first-order modifier:

($\exists$ male fulmar) such that
(male fulmar) Mat (subject female) | ξ (nesting site) (subject female)
and
$\sim$(male fulmar) Mat (subject female) | $\sim\xi$ (nesting site) (subject female),

that is, unless the ledge is available, the female will not lay her eggs and so the male cannot be a mate.

When threatened a fulmar will vomit or spit foul-smelling stomach-oil, not directly at the intruder but simply in the direction in which it is looking at the time. A baby fulmar not yet out of its shell has been observed to vomit through a small chink when disturbed by the observer. The glaucous gull *(Larus hyperboreus)* will readily eat fulmar eggs and fledglings if the parents are away from the nest. The gull is classified as a predator in the environment of a subject fledgling fulmar:

H (fledgling) is decreased and H (gull) is increased | ξ (gull) (fledgling).

The fledgling, in turn, is classified as a resource in the environment of a subject gull:

H (gull) is increased and H (fledgling) is decreased | ξ (fledgling) (gull).

Notice that in this case the term 'H (fledgling) is decreased' is included in the defining sentence, in contrast to the two previous examples of resources in which the resource was not an animal.

The stomach-oil emitted by a subject fledgling fulmar when disturbed by a gull is a negative first-order modifier:

($\exists$ gull) such that (gull) Pred (fledgling) | $\sim\xi$ (stomach-oil) (gull) and
$\sim$ (gull) Pred (fledgling) $|\xi$ (stomach-oil) (gull).

The fledgling is modifying its own environment by producing the stomach-oil; it is a positive second-order modifier:

$(\exists$ stomach-oil$)$ such that
(stomach-oil) Mod^1 (fledgling) $|\xi$ (fledgling) (fledgling) and $\sim$ (stomach-oil) Mod^1 (fledgling) $|\sim\xi$ (fledgling) (fledgling).

Here we assume that the fledgling is interacting with itself in the sense of the primitive term ξ to produce the stomach-oil. The parent bird which protects the fledgling from the gull is a negative first-order modifier:

$(\exists$ gull$)$ such that (gull) Pred (fledgling) $|\sim\xi$ (parent) (fledgling)
and $\sim$ (gull) Pred (fledgling) $|\xi$ (parent) (fledgling).

It is the case here that both the parent and the fledgling are acting to protect the fledgling against the predacious gull, but the fledgling acts via an intermediate object (the stomach-oil) whereas the parent acts directly on the predator, hence the classifications are different.

Other examples, taken from the ecology of animals ranging from a sponge to a non-human primate, are given in Niven (1987a, 1988a, b, c, d, Niven and Stewart 1987). The definition is unsuited to human beings, since the cultural and psychological factors which are of such importance to humans are not sufficiently stressed in the defining sentences of an animal's environment.

Species

In a series of articles Paterson and his colleagues have developed a non-mathematical definition of an animal species (Paterson, 1980; Paterson 1981, Paterson 1985, Paterson and Macnamara 1984, Lambert and Paterson 1985). Paterson's definition is dependent on the notion of specific-mate-recognition necessarily occurring in a particular habitat and arose via a careful consideration of evolutionary concepts. A mathematical definition based on Paterson's work is given in Niven (1989). The animal species S_a at the time 't' which includes a subject animal 'a' is the set as follows:

$$S_a =_{df} \{x : x = a \ \mathrm{V} x \ \mathrm{Mat}_t a \ \mathrm{V} x \ \mathrm{Mat}_t \mathrm{Mat}_t a | \mathrm{An}\ (a) \ \&$$

$$\mathrm{An}\ (x) \ \& \ \mathrm{B} \ \mathrm{Hab}_t \ (x \ \& \ a)\}.$$

For hermaphroditic animals the terms 'x $\mathrm{Mat}_t\mathrm{Mat}_t a$' is redundant. The sub-index 't' may be replaced by 'δt' if, for example, we wish to include juvenile animals which will become (potential) mates of 'a' during the interval of time δt.

As examples, first consider the case of chimpanzees *(Pan troglodytes)* and, to begin with, choose the Gombe National Park in East Africa to be the habitat 'B'. Since female chimpanzees have marked sexual cycles the sub-index 'δt' should replace 't' in this case in order to ensure that all the animals are included (Lemmon and Allen, 1978; Tutin and McGrew, 1973; van Lawick-Goodall, 1971). Then if we choose as our initial animal 'a' some mature female chimpanzee we have that the species S_a is the set of objects x where either x is a (potential) mate of 'a' or a mate of a mate of 'a' during the time interval 'δt', given that 'a' is an animal and the 'x's' are all animals and that 'a' and all the 'x's' are in the Gombe National Park. In order to include all the animals normally thought of as being of species *Pan troglodytes* we simply extend 'B' to include the Mhale mountains and other suitable areas. It is not necessary for the theory that these areas are connected.

If now we are working with the hermaphroditic earthworm *Lumbricus terrestris* (Edwards and Lofty 1972) then the mate of our initial subject worm is simply another mature adult and it is unnecessary to consider the mates of its mates.

In the case of a perpetually self-mating animal the definition reduces to just the animal 'a' which is in habitat 'B'; thus the definition is not suitable for animals which reproduce parthenogenetically. In the case of an animal which has only daughters for several generations, followed by normal bisexual reproduction for one or two generations the mathematical definition covers only the latter case.

Paterson deals with animals in the wild state. If the biologist should so desire the habitat 'B' in the mathematical definition could be some artificial place, such as a cage in a zoo, thus leading to the classification of animals such as lions and tigers, dogs and jackals, or mallard and pintail ducks, being defined as being of the same species. However these are very peculiar cases and, although they are logically valid, they seem unlikely to be of any practical use. Another peculiar and artificial case is that of artificial insemination. The mathematical definition can be 'forced' to cover this case by making both the habitat 'B' and the time interval 'δt' large enough to include both parents.

It does not follow from the formal definition that either the parents or offspring of the animal 'a' are elements of the set S_a. Thus mutations resulting in some change of mate recognition in at least one pair of offspring may well result in a different species.

Unlike the definition of 'environment' the mathematical definition of 'species' is valid also for humans. The inclusion of the probabilistic sentence used to define 'mate' implies that the definition of 'species' is stochastic.

The definition of the animal niche

The animal niche is the relation of that animal (species) to the environment of individuals of the species. Roughly speaking, the niche gives us some idea of the place of the species in the biotic milieu; it provides information about the status of the species in the community. It is sometimes useful to think of the niche as the 'profession' of the species (Elton 1927, Andrewartha and Birch 1984). So the niche is to do with the animal's functional relations with some of the objects in the environment.

When we observe a particular species of animal we usually find that all members of the species eat much the same kind of food, have more-or-less the same enemies and so on. In fact we expect all the adults of the same sex to have the same (potential) resources, mates, predators and malentities and apart from modifying one another's environments as competitors or predators, the same modifiers. In practical ecology it is not feasible to examine all possible objects in an animal's environment and some intuitive selection has to be made by the ecologist of those objects which seem to be the most important (Dennison and Hodkinson 1984).

A relation is formally defined in mathematics as a class of ordered pairs (Kuratowski and Mostowski 1976). Rather than speak of modifiers of order zero and greater ecologists prefer the terms 'centrum' and 'web' (Andrewartha and Birch 1984) so it is convenient to specify the niche as a class of triplets instead of pairs. Thus the niche of animal species S is defined as a class of one or more ordered triplets as follows:

(i) The first member of a triplet is an animal species.
(ii) One of the triplets has S as first member.
(iii) The second member of each triplet is either empty or an ordered set of objects in the centrum of the animals belonging to the first element.
(iv) Objects in the i-th place of the second member are all of the same kind *i.e.* they belong to the same well-defined class of objects; furthermore they are all resources or all mates or all predators or all malentities.
(v) The third member of each triplet is either empty or an ordered set of objects in the web of the animals belonging to the first element.
(vi) Objects in the i-th place of the third member are all of the same kind *i.e.* they belong to the same well-defined class of objects; furthermore they are all of the same modifier order.
(vii) At least one of the second or third elements is not empty.
(viii) A zero-order niche is one in which all third elements are empty.
(ix) An n-th-order niche contains n-th order modifiers in the third element of each triplet and does not contain modifiers of order greater than n.
(x) A simple niche contains only one modifier in the third element of each triplet; multiple niches contain more than one.

Examples of animal niches

1. The first example is taken from Elton (1927). Consider the arctic fox which subsists on eggs of guillemots but in winter relies partly on remains of seals killed by polar bears. The eggs and remains of dead seals are resources. The guillemots and polar bears, as providers of resources, are first-order modifiers. The associated ordered triplet is:

<arctic fox; guillemot eggs, seal remains; guillemots, polar bears>.

Now consider the African spotted hyaena which eats ostrich eggs and also the remains of zebras killed by lions. The eggs and zebra remains are resources and the ostriches and lions first-order modifiers. The triplet is:

<spotted hyaena; ostrich eggs, zebra remains; ostriches, lions>.

Elton clearly considers the two species to belong to the same niche and indeed we may write the two triplets with objects occupying the same places in the second and third elements being: (a) eggs, (b) carcasses, (c) birds and (d) large predators. Thus we have a niche containing two ordered triplets:

<arctic; guillemot, seal; guillemots, polar bears>
fox eggs remains

<spotted; ostrich, zebra; ostriches, lions>
hyaena eggs remains

Since the modifiers are all of first order and there are two of them in each triplet the niche is a first-order double niche. Notice that there are two distinct habitats. We may refer to this niche as either 'the niche of the arctic fox' or 'the niche of the spotted hyaena'.

2. Now consider a second example from the same source. This is the niche of animals which eat ticks off other animals. Three species are included by Elton: (i) The African oxpecker, which sits on the back of wild African ungulates, picks off the ticks and eats them, (ii) the English starling which eats ticks off sheep and (iii) the scarlet land crab which takes ticks from the great aquatic lizard. So the niche is the class:

<oxpecker; ticks; ungulates>
<starling; ticks; sheep>
<crab; ticks; lizards>

The second elements in the ordered triplets are all ticks which are resources of animals in the first elements and the third elements are all vertebrates which are first-order modifiers. Thus the niche is a first-order simple niche.

Elton contrasts this niche with that of the African cattle egret which follows buffalo or other ungulates in order to catch and eat grasshoppers. The modifier chain for a subject egret is:

buffalo → kinetic energy → grasshopper → egret

since without the buffalo that particular energy package does not come into existence and without the movement the grasshopper is not a resource. The corresponding niche triplet is:

<egret; grasshoppers; kinetic energy, buffalos>.

Since a second-order modifier appears in the third element and there are two modifiers named the niche is a second-order double niche. It contrasts sharply with the previous case by including the energy component which shifts the buffalo into a higher order of modifiers.

3. We now turn to a study of Wolf spiders by Vogel (1972). The two species *Pardosa falcifera* and *P. sternalis* are often found in the same place, however *P. falcifera* is very much more dependent on cover such as fallen leaves which serve to protect the spiders from predators, like birds. In Cochise County, Arizona, a marked change in conditions at Lake Cienaga from a lush green marsh in 1963 to a nearly dry overgrazed pasture in 1970 showed how dependent *P. falcifera* is on cover. In 1963 one collection of the spiders contained twenty-three times as many *P. falcifera* as *P. sternalis*. In contrast a collection made in the same place in 1970 contained thirty-six times as many *P. sternalis* as *P. falcifera*. The exact mechanism is unknown; it was observed, however, that these spiders have a 'territory sphere' surrounding them, into which they do not allow another spider to enter. We shall assume here that both species are subject to predation by the same predatory birds, that both would use cover readily available in the habitat, but that *P. falcifera* is able to drive *P. sternalis* away from cover, whereas *P. falcifera* by its own actions is able to use the cover to protect itself against the predators. Thus for both species the cover is a first-order modifier of predators. *P. falcifera* is a second-order modifier of cover in its own environment and also a second-order modifier of cover in the environment of *P. sternalis*. The two ordered triplets are:

<*P. falcifera*; predatory birds; cover, *P. falcifera*>
<*P. sternalis*; predatory birds; cover, *P. falcifera*>

Since there are two modifiers in each third element and the second of these is of second order the niche is a second-order double niche. In contrast to Elton's examples the two species are found in the same habitat.

4. The predatory bark beetles *Olophrum piceum* and *Lathrobium brunnipes* have both been found in a wood near Liverpool, England, according to Dennision and Hodkinson (1983). *O. piceum* feeds on Collembola and *L. brunnipes* on mites. The two triplets are:

<*O. piceum*; Collembola; —>
<*L. brunnipes*; mites; —>

Both second elements contain resources which are arthropods and both third elements are empty. The niche is therefore of zero order. The habitat is the same for both species.

5. The marine copepods *Calanus* and *Eucalanus* were observed by Boyd and Smith (1980) at a station in the Peruvian upwelling system. *Eucalanus* were sometimes found in water below the surface layers which had very low oxygen concentration. These layers were avoided by *Calanus*. The copepods are detritus feeders; *Calanus* fed both day and night in a fairly even pattern but *Eucalanus* moved near the surface at night and reduced its feeding intensity. Clearly water with low oxygen concentration (WLO) is a malentity and detritus a resource for both species. Both species modify their food by moving to suit the feeding requirements; they are thus first-order modifiers of resources in their own environment. If we work over a period of time long enough to accommodate the migrations, say twenty-four hours, then the two triplets are:

<*Eucalanus*; WLO, detritus; *Eucalanus*>
<*Calanus*; WLO, detritus; *Calanus*>

The niche is a first-order simple niche.
If we wish to show up the difference in the night-time position then we reduce the time period to, say, the twelve hours of darkness and introduce the objects 'water with low detritus concentration' (WLD) and 'water with high detritus concentration' (WHD). These objects, which provide resources at the required levels, are then first-order modifiers. The animals are first-order modifiers in their own environments, since they locate themselves in the preferred places. For convenience we leave out the malentities WLO. Then the two triplets are:

<*Eucalanus*; detritus; WLD, *Eucalanus*>
<*Calanus*; detritus; WHD, *Calanus*>

We have now written down a second-order double niche for the same species in the same habitat, but using a different time interval. This example clarifies two points (i) the environment classification and therefore the niche classification are both critically dependent on the time chosen by the observer and (ii) the observer's choice of object (high or low detritus layers) and the accuracy and completeness of the natural history (*e.g.* night-time behaviour of *Eucalanus*) are also critically important when classifying a niche.

6. The waterfleas *Daphnia magna, D. pulex* and *D. longispina* were found together in a freshwater rock pool in an archipelago near the Gulf of Finland by Ranta (1979). The animals are filter feeders and unable to select food particles so the size of the ingested particles is controlled by the density of the filtering combs and the width of the carapace crevice. These measurements relate to the body length. The maximum body lengths of the three species observed were:

D. magna 5.0 mm; *D. pulex* 3.5 mm;
D. longispina 2.5 mm.

If we classify particles as large, medium or small then the three sorts of particles will be resources for the three species, the animals themselves acting as first-order modifiers of these resources. The corresponding niche triplets are:

<*D. magna*; large particles; *D. magna*>
<*D. pulex*; medium particles; *D. pulex*>
<*D. longispina*; small particles; *D. longispina*>

The niche is a first-order simple niche.

The principle of competitive exclusion

In the context of this paper the Principle of Competitive Exclusion is that the second and third elements of any one triplet are unique to the species. It would seem to be very likely that if a large number of objects are named in the triplet then the principle would be true. One has only to imagine two n-th order triplets for which the second and third elements were identical but the species of the first elements different; for n large enough it seems highly likely that we could find a pair of (n+1) th-order modifiers which differ from one another.

However the Principle clearly does not hold for zero-order niches. Consider as a counter-example No. 3 above on Wolf spiders. A zero-order niche would be:

<*P. falcifera*; predatory birds; —>
<*P. sternalis*; predatory birds; —>

Thus when invoking the Principle we should be careful to state precisely what order of niche is being studied. Between the limiting cases of zero-order and n-th order for n large there is a grey area in which the Principle may or may not hold.

Discussion

The untutored peasant, gazing bucolically at a frog and a bird, may dismiss as fanciful and unnecessary the Latin nomenclature of modern animal taxonomy. In contrast the trained zoologist is well aware of the necessity for such classification. In science in general and ecology in particular classification is essential. The main practical use of the mathematical definition of niche given in this paper is that a method of classifying niches is provided which is both well-defined and simple to write down.

On the theoretical side defining the niche as a functional relation between animals and their environment matches Elton's original concept and answers Alley's severe criticism. However we may well ask whether the niche concept is likely to lead to further development of a mathematical basis for ecology and here the answer is at present an unqualified negative for the following reason. In any useful branch of pure mathematics an axiom asserting the existence of an identity operator is essential. An example of an identity operator is the multiplication by the unit in ordinary arithmetic. This operation on any number yields that same number as the answer; the identity operator sends a number back to itself. The identity operator for new ecological mathematics is readily available; it is the mathematical object '$E^{-1}E$' where by '$E^{-1}B$' we mean the animal whose (formalized) environment is B and by 'Ea' we mean the environment of the animal 'a'. The uniqueness of an animal's environment (Niven 1983) leads naturally to the axiom. In ordinary English we may say "The animal whose environment is the environment of animal 'a' is in fact that same animal 'a' ". This axiom applies immediately when we construct new mathematics for animal communities and, by extension, for ecosystems, the latter assuming that an equivalent to 'environment of an animal' will be found for plants and modules when the formalization of plant and module ecology is undertaken (Niven 1988e). Unfortunately we cannot extend the uniqueness of the environment of an individual animal to a set of animals such as a species. Consider as an example three frogs of the same species F_1, F_2, and F_3 sitting next to each other. F_2 and F_3 appear in F_1's environment as first-order modifiers of food and other objects. Similarly F_1 and F_3 are in F_2's environment and F_1 and F_2 in F_3's environment. In order to obtain a set of objects, a pseudo-environment, say, which is unique to the set $\{F_1, F_2, F_3\}$ we need to exclude certain objects. Including the frog F_4 further complicates the situation. So the construction of a biologically meaningful mathematical object which will send the set of frogs back to itself is certainly very difficult and may well be impossible. Without an axiom asserting the existence of an identity operator we are left with the prospect of handling ecological mathematics in which a unique inverse does not exist. Such branches of pure mathematics are difficult to handle in practice and are unlikely to be useful in scientific work.

Nevertheless the concept of niche may well continue to be useful in field ecology. As McIntosh (1982) writes "(the question now is) how similar can (species) be and still coexist?" In the cases in which suitable metrics exist, such as the particle sizes of example 6 above on *Daphnia* spp., well-tried methods of statistical univariate and multivariate analysis may be used to ascertain the separation of the triplets. Such methods of niche separation are already in wide use (McIntosh 1982, 1985; Whittaker and Levin, 1975). However it should be noted that not all field workers agree that the niche is a useful concept. For example Johnson (1984) writes "One of the problems facing a niche analyst is that niche differences can nearly always be found, provided that enough niche parameters are examined". Johnson investigated the coexistence of two flycatchers in the Nigerian rain forest, between which, in spite of their close proximity, competition appeared to be absent. He writes "If niches are at least partially genetically... determined, then the occasional high niche overlap is an unremarkable certainty".

The niche is a dynamic concept. In the present formalization the time-dependence of the environment is provided by the primitive terms. This time-dependence is, therefore, incorporated in the definition of niche. Similarly the defined niche is stochastic at a foundational level.

The mathematical definition of species used in the niche definition is habitat-dependent. (In practice we usually work with the museum concept of species which is not). However the mathematical definition of environment is independent of habitat. In ordinary English we refer to *potential* resources, *potential* mates, *potential* predators, *potential* malentities and *potential* modifiers. Thus it is strictly correct to specify a triplet in which the first element (the species) is restricted to a particular habitat, but the objects of the second and third elements are not restricted to the same habitat.

The original concept of niche as described by Elton included animals only; this is clearly an unnecessary restriction. Elton's concept, however, also enabled us to compare species in several quite different habitats and this flexibility has been incorporated into the formalization since it may well prove suggestive to write down several triplets which refer to a variety of habitats. The exercise could point the way to further study on important objects which have been observed in one place but missed in another.

It should be noted that according to the definition it is not possible to have an empty niche. The question as to how many niches might exist does not seem to be profitable. Presumably a clever genetic engineer could tailor a new species to almost any given subset of the objects in a habitat and so the number of possible niches within a given habitat, although not infinite, is certainly very large.

REFERENCES

Alley, T.R. 1982. Organism-environment mutuality epistemics, and the concept of an ecological niche. Synthese 65 411-444.

Andrewartha, H.G. and L.C. Birch. 1954. *The distributio and abundance of animals.* The University of Chicago Press Chicago.

Andrewartha, H.G. and L.C. Birch. 1984. *The ecological web more on the distribution and abundance of animals.* Th University of Chicago Press, Chicago.

Boyd, C.M. and S.L. Smith. 1980. Grazing patters of copepod in the upwelling system of Peru. Limnol. and Ocean 25 583-596.

Church, A. 1956. *Introduction to mathematical logic.* Princeton University Press, Princeton, New Jersey.

Dennison, D.F. and I.D. Hodkinson. 1983. Structure of the predatory beetle community in a woodland soil ecosystem. I Prey selection. Pedobiologia 25: 109-115.

Dennison, D.F. and I.D. Hodkinson. 1984. Structure of the predatory beetle community in a woodland soil ecosystem. V Summary and conclusions. Pedobiologia 26: 171-177.

Edwards, C.A. and J.R. Lofty. 1972. *Biology of earthworms* Chapman and Hall, London.

Elton, C. 1927. *Animal ecology.* Sidgwick and Jackson Ltd Reissued 1966 by Methuen and Co. Ltd: Science Paperbacks

Elton, C. 1966. *The pattern of animal communities.* Methuen, London.

Fisher, J. 1952. *The fulmar.* Collins, London.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22: 415-427.

Johnson, D.N. 1984. The co-existence of the Red-bellied Paradise Flycatcher *Tchitrea rufiventer* and the Chestnut Wattle-eye *Dyaphorophyia casanea* in Nigerian rain forest. In: Proc. V. Pan-Afr. orn. Congr. pp. 263-274.

Kuratowski, K. and A. Mostowski. 1976. *Set theory: with an introduction to descriptive set theory.* PWN - Polish Scientific Publishers, Warszawa; North-Holland Publishing Company, Amsterdam.

Lambert, D.M. and H.E.H. Paterson. 1984. On 'Bridging the Gap between Race and Species': The isolation concept and an alternative. Proc. Linn. Soc. N.S.W. 107: 501-514.

Lemmon, W.B. and M.L. Allen. 1978. Continual sexual receptivity in the female chimpanzee *(Pan troglodytes).* Folia Primatol 30: 80-88.

Margulis, L. and K.V. Schwartz. 1982. Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth. Freeman, San Francisco.

May, R.M. 1974. *Model Ecosystems.* 2nd ed. Princeton University Press, Princeton, New Jersey.

McIntosh, R.T. 1982. The background and some current problems of theoretical ecology. In: Saarinen E. (ed.), *Conceptual issues in ecology.* D. Reidel, Dordrecht, Holland.

McIntosh, R.T. 1985. *The background of ecology: concept and theory.* Cambridge University Press, Cambridge, England.

Niven, B.S. 1980. The formal definition of the environment of an animal. Australian Journal of Ecology 5: 37-46.

Niven, B.S. 1982. Formalization of the basic concepts of animal ecology. Erkenntnis 17: 307-320.

Niven, B.S. 1983. Two different animals may not have the same environment. J. theor. Biol. 105: 369-370.

Niven, B.S. 1987a. The Logical Synthesis of an Animal's Environment. I. Primitive terms and definitions. Aust. J. Zool.: 35, 597-606.

NIVEN, B.S. 1988a. The Logical Synthesis of an Animal's Environment. III. The Rat tapeworm *(Hymenolepis diminuta)*. Aust. J. Zool. 36: 1-14.

NIVEN, B.S. 1988b. The Logical Synthesis of an Animal's Environment. IV. The Common octopus *(Octopus vulgaris)*. Aust. J. Zool. 36: 15-27.

NIVEN, B.S. 1988c. The Logical Synthesis of an Animal's Environment. V. The Cane toad *(Bufo marinus)*. Aust. J. Zool. 36: 169-194.

NIVEN, B.S. 1988d. The Logical Synthesis of an Animal's Environment. VI. The chimpanzee *(Pan troglodytes)*. Aust. J. Zool. 36: 195-208.

NIVEN, B.S. 1988e. The ecosystem as an algebraic category: a mathematical basis for theory of community and ecosystem in animal ecology. Coenoses: 3, 83-87.

NIVEN, B.S. 1989. Formalization of the Paterson concept of an animal species. Rivista di Biologia. (In press).

NIVEN, B.S. and M.G. STEWART. 1987. The Logical Synthesis of an Animal's Environment. II. The freshwater sponge *(Spongilla lacustris)*. Aust. J. Zool. 35: 607-624.

PATERSON, H.E.H. 1980. A comment on 'mate recognition systems'. Evolution 34: 330-331.

PATERSON, H.E.H. 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. South African Journal of Science 77: 113-119.

PATERSON, H.E.H. 1985. The recognition concept of species. In: Vrba E.S. (ed.), *Species and speciation*, pp. 21-29. Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria.

PATERSON, H.E.H. and M. MACNAMARA. 1984. The recognition concept of species. South African Journal of Science 80: 312-318.

RANTA, E. 1979. Niche of Daphnia species in rock pools. Arch. Hydrobiol. 87: 205-223.

RUSSELL, G. 1953. Mathematics and the metaphysicians. In: Russell, B. *Mysticsm and logic*. Penguin Books Ltd., Harmondsworth, Middlesex.

TUTIN, C.E.G. and W.G. MCGREW. 1973. Chimpanzee copulatory behaviour. Folia Primatol 19: 237-256.

VAN LAWICK-GOODALL, J. 1971. *In the shadow of man*. Houghton Miffin, Boston.

VOGEL, B.R. 1972. Apparent niche sharing of two *Pardosa* species. (Araneida: Lycosidae). Vogel, 2505 Ashdale Drive, Austin, Texas.

WHITEHEAD, A.N. and B. RUSSEL. 1925. *Principia Mathematika*. 2nd ed. The University Press, Cambridge, England.

WHITTAKER, R.H. and S. LEVIN. (eds.). 1975. *Niche: theory and application*. Dowden, Hutchinson and Ross, Stroudsberg, Pennsylvania.

WILLIAMS, M.B. 1970. Deducing the consequences of evolution: a mathematical model. J. theor. Biol. 29: 343-385.

WOODGER, J.H. 1937. *The axiomatic method in biology*. Cambridge University Press, Cambridge, England.

WOODGER, J.H. 1939. The technique of theory construction. In: *International Encyclopedia of Unified Science*, Vol. II, No. 5. The University of Chicago Press, Chicago.

WOODGER, J.H. 1952. From biology to mathematics. Brit. J. Phil. Sc. 3: 1-21.

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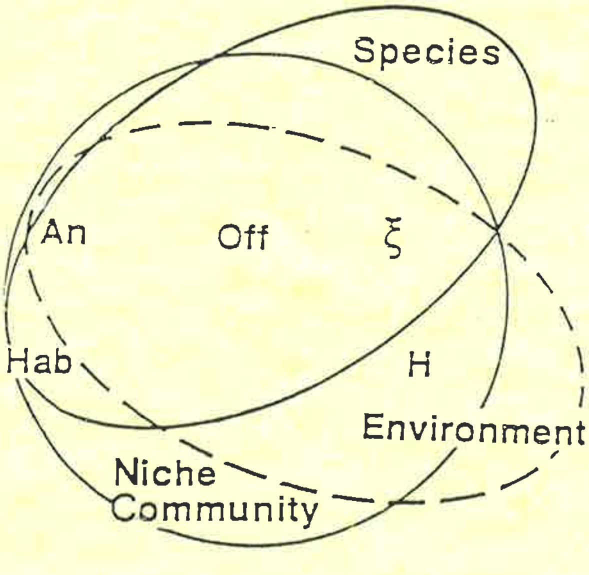
APPENDIX

>	greater than
<	less than
≤	less than or equal to
x_t	x at time t
x_{t-}	x just before time t
A|B	A given that B
~	negation
ϵ	element of
⊃	The subjunctive conditional; read 'x⊃y' "if x then y".
$=_{df}$	Definition; read 'x $=_{df}$ y' "x is interchangeable with y" or "x is equal by definition to y".
&	Conjunction; read 'A & B' "A and B".
V	Disjunction; read 'A V B' "A or B" (or both).
∃	The existential quantifier; read '∃x' "there is at least one x (such that)...".

TOWARDS A MATHEMATICALLY-BASED THEORY OF ECOLOGY

B. S. NIVEN



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Cover diagram. This diagram shows how community and population concepts in animal ecology are closely linked at the foundational level by the primitive terms An, Off, ξ, Hab and H. (See Section X).
All three diagrams in this Monograph were drawn by CALT Graphics Section, Griffith University, under the guidance of Mr Richard Blundell.

TOWARDS A MATHEMATICALLY-BASED THEORY OF ECOLOGY

A Monograph

by

B.S. Niven

Pure Mathematics is the class of all propositions
of the form "p implies q".

Bertrand Russell
The Principles of Mathematics

CONTENTS

PREFACE

This short monograph started as a brief review of my work on formalized theory of animal ecology. I had published over forty articles in a wide variety of journals, ranging from 'Erkenntnis' (a journal of analytic philosophy) to the 'Australian Journal of Ecology'. I felt the need both to explain the central theme which guided my work and to bring the results in all these scattered articles together. I have written for biologists. Mathematicians will find such things as my explanation of the difference between a formalization and a model-building exercise boring, naive and unnecessary. The diagram of section X (repeated on the front cover) has not been published elsewhere.

My overall approach is encapsulated in the quotation from Bertrand Russell's "Principles of Mathematics" on the title page. I do not know whether this statement is true. I have found it useful. It has been the guiding light for all my studies described here. Far from restricting myself to first-order logic as is usual in a formalization I have not hesitated to draw on any branch of existing mathematics which seemed useful, so at various stages of the work I have used ideas and symbolism from engineering mathematics, probability theory, modern algebra, set theory and symbolic logic. At an early stage I became convinced that a basis of mereology (the axiomatic theory of the part-whole relation) rather than set theory was the more appropriate for ecological mathematics. I made myself fully familiar with the 198 theorems of Stanislaw Lesniewski, to the extent that even his notorious Theorem CIV "If P is the class of objects a and Q is the class of objects not a, then (P is the class of objects or Q is the class of objects)" became intuitively obvious to me. However my attempt to give the foundational mathematics of ecology a mereological basis was a failure. Furthermore until the relation between mereology and such modern mathematics as probability theory and the algebra of categories becomes clear I do not think it feasible to proceed along these lines. For the record, I am convinced that a mereological basis for ecological mathematics would be preferable and I hope some other mathematician will succeed where I have failed.

Many people have encouraged and supported me in the work and to them I am grateful. They include : the logicians I D Barnett, I C Hinckfuss, Richard Sylvan(Routley) and Ryszard Wojcicki; the mathematical biologist W T Williams; the computer scientist D E Abel; the animal ecologists H G Andrewartha, T O Browning, L C Birch, R L Kitching, W J Lawson, D A Maelzer, H E H Paterson and Georg Ribi; the plant ecologists J L Harper and M J Liddle; the zoologist-biochemist Clyde Manwell; the argricultural scientist C M Ann Baker; the social anthropologist and business management expert F J Willett. In addition many experts on the various species included in my series 'The Precise Environment of Some Well-Known Animals' went out of their way to assist the understanding of an alien mathematician; in particular I am grateful to : the parasitologists M.D.B. Burt and Larry S. Roberts, the octopus expert R F Ambrose, the Monarch butterfly expert Myron P. Zalucki and that great Australian "froggy bloke" Michael J. Tyler. Without the expert assistance of the Griffith University Academic Librarian W J Lawson I think I might have given up under the weight of the biology literature.

Finally I wish to record my thanks also to my Griffith University colleague R J Henry, who kept insisting that he understood neither mathematics nor biology, but nevertheless supported me constantly with legal and other advice.

March 1989

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I INTRODUCTION

Any statement which can be written in English can be written in a formalized language and half a century ago J H Woodger (1937) urged that a formalization of biology would yield a worthwhile contribution to the progress of research in the biological sciences. We should not expect that only one formalized language would convey the richness of English or any other natural language. Rather it is necessary to choose a relatively small subset of sentences in the natural language to be translated into a formalized language which is constructed for just that restricted purpose. For instance if we wish to talk about points, lines and triangles we use geometry; for talking about integers we use number theory; for arrays of numbers matrix algebra. The richness of natural language is lost, but we gain precision, conciseness and exactness of communication. Faulty thinking is more noticeable and more easily corrected within a formalized language and obscure ideas are necessarily clarified by the requirement to write definitions at least partly in symbols and according to strict rules, (Quine, 1967). Woodger's work towards formalization in the biological sciences was difficult for biologists to read and understand; its inaccessibility, combined with the increasingly multipartite nature of modern universities which have separated pure mathematics and logic from biology, has resulted in the method being less widely known even among biomathematicians than one might expect. An exception is a formalized system for evolutionary theory constructed by Williams (1970). The Williams system has become well-known among logician-philosophers, perhaps somewhat less so among biomathematicians. However it seems to have had negligible impact among evolutionists.

The techniques for the construction of a formalized language, in particular for a new branch of mathematics, are readily available in any modern text on foundational mathematics or logic, e.g. the text by

Church (1956). There is a foundational semantic basis, the universe of discourse, which consists of the individuals of the system, the things we talk about. Thus in Euclidean geometry we talk about the points, lines and shapes of "flat" space; squares in two dimensions, cubes in three dimensions, tesseracts and hypercubes in four or more dimensions. At the basis of the formal system we have primitive terms; these are terms which are not formally defined and which we explain by drawing pictures, indicating type objects or simply talking about them; 'point' is a primitive term in Euclidean geometry. The formal definitions of the system include the primitive terms. The axioms of the system are sentences which contain primitive terms and definitions; they are assertions for which there is usually some evidence from the senses or from experiment. Thus in Euclidean geometry a straight line is defined in terms of two points and it is asserted that such a line will not cross itself. From axioms we proceed to theorems, which are sentences derived by the rules of inference which also belong to the system. In sciences such as astronomy the theorems of various formalized languages are useful for explanation and prediction, for instance the Russell-Vogt theorem (see below).

In this monograph I use some standard symbols long used in symbolic logic. They are:

(i) the existential quantifier $\exists$, so '$\exists$ crab' means "there is at least one crab,"

(ii) the negation $\sim$, meaning "it is not the case that", so '$\sim$ ($\exists$ crab)' means "it is not the case that there is at least one crab" and

(iii) the subjunctive conditional $\supset$; 'octopus ink $\supset$ octopus' means "if there is octopus ink then there is an octopus.

I also use the symbols $>$ and $\leq$ from ordinary arithmetic and as a subindex t_-; 'event$_{t_-}$' means "the event just before t". The 'hard' conditional '|', meaning "given that" is also used. This is the conditional used by statisticians for conditional events and conditional probabilities (Feller, 1959). By 'octopus will eat crab|octopus can find crab' we mean "the octopus will eat the crab given that the octopus can find the crab." There are five primitive terms in the system derived from biology. They are:

(i) 'Off' meaning "Offspring"
(ii) 'An' meaning "animal"
(iii) 'Hab' meaning "habitat"
(iv) the survival and reproduction primitive 'H', which is a number and,
(v) The directed interaction primitive 'ξ ' which ensures that the system is totally interactive.

Explications of all primitives are given below.

II MATHEMATICAL MODELS CONTRASTED WITH MATHEMATICAL FORMALIZATION.

Mathematical modelling in ecology consists of using a known branch of pure mathematics to write sentences about ecology. An example is the model for niche proposed by Hutchinson (1957). This model is an n-dimensional Euclidean space, in which the number of dimensions n is usually at least four. Ecological statistics such as measurement of length of animal or height above the ground of egg depository are plotted along the axes. The model was seen as simplifying a complex situation and has stimulated a great deal of field work. However there are a number of difficulties inherent in such a model. Perhaps the most important of these is the difficulty of visualizing a shape in four or more dimensions. Even the simple tesseract, the four-dimensional extension of the cube, is very difficult to visualize. One can attempt to do it by imagining eight ordinary three-dimensional cubes each of which form a 'side' of the four-dimensional figure. Thus, suppose we refer to the four axes as the w,x,y and z axes. Then there are sixteen 'corners' of the tesseract where all possible combinations of the two values of w,x,y and z meet. Also the 'sides' occur at lower and upper values of w,x,y and z, so there are eight 'sides' altogether, each of which is a cube. It is possible to construct a three-dimensional graph which will give us some idea of the appearance of a tesseract in much the same way as we can represent a cube on a flat surface, but it is not possible to represent a five-dimensional hypercube, with its thirty-two 'corners' and ten 'sides' each of which is a tesseract. Now the cube and its extensions are very simple shapes, far simpler than the complex tangled snarl which we have in ecology. The model is thus inadequate in this conceptual sense and indeed we may easily be deceived into misrepresenting the 'space' of the observed niche by inadequately chosen cross-sections or projections on to more easily visualized two-or three-dimensional spaces.

Another disadvantage of the Hutchinson model for niche is that it does not represent in a natural way the functional relations among the organisms. We may attempt to do this by, say grouping all the statistics to do with predation along one subset of the axes and the statistics of nutriment along another subset; the result is unsatisfactory since a change in the angle of perception immediately returns us to a confusion between the two classes.

These criticisms of the model arise from the fact that Euclidean geometry was originally devised to deal with concepts of physical space in three dimensions. There was no intention to use the language of geometry for living organisms and so reference to biology was not built in at the foundational level. These remarks apply to some extent at least to all mathematical modelling. Population dynamics in animal ecology makes use of the differential and integral calculus and the theory of differential equations, all of which were developed for the physical sciences. The use of matrix algebra has led to confusion because the standard theory allows the use of negative numbers as elements of a matrix; so some of the theorems do not apply because we cannot have negative numbers of animals in a population.

This is not an argument for ceasing to use mathematical models. The Hutchinson model has resulted in much good field work being undertaken. In population dynamics it was shown twenty-five years ago that a systems analysis (difference equations) for *Tribolium* populations correctly predicted the outcome of a two-species interaction (Niven, 1967, 1969). Furthermore just the effort required to write down a symbolic model often helps to clarify the situation; models are useful for sorting out the mess; until we have something better they should continue to be used in ecology.

In contrast mathematical formalization in ecology consists of the construction of a new branch of pure mathematics specifically for ecology. The universe of discourse contains objects belonging to biology and the primitive terms and definitions refer directly to the biological sciences. As Quine (1967) wrote "The less a science has advanced, the more its terminology tends to rest on an uncritical assumption of mutual understanding ... To be satisfactory ... a definition ... not only must fulfill the formal requirement of unambiguous eliminability, but must also conform to the traditional usage in question." Axioms and theorems should be sentences which assert things about ecology. Woodger (1952) wrote, when contrasting the two approaches, "In considering the relation of mathematics to biology we must distinguish between the process of applying existing mathematics to biology, and the less familiar process of letting the biological statements suggest new mathematical ones."

It has been stated often that there is something 'natural' and 'obvious' about the development of an appropriate mathematical basis for physics, in particular astronomy, and that by contrast biology in general and ecology in particular are not suited to the development of appropriate mathematics, that the best we can do is make shift with models taken from the physical sciences. It is not the case that early geometry arose naturally and easily. Early Polynesians were great astronavigators, the Mayas developed a magnificent solar-based calender, the Chinese were superb visual astronomers. But it was left to the Greek Scholars to make the deliberate intellectual attempt to develop geometry; this did not happen by chance, nor could it have been easy. A comparison of Aristotle's works, written two thousand years ago, both about living organisms and about astronomy, makes the point that we have failed to develop appropriate mathematics for the biological sciences. On that octopus which we now call *Octopus vulgaris*, Aristotle (Peck, 1965) wrote "The octopus discharges its eggs into its lurking - place, or into some old pot or other hollow object; they resemble the twisted inflorescence of a grape-vine, or the fruit of the white poplar... Once the parent has laid them, they cling on all round the receptacle." Two thousand years later, Mangold (1983) wrote "...most eggs are probably laid in shallow water... They are always attached to a substrate... On sandy or muddy bottom, eggs are laid in empty mollusc shells or in man-made objects, such as cans, tins, bottles, tyres, boots and amphorae... In the aquarium, the egg strings are stuck to the wall of the tank if no suitable home in provided... the chorion is drawn out into a stalk by which the eggs are interwoven to form a string." The modern article contains more detail, the animals are given Latin names, even some simple mathematical models are presented, but a contemporary of Aristotle would have little difficulty in understanding Mangold's article. Contrast this with the situation in astronomy. Aristotle (Stocks, 1930) wrote at length to convince his readers that "it is clear that the earth does not move and does not lie elsewhere than at the centre" (of the universe). The complex mathematical calculations, using the modern formalized languages of dynamics and calculus, which were necessary for the Voyager spacecraft explorations of the solar system would have been incomprehensible two thousand years ago. Once again modern dynamics, calculus and computer science did not arise easily and naturally; they required the whole-hearted full-time attention of some of our very greatest thinkers. We can only ask the question: "Why have ecologists failed to develop a mathematically based science?" The answer may be simply that it is so much easier to study another plant, or another animal, than develop hard theory. It is not so easy to study another star, or another galaxy, without developing a mathematical basis.

Finally, on this theme, it should be stated that in contrast to most mathematical models a mathematical formalization is realistic, precise *and* general (Levins, 1968).

III A SMALL BEGINNING: THE NOTION OF A RESOURCE

The first concept of ecology to be formalized was the notion of a resource based on a non-mathematical analysis of the idea of a resource in animal ecology which was published by Andrewartha and Browning (1961). The authors presented the point of view that resources are objects which are "material necessities of life." A resource was deemed to be an object which would increase the expectation of life of the animal or the probability of reproducing. In other words, a resource is an object which, on interacting with the animal, results in an increase in the chance that the animal will survive and reproduce. Examples of resources are given by Andrewartha and Birch (1954,1984) and others. They may be food, water, a place to oviposit, oxygen, light energy, thermal energy... In each of these cases the interaction with the animal results in an increased chance of survival and reproduction. Once this notion of a resource is accepted we are in a position to formalize. Let us choose a universe of discourse which is the set of all substantive objects, including units of energy. Then the object 'r' is defined to be a resource of the subject animal 'a' in the case that:

$$H_t(a) > H_{t_-}(a) \mid \xi_t ra \;\&\; [An_t(r) \supset \{H_t(r) \leq H_{t_-}(r)\} \mid \xi_t ra].$$

This string of symbols is a (mathematical) sentence which reads: The survival or reproductive ability of the subject animal at a particular time t is greater than its survival or reproductive ability just before t given that at time t the object acts significantly on the animal; furthermore if it is the case that the object is itself an animal then the survival or reproductive ability of the object at the time t is less than or equal to its survival and reproductive ability just before t given that at time t the object acts significantly on the animal. The mathematical sentence includes three primitive terms derived from the biological sciences: H, ξ and An. The explications are:

(i) The survival-and-reproduction primitive $H_t(a)$ is a positive real number which is a non-decreasing function of:
  (a) the expectation of life of the individual animal 'a' at birth or on entering its present stage of the life cycle, and
  (b) the probability that 'a' will have offspring.

(ii) The directed interaction primitive $\xi_t xy$ means that an interaction occurs between the object 'x' and the object 'y' which evokes immediately in 'y' some physical, physiological or behavioural response or a change of position and no other object (other than 'x') reduces or enhances this effect of 'x' on 'y' i.e. 'x' affects 'y' directly. The objects 'x' and 'y' must be elements of the universe of discourse; in particular they may be animals, including the animal 'a'. Judgement as to whether the response is significant is to be made by the ecologist.

(iii) An_t (r) is used to mean that the object 'r' is an animal. We may regard living organisms as being plants, animals or protists. Apart from a few rare occasions, it is quite clear in the field or laboratory to which of these three categories the organism of interest belongs.

If it is convenient to work in an interval of time 'δt' instead of an instant of time 't' then the subindex 't' should be replaced by 'δt'.

The inclusion of H as a primitive term implies that this definition, other definitions of the direct environment (see below) and hence the entire system, are all stochastic at a foundational level. The inclusion of the directed interaction ξ, which is incorporated in all definitions of the system, ensures that the system is totally interactive at the foundational level. The time-dependence of the primitives implies that the system is dynamic. The use of the conditional | (given that) means that an object classified as a resource is, in ordinary English, a potential resource. So if a chimpanzee is observed to eat a particular species of ant in the Gombe National Park then that same species of ant is classified as a resource for a chimpanzee living in the Mahale area. In the formal sense, therefore, the mathematical definition of a resource is independent of the animal's habitat. Thus in one line of symbols we have expressed a complex idea which applies widely to all animals and a very large set of objects. There is no need to be quite so formally symbolic when we use the mathematical definition in practice. For example, the chimpanzee is known to eat bark. The semi-formal sentence:

$$H(\text{chimp.}) \text{ is increased } \mid \xi(\text{bark})(\text{chimp.})$$

justifies the classification of bark as a resource. (Niven, 1988d) Chimpanzees also eat ants - another animal. A semi-formal sentence is:

$$H(\text{chimp.}) \text{ is increased and } H(\text{ant}) \text{ is decreased } \mid \xi(\text{ant})(\text{chimp.})$$

In the latter case H(ant) is decreased because when the ant is eaten its life expectancy drops abruptly. We assume in both cases that the resource (bark or ant) is nutritious, so H(chimp.) is increased via either the chimpanzee's life expectancy or its ability to reproduce. Since chimpanzees prefer a particular temperature range, any specific unit of thermal energy corresponding to that particular temperature range constitutes a resource. We have:

$$H(\text{chimp.}) \text{ is increased } \mid \xi(\text{heat})(\text{chimp.})$$

In this case H(chimp.) increases because either the animal's life expectation or its chance of reproduction is increased. A different unit of thermal energy corresponding to higher or lower temperatures would not be a resource, but a malentity (see below). Notice that, following the practice of modern physics, units of heat belong to the specified universe of discourse; we cannot work with 'quantities of cold'.

A resource need not necessarily be on object which is assimilated by the subject animal. The freshwater sponge *Spongilla lacustris* must find a suitable piece of substrate, otherwise its expectation of life is drastically reduced, thus a particular piece of substrate is classified as a resource:

> H(sponge) is increased $|$ ξ(substrate)(sponge). (Niven & Stewart, 1987).

'Shelter' could be seen superficially to be classifiable also as a resource. However it is a modifier of other objects in the environment of the subject animal. The animal thrives because it is protected from predators or malentities, so the shelter is a first-order modifier as explained below.

Poisoned food may seem to present a difficulty. Confusion here is avoided if the constituents are treated separately, the protein, say, as a resource, the poison as a malentity.

An animal may not be a resource of itself. If the mathematical definition given above is rewritten, but replacing the symbol 'r' by 'a', a contradiction appears; $H(a)$ is required simultaneously to increase and to decrease or remain unchanged.

IV OTHER KINDS OF OBJECTS WHICH DIRECTLY AFFECT AN ANIMAL

Things which have the potential to affect the animal directly were called the 'direct environment' by Niven (1980) and the 'Centrum' by Andrewartha and Birch (1984). When developing the mathematics of the system it is convenient to refer to this set of objects as 'modifiers of order zero.' There are four subsets of the centrum: resources (dealt with above); predators, for which the H of the subject animal is decreased and the H of the predator increased given that a significant interaction occurs, i.e. given that ξ(object) (animal); malentities, for which the H of the subject animal is decreased and the H of the object decreases or remains unchanged given that a significant interaction occurs; finally, mates, which are objects such that an interaction with the subject animal has the chance of resulting in offspring. It is convenient to use 'offspring' as another primitive term for this definition, its explication being the ordinary English semantic definition of the word. Of the four definitions for resources, mates, predators and malentities that for mates is the only one which is explicitly probabilistic. The other three definitions are implicitly probabilistic since they all include the primitive term H.

Something should be said about symbionts here, since they appear to have been left out of the direct environment. In practice, however, it seems that, apart from when mating occurs, when two animals interact in such a way that both the H values increase the interaction is not direct but *via* other objects. Typically one animal secretes a resource for the second animal, which supplies protection from predators in return. So the animals are interacting indirectly through resources or predators of each other; they are first-order modifiers in each others environment (see below).

As in the case of resource, it greatly assists correctness of classification to use the semiformal versions of the mathematical definitions (Niven, 1987). Thus if the subject animal is an adult female chimpanzee in oestrous at the time of classification then any one particular adult male chimpanzee, providing it is not sterile, is a (potential) mate. We may write:

An offspring of both individuals will be produced with
prob.>0|ξ(male chimp.)(subject chimp.).

The same female chimpanzee will not have mates in its environment in this formal sense when is is not in oestrous.
The rat tapeworm (*Hymenolepis diminuta*) customarily self-reproduces, so for a subject tapeworm we may write:

An offspring of the subject tapeworm will be produced with
prob >0|ξ(tapeworm)(tapeworm).

The interaction primitive ξ is used here in the sense that the subject animal is interacting with itself (Niven, 1988a).

Predacious caddis flies are formally (potential) predators of the freshwater sponge (*Spongilla lacustris*). We have:

H(sponge) is decreased and H(caddis fly) is increased
|ξ (caddis fly) (sponge)

(Niven & Stewart, 1987).

Snails and other crawling or browsing animals sometimes damage sponges accidently, so a snail, say, is a malentity in the environment of a subject sponge:

H(sponge) is decreased and H(snail) is unchanged |ξ (snail) (sponge)
(Niven & Stewart, 1987).

If 'm' is a mate of animal 'a' then it follows from the symmetry of the definition that 'a' is a mate of 'm', provided that 'm' is indeed an animal. (The mathematical definition allows 'm' to be an artefact.) As noted above an animal may be a mate of itself, however it may not be a predator of itself; as in the case of a resource a contradiction appears in the mathematics in this case. An animal may formally be a malentity of itself; in this case H(subject animal) must decrease due perhaps to some biochemical interaction within the animal. In practice this is an unlikely event.

V OBJECTS WHICH AFFECT AN ANIMAL INDIRECTLY

Things which we call 'modifiers', or 'Maelzer modifiers' after D A Maelzer who introduced the idea into the literature (Maelzer, 1965) affect the subject animal *via* the direct environment (centrum) or other modifiers. The set of modifiers was called the 'indirect environment' by Niven (1980) and the 'web' by Andrewartha and Birch (1984). A first-order modifier modifies an object in the centrum of the subject animal i.e. it modifies a resource, a mate, a predator or a malentity. A positive first-order modifier acts so as to include the object within the centrum; a negative first-order modifier causes the object to disappear from the centrum. An example of a negative first-order modifier is as follows:

> The common octopus (*Octopus vulgaris*) when presented with a crab of species *Dardanus arroser*, will eat the crab unless it is 'protected' by the anemone *Calliactis parasitica*; in the latter case, the crab is never taken (Niven, 1988b). The anemone is a negative first-order modifier of the crab, which is a resource in the environment of the octopus.

We may write:

$$
\begin{aligned}
(\exists\ \text{crab})[(\text{crab})\text{Res}(\text{octopus}) \mid {\sim}\xi(\text{anemone})(\text{crab})\ \&\ {\sim}(\text{crab})\text{Res}(\text{octopus}) \\
\mid \xi(\text{anemone})(\text{crab})].
\end{aligned}
$$

The symbol '∃' is the existential quantifier of modern formal logic. The sentence reads:

> There is at least one crab such that the crab is a resource of the octopus given that (at time t) it is not the case that the anemone acts significantly on the crab and it is not the case that the crab is

> a resource of the octopus given that the anemone acts significantly on the crab. Notice that the square brackets enclose the entire sentence outside the first round brackets '(∃ crab)' indicating that the existence of that crab applies to the entire phrase.

Oxygen consumption by the freshwater sponge (*Spongilla lacustris*) kept in the light is lower than that for sponges kept in the dark. This difference is probably the result of algal photosynthesis; oxygen produced by endocellular algae reduces the demand on that carried through the aquiferous system. Thus, for a subject sponge, a specific unit of oxygen is a resource which is modified (negatively) by an individual zoochlorella, which in turn is positively modified by a specific unit of light energy (kinetic energy in the form of light). In the presence of the light energy, the zoochlorella 'interferes' with the oxygen resource; in the absence of the light energy it does not. We may write first that the zoochlorella is a negative first-order modifier in the environment of the subject sponge:

$$(\exists O)[(O)\mathrm{Res}(\mathrm{sponge}) \mid {\sim}\xi(\mathrm{zoo.})(\mathrm{sponge}) \;\&\; {\sim}(O)\mathrm{Res}(\mathrm{sponge}) \mid \xi(\mathrm{zoo.})(\mathrm{sponge})].$$

The sentence reads:

> There is at least one unit of oxygen such that this oxygen is a resource of the sponge given that it is not the case that the zoochlorella acts significantly on the sponge and it is not the case that the unit of oxygen is a resource of the sponge given that the zoochlorella does act significantly on the sponge. Furthermore the light energy is a positive second-order modifier in the environment of the sponge:

$$(\exists\ \mathrm{zoo.})\ [(\mathrm{zoo.})\mathrm{Mod}^{1}\ (\mathrm{sponge}) \mid \xi(\mathrm{l.e.})(\mathrm{zoo.}) \;\&\; {\sim}\ (\mathrm{zoo.})\mathrm{Mod}^{1}(\mathrm{sponge}) \mid {\sim}\ \xi(\mathrm{l.e.})(\mathrm{zoo.})].$$

The sentence reads:

> There is at least one zoochlorella such that the zoochlorella is a first-order modifier in the environment of the sponge given that the particular unit of light energy acts significantly on the zoochlorella and it is not the case that the zoochlorella is a first-order modifier of the sponge given that it is not the case that the light energy acts significantly on the zoochlorella. (Niven & Stewart, 1987).

VI THE TOTAL ENVIRONMENT

The environment of an individual animal has thus been defined as a structured set of material objects, which has the subsets 'centrum' or direct environment and 'web' or indirect environment. The centrum contains four subsets:

resources, mates, predators and malentities.

The web is the set of modifiers:

first-order, second-order, third-order and so on.

An nth-order modifier is separated from the subject animal by n objects; the modifiers suggest the idea of an 'ecological distance' from subject animal to object. A connected set of modifiers, in order, form a modifier chain. In a practical case we choose which value of n to use (see analysis of 25-animal study below). The modifier chains may continue indefinitely or loop back on themselves; they are cross-linked, since an object may lie in two or more modifier chains attached to the same subject animal. Since in the centrum all cases of increasing or decreasing values of H are included for both subject animal and object the definition is 'complete' in this sense. The symbolic definition makes it clear that we have mot left any objects out. The modifier chains link animals together, possibly passing through plants or inanimate things *en route*; they thus provide the linking structure of animal communities and of ecosystems (Niven, 1988e). In order to define an animal community it is convenient to refer to elements of the centrum as 'zero-order modifiers'; the total environment of an individual subject animal is thus the structured set of all modifiers, with n taking the values 0, 1, 2, 3, ...

An example of the complex cross-linkages which occur in the environment is illustrated by the occurrence of the flatworm *Schistocephalus solidus* in the environment of the three-spined stickleback *Gasterosteus aculeatus* (Niven & Stewart, 1981-1983).

(i) The worm is in the centrum (is a zero-order modifier) as a predator, since the stickleback will become ill or die from an infestation:

$$\mathrm{H(stickleback)\ is\ decreased\ and\ H(worm)\ increased}\\ |\xi\mathrm{(worm)\ (stickleback)}.$$

(ii) A predator of the stickleback is a fish-eating bird. The stickleback which is infested by the worm swims higher in the water than otherwise and so is easier prey. Thus the worm is a positive first-order modifier:

$$(\exists \mathrm{bird})[(\mathrm{bird})\mathrm{Mod}^{\circ}(\mathrm{stickleback})|\xi(\mathrm{worm})(\mathrm{stickleback}) \quad \& \quad \sim(\mathrm{bird})\mathrm{Mod}^{\circ}\\ (\mathrm{stickleback})|\sim\xi(\mathrm{worm})(\mathrm{stickleback})].$$

(iii) The worm is a parasitic burden on the stickleback's oxygen consumption, oxygen being a resource of the stickleback. So the worm is a negative first-order modifier (since extra oxygen is required):

$$(\exists \mathrm{oxygen})[(\mathrm{oxygen})\mathrm{Mod}^{\circ}(\mathrm{stickleback})|\sim\xi(\mathrm{worm})(\mathrm{stickleback}) \ \& \ \sim\\ (\mathrm{oxygen})\mathrm{Mod}^{\circ}(\mathrm{stickleback})|\xi(\mathrm{worm})(\mathrm{stickleback})].$$

(iv) The worm is also a parasitic burden on the stickleback's food consumption, a particular (extra) item of food being a resource of the stickleback; this is like the case above, oxygen being replaced by food.

(v) The worm may affect the production of nest glue by the male stickleback. Here, the worm is acting as a negative third-order modifier, the chain being subject male stickleback-adult female as mate - nest - kidney glue - worm. The informal classifying sentences are:

(a) the female is a mate (a zero-order modifier):
An offspring of both individuals will be produced with
$\text{prob.}>0 \mid \xi(\text{female})(\text{male stickleback})$.

(b) A nest is a positive first-order modifier:
$(\exists\text{female})[(\text{female})\text{Mod}^{\circ}(\text{m.stick.})|\xi(\text{nest})(\text{female})$
$\& \sim(\text{female})\text{Mod}^{\circ}(\text{m. stick.})|\sim\xi(\text{nest})(\text{female})]$
(c) Kidney glue is a positive second-order modifier:
$(\exists\ \text{nest})[(\text{nest})\ \text{Mod}^{1}(\text{m. stick.})|\xi(\text{glue})(\text{nest})$
$\& \sim(\text{nest})\ \text{Mod}^{1}(\text{m. stick.})|\sim\xi(\text{glue})(\text{nest})]$.
(d) The worm is a negative third-order modifier:
$(\exists\text{glue})[(\text{glue})\text{Mod}^{2}(\text{m.stick.})|\sim\xi(\text{worm})(\text{m.stick.}) \ \& \sim (\text{glue})\text{Mod}^{2}$
$(\text{m. stick.})|\xi(\text{worm})(\text{m. stick.})]$

Notice that in (d) we use the form of the modifier definition which enables us to pass over the next lowest item in the chain to write '$\xi(\text{worm})(\text{male stickleback})$'.

(vi) Finally, the worm is a negative third-order modifier since with a severe infestation the female may break up the nest, while spawning, because of her increased bulk. In the absence of the worm some minor damage may occur, but devastation is unlikely:

As in (v) the female is a mate and the nest is a positive first-order modifier. Furthermore an enlarged adult female is a negative second-order modifier:

$(\exists\ \text{nest})[(\text{nest})\text{Mod}^{2}(\text{m.stick.})|\sim\xi(\text{enlarged female})(\text{nest})$
$\& \sim (\text{nest})\text{Mod}^{1}(\text{m. stick.})|\xi(\text{enlarged female})(\text{nest})]$.

The nest, in fact, disappears from the environment of the male stickleback. The worm, then, is a negative third-order modifier:

$$(\exists\ \text{female})[(\text{female})\text{Mod}^2(\text{m.stick.})|\sim\xi(\text{worm})(\text{female})$$
$$\&\ \sim(\text{female})\ \text{Mod}^2(\text{m. stick.})|\xi(\text{worm})(\text{female})].$$

This complex inter-linkage of modifier chains is shown in figure 1.

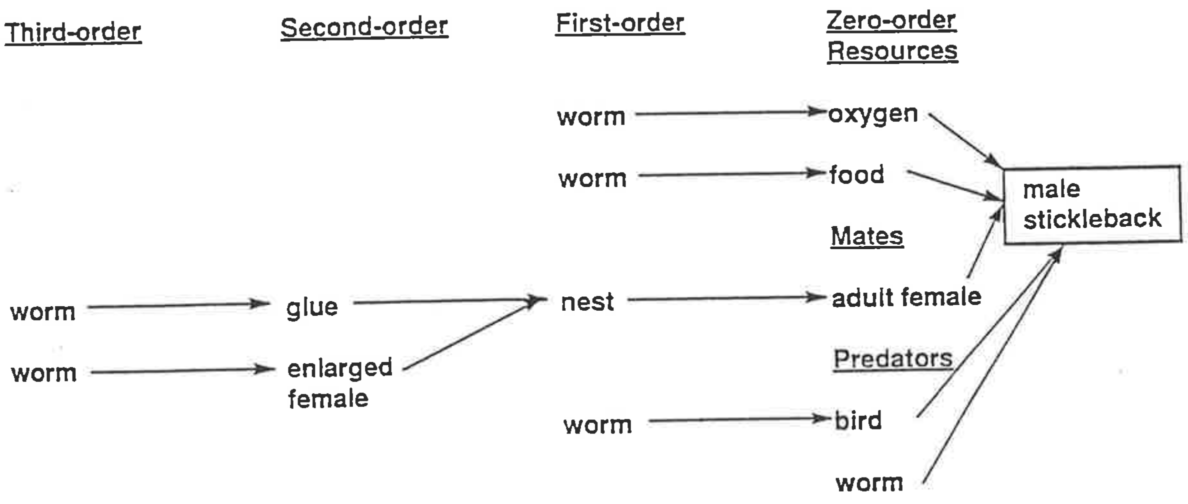

Fig 1. A particular individual parasitic worm *Schistocephalus solidus* has the potential (at some particular time) to interact with the subject male stickleback from at least six different 'positions' in the environment of the stickleback.

VII THE ENVIROGRAM

The realization of the mathematical definition of an animal's environment is called an 'envirogram'. These diagrams were developed by Andrewartha and Birch (1984) using early formulations of the mathematical definition (Niven 1980,1982). Each envirogram is drawn up for a specific life-stage of a particular animal species. The mathematics defines the environment of an individual animal, however the envirogram concatenates field and laboratory results of many animals. The diagram displays the four subsets of the centrum in a vertical column. The subject animal is named on the extreme right, with arrows linking it to elements of the centrum. First-order modifiers are in a vertical column to the left of the centrum, followed by second-order modifiers left of first-order and so on. The modifier chains are shown by connecting the elements from the highest order modifier on the diagram through to the subject animal. Unfortunately an envirogram does not easily display the complex cross-linkages implicit in the mathematical definition. Nevertheless it is a useful diagram and has been used to display the environments of the twenty-five species listed in Appendix I and the nine species of Appendix II. An example for *Octopus vulgaris* is given in Figure 2. The separate envirograms for egg and larva, which are sparse, have been superimposed on the adult envirogram. A full account of the environment of this animal is available (Niven 1988b). Andrewartha and Birch found that "when the theory in respect to any particular species..... is presented graphically in the form of an envirogram, the problems in the ecology of that species seem to be illuminated and to stand out clearly".

All envirograms mentioned in this paper were drawn by hand. However work is presently in progress to produce a computer package for drawing envirograms, which will also be used as a teaching tool for undergraduate courses in ecology. The package will allow for successive updating as new results are received.

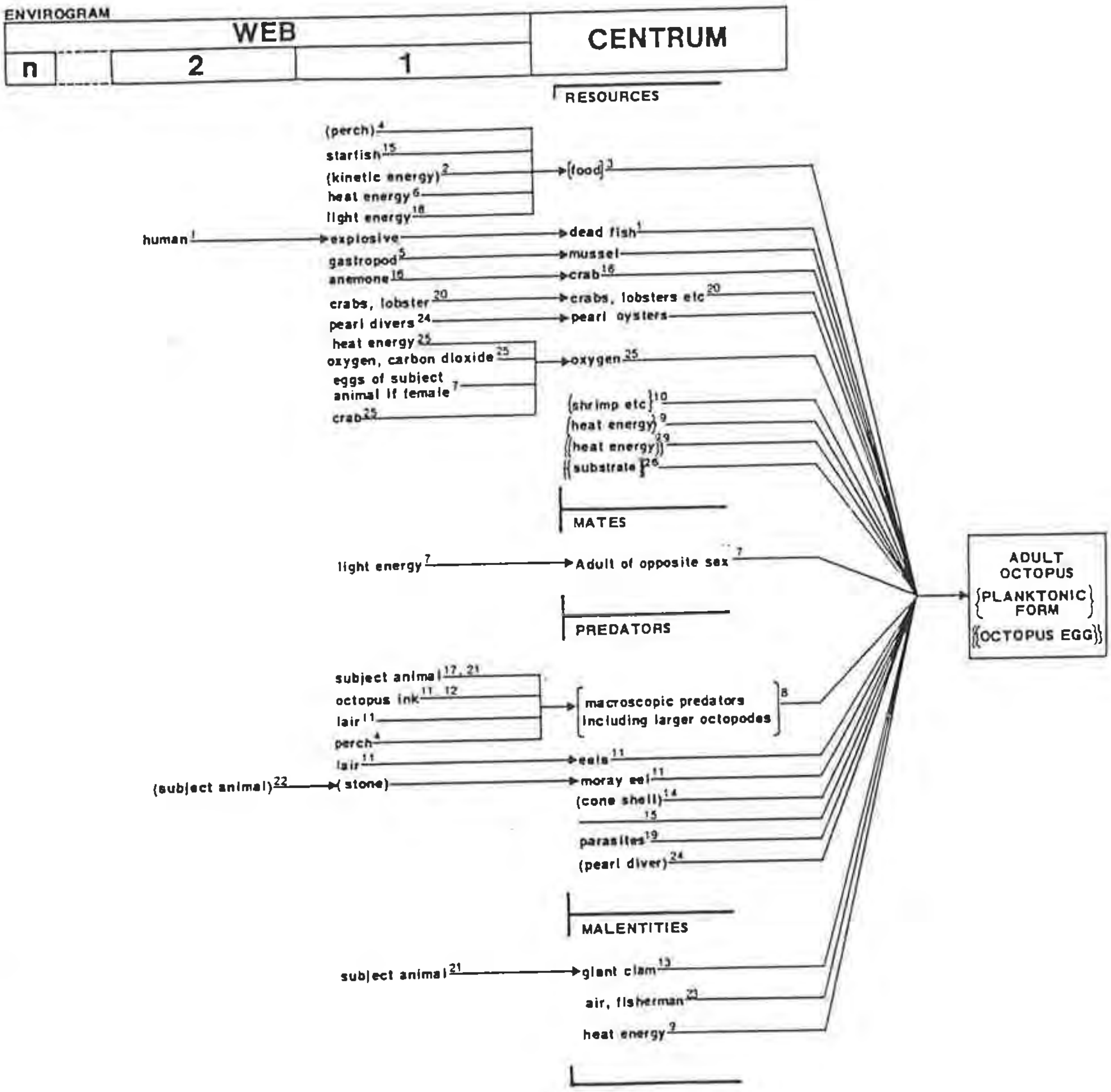

Fig 2. An envirogram for *Octopus vulgaris*. The numbers refer to the notes on the envirogram given in Niven (1988b). Notice the modifier chain anemone - crab - adult octopus which is referred to in the text of this article.

VIII THE TWENTY-FIVE ANIMAL STUDY.

A careful check of the environment definition was undertaken by choosing twenty-five well-known species of animal, searching the literature and classifying all objects deemed by the authors to be part of the animal's environment. In no case was an object recorded in the literature which could not be classified according to the mathematical definition. The formulation used for this exercise was the one published in 1982; this was found to be rather difficult to use in practice and even experienced logicians made the occasional mistake. For this reason a new formulation was developed during the later stages of the twenty-five animal study and five of them have been updated (Niven 1987, Niven & Stewart 1987, Niven 1988a,b,c,d).
The list of the twenty-five species is given in Appendix I. There are five lower invertebrates: sponge, coral, sea gooseberry, tapeworm, earthworm; six arthropods:; copepod, waterflea, mosquito, honeybee, blowfly, butterfly; five higher invertebrates: freshwater snail, terrestrial snail, squid, octopus, brachiopod; nine vertebrates: fish, frog, toad, fulmar, penguin, wallaby, dolphin, gorilla, chimpanzee.

These species were chosen because they were well-known, the information was easily accessible, the range of animal phyla was well-represented and colleagues in the biological sciences were at hand to provide occasional expert advice. Several comparable pairs were included for future comparative studies, e.g. squid and octopus. At least one envirogram was constructed for each species. In the case of the insects separate envirograms were constructed for egg, larva, pupa and adult, except the honeybee for which there are envirograms for worker, queen, drone and larva. Two or three envirograms were constructed for some of the other species.

Among the five lower invertebrates the envirograms for the coral

(*Pocillopora damicornis*) and the sea gooseberry (*Pleurobrachia pileus*) were both sparse, pointing to a lack of research on these animals although they are relatively well known within their phyla. The coral envirogram lacked modifiers of food resources. There was very little reported on the reproductive system.

Envirograms for the tapeworm (*Hymenolepis diminuta*) and the earthworm (*Lumbricus terrestris*) displayed greater range of research interest. There was an obvious gap in the two tapeworm envirograms for adult and larva; in both cases the class 'predators' had to be marked 'none known'. This is to say that it is not known whether this animal is attacked by diseases or parasites or eaten by larger animals. There is a lack of predator modifiers on the earthworm envirogram. An interesting modifier chain for the tapeworm is 'riboflavine - host rat - glucose - subject adult tapeworm.' This refers to the observation that when the host rat is fed a diet lacking riboflavine the tapeworm grows larger. This seems to be because more glucose is available to the tapeworm, since the host's ability to absorb glucose is reduced when it is fed a riboflavine-deficient diet. Riboflavine is thus a modifier of the host rat which in turn is a modifier of glucose as a resource in the tapeworm's environment. A modifier chain for the freshwater sponge (*Spongilla lacustris*) is 'kinetic energy (water currents) - sediment - particles capable of blocking ostia and porocytes - subject sponge.' The particles act as malentities of the subject animal. They are modified by (provided by) the sediment, or any other source of large particles; the sediment is stirred up and carried by water currents.

The envirograms for the six arthropods were extensive, reflecting greater interest in this phylum. Relatively little was known about the ecology of the larva and egg of the marine copepod (*Calanus finmarchicus*). A modifier chain for the adult copepod is 'iceberg - kinetic energy (upwelling) - diatoms - subject copepod'. The copepod eats diatoms which are modified by upwelling currents induced by an iceberg. The literature on the ecology of the waterflea (*Daphnia magna*) mentioned no modifiers of predators. A very well-known modifier chain for the yellow fever mosquito (*Aedes aegypti*) is 'human - small container - standing water - adult male - subject adult female. The male is a mate of the female and is modified by the presence of standing water in a small container provided by the human. Notice that the male as well as the female does not have offspring unless water is available for breeding. This modifier chain forms the basis for public health measures in places where the mosquito is found; householders are required to control and check bird baths, vases etc. The honeybee (*Apis mellifera*) is probably the best known insect (ecologically speaking). The worker envirogram in particular is relatively large. A nice modifier chain is 'wasp - wax moth - wax comb - honey - worker'. The honey is a food resource of the subject worker bee. Honey is stored in the wax comb of the hive, this is attacked and often destroyed by the Greater Wax Moth (*Galleria mellonella*) which is in turn attacked by the wasp *Apanteles galleriae*. The envirograms for the Monarch butterfly (*Danaus plexippus*) and the sheep blowfly (*Lucilia cuprina*) are also large. A modifier chain from the latter is 'other animal - pasture - helminth - faeces - bacteria - odour - sheep - subject adult female blowfly'. The female lays eggs on the sheep, which is thus a resource. The blowfly is attracted to the sheep by the ammoniacal odour produced by ammonia-producing bacteria living in the faeces. The presence of helminths tends to promote breech soiling with soft wet faeces. The pasture affects the helminths and is in turn modified by other animals.

Among the five higher invertebrates the envirograms for the squid (*Loligo opalescens*) and the brachiopod (*Lingula anatina*) were relatively sparse. The latter was surprising, since the animal is a standard reference in undergraduate zoology texts because of its fossil record which dates back to pre-Cambrian times. It is astonishing that the ecology of such an important animal, which one would expect to be of significance also to evolutionary studies, has been so grossly neglected. It is readily available, with world-wide distribution in very shallow sea water. The envirogram of a subject brachiopod lacks first-order modifiers of both food and predators and there does not even seem to be a definitive food list. Both snails have been well studied. An example of a modifier chain from the environment of the Wandering snail (*Lymnaea peregra*) is 'herbicides - decaying vegetation - bacteria - oxygen in water - subject adult snail'. The oxygen is a resource, for which the bacteria are competitors; the decaying vegetation is a resource for the bacteria (and hence a modifier for the subject snail); it is in turn modified by herbicides. For the Giant African snail (*Achatina fulica*) a modifier chain is 'legislation --- market gardener --- soil removed by erosion --- plant material --- subject snail'. Here, in order to comply with the restriction of the universe of discourse, the object 'legislation' has to be interpreted as the 'marks on paper' of the nominalist. Chinese market gardeners in Sarawak are required to keep their plots so clean all the year round that excessive soil erosion results, thus reducing feed for the snail. The common octopus (*Octopus vulgaris*) has been studied extensively for a very long time. Aristotle (1965) devotes several paragraphs to the animal. Predators, the moray eel and others, are well known. The envirogram includes the interesting modifier chain 'anemone - crab - subject adult octopus, given above. (See also the envirogram in the previous section.)

All nine vertebrates have been well studied. The three-spined stickleback (*Gasterosteus aculeatus*) has been used in numerous laboratory experiments by animal behaviourists in addition to being studied in the wild. The Leopard frog (*Rana pipiens*) presented taxonomic difficulties; these were overcome by restricting the envirogram to observations made in the northeast United States. An interesting double classification of the subject adult frog in its own environment occurs when we consider the behaviour of the animal during the winter, when it hibernates in an ice-covered pond. The frog excavates a pit in the mud at the bottom of the pond. From time to time it moves slightly. The action flushes the pit, renewing the oxygen supply and removing silt from the sides of the body to allow easier breathing. The same action attracts predators such as the Rainbow trout (*Salmo gairdneri*). So the animal is modifying, by its one action, both a resource and a predator. The envirogram for the Cane Toad (*Bufo marinus*) is considerably larger than the frog envirogram. A modifier chain is 'chicken - monitor lizard - coconut crab - Giant African snail - subject adult toad'. This chain refers to a situation on Guam. The snail is eaten by the toad. The coconut crab also feeds on the snail; the crab is in turn eaten by monitor lizards which also attack chickens. The Atlantic fulmar (*Fulmarus glacialis*) and the penguin *Aptenodytes patagonica* are the two birds of the study; the fulmar seems to be the better known. A modifier chain from the fledgling fulmar envirogram is 'subject animal - vomit - gull - subject fledgling. This refers to the predation of fledgling fulmars by the Great Blackback gull (*Larus marinus*); the fledgling, when threatened, will vomit a foul-smelling stomach-oil in defence, thus acting as a positive second-order modifier in its own environment. The Rottnest quokka (*Setonix brachyurus*) is the best known wallaby and the envirogram is relatively large. The Bottlenose dolphin (*Tursiops truncatus*) has been well studied both in captivity and in the wild. A modifier chain is 'subject animal - sound energy - fish - subject adult dolphin'. The fish are resources; the subject dolphin is able to locate them by producing ultrasonic signals for ecolocation. Both the mountain gorilla (*Gorilla gorilla beringei*) and the chimpanzee (*Pan troglodytes*) have been extensively studied. The envirograms refer mainly to observations in the wild. A modifier chain from the chimpanzee study is 'leopard - dead antelope - chimpanzee' which refers to observations of a chimpanzee searching for and then eating dead bushbuck which had been killed and left in a tree by a leopard the previous night. It is noteworthy that the mathematical definition accommodates well to observed chimpanzee behaviour, an exception being 'social grooming', which, if not undertaken for fleas, salt or small pieces of skin, but solely for the sake of increasing the H of both animals for some 'psycho-social' reason, is not covered by the definition. For this reason it may be necessary to use the formalized theory of human ecology (see below) for these animals, however hard evidence for the existence of purely 'social' grooming should first be obtained.

The structure of the observed modifier chains is of theoretical interest for the future mathematical development of ecology theory. There seem to be four main types:

(i) The chain continues indefinitively.
(ii) It ends in the sun (it seems pointless to continue beyond this point).
(iii) After passing through a number of other objects the chain loops back to the subject animal.
(iv) The chain loops back to the subject animal immediately because it is a first-order modifier in its own environment.

IX FROM ONE ANIMAL TO MANY: COMMUNITY; SPECIES; NICHE.

The modifier chains of the formalized environment tie animals together into a functional network. Consider as an example the chain 'anemone - crab - octopus' given above. Here we have three animals which are functionally related; furthermore we can write down precise mathematical expressions for those relations. The conditional form of those expressions implies that we are not limited to a particular habitat, so that a crab of the correct species is classified as a (potential) resource of the octopus even if one animal is in the Mediterranean and the other in the Pacific. However when we study an animal community we usually restrict our concept to a particular habitat; it is convenient, therefore, to introduce at this point a fifth biologically-based primitive term. Elton's notion of habitat is a useful one: "...a place that might be habitable for the animal whose ecology is being studied. The boundaries of the habitat and the qualities that determine the boundaries are fixed arbitrarily by the ecologist" (Elton, 1949). This is the 'habitat' used by Andrewartha and Birch (1984). So the primitive term 'Hab' is used in the formalized system to mean a specific place, not a class of places. The way is now clear to define an animal community (Niven, 1988e). All we have to do is change our perspective; instead of animals like the anemone and crab modifying the environment of a subject octopus we view the three individual animals as interacting with each other. Instead of saying 'the crab is in the direct environment of the octopus' or 'the crab is a zero-order modifier of the octopus' we can say 'the two animals, which are zero-order modifiers of each other, form a zero-order community'.

Consider for example a small habitat in the Mediterranean containing an octopus lair. The animals present are: 1 *Octopus vulgaris*, 2 *Dardanus arroser* of opposite sex, 1 *Calliactis parasitica*, 1 *Gymnothorax mordax* (the moray eel) and 2 passing anonymous fish.

It is convenient to use the language of modern algebra; instead of writing '(octopus) Pred ($crab_1$)' (the octopus is a predator of $crab_1$) we shall say "the morphism 'Predator' sends the octopus to $crab_1$," and write:

$$\text{Pred: Octopus} \rightarrow crab_1,$$

Similarly Pred: octopus → $crab_2$
Res : $crab_1$ → octopus
Res : $crab_2$ → octopus
Mat : $crab_1$ → $crab_2$
Mat : $crab_2$ → $crab_1$,

where 'Res' means resource and 'Mat' means mate. All these morphisms are derived from zero-order modifiers, so we call the set

$$\{octopus, crab_1, crab_2\}$$

a zero-order community in the habitat. Similarly the set

$$\{octopus, crab_1, crab_2, eel\}$$

is a first-order community in the habitat, and the set

$$\{octopus, crab_1, crab_2, anemone\}$$

is a second-order community in the habitat since in the environment of the anemone the crabs are first-order modifiers by conveying the anemone to its food so the octopus is a second-order modifier in the environment of the anemone. There is an asymmetry here; the anemone is only a first-order modifier in the environment of the octopus, but when we define a community we should look at the relation of anemone to octopus as well as the relation of octopus to anemone. Finally, the set

$$\{octopus, crab_1, crab_2, eel, anemone\}$$

is a third-order community in the habitat. The two passing fish may possibly enter into the scheme if high-order morphisms are considered, or if the fish happen to be suitable octopus prey. However two large fish are unlikely to be elements of an animal community of low order in this habitat. They may form a separate low-order community of their own. The octopus lair should be included when we consider the ecosystem.

An interesting mathematical object within an animal community is the product $X^{pred}Y$ where X and Y are sets of animals of the same species and for every individual animal x and y in X and Y we have that $Pred:x \rightarrow y$. This product is very like the Cartesian product of the algebra of real numbers. In ecology it is called a 'food web' and we often extend to more than two sets.

For further comments on animal communities see Niven (1988e)

We may consider the niche to be the relation of an animal species to its environment (Niven, 1989b). So when defining the niche we require a mathematical definition of species as well as environment. The ideas of Paterson (1985) fit very well into the scheme being developed; we may use the five biologically-based primitive terms given in this paper to construct a mathematical definition (Niven, 1989a). This definition reads, in words, that the animal species X is a set such that every element of X is an animal and is either a mate or the mate of a mate of a subject animal 'a', given that the animals are all in a specific habitat. The specific-mate- recognition notion of Paterson is dependent on the idea that the recognition response of a potential mating partner is of supreme importance; without such a response the probability of mating is negligibly small. The use of a specific habitat is a necessary feature of the recognition response and this is catered for in the mathematical definition by the use of '|' (given that). The mathematical definition given by Niven (1989a) covers the case of hermaphrodites. It also caters for mutations which result in some change of mate recognition in at least one pair of offspring in the same habitat which then lead to the establishment of a different species. The mathematical definition is not suitable for animals which are perpetually self-mating. In the case of an animal which has only daughters for several generations, followed by normal bisexual reproduction for one or two generations, the mathematical definition covers the latter case and can be 'forced' by making the time interval attached to the interaction primitive large enough. The definition is suitable for humans, unlike those for environment niche and community (see below).

Once species is mathematically defined we may proceed to the formal definition of niche by simply using the standard mathematical definition of a relation as a class of ordered pairs (Kuratowski & Mostowski, 1976). At the time of writing it seems very doubtful as to whether the concept of niche will, in the long run, be retained within ecology (see Niven 1989b and final section in this paper). Nevertheless many present-day field ecologists find the notion useful so the mathematical definition was constructed as part of the system. It is convenient to separate direct and indirect environments, so we extend the normal definition of relation to be a class of one or more ordered triplets. An an example we give a niche mentioned by Elton (1927) of the African spotted hyaena which eats ostrich eggs and also the remains of zebras killed by lions. The eggs and zebra remains are resources of the hyaena and the ostriches and lions first-order modifiers. The triplet is:

<spotted hyaena; ostrich eggs, zebra remains; ostriches, lions>

Elton considers as part of the same niche the arctic fox which subsists on eggs of guillemots but in winter relies partly on remains of seals killed by polar bears. So the niche is the class of ordered triplets:

< spotted hyaena; ostrich eggs, zebra remains; ostriches, lions >
< arctic fox ; guillemot eggs, seal remains ; guillemots, pol. brs >

Since the modifiers are all of first order and there are two of them in each triplet the niche is a first-order double niche. Notice that there are two distinct habitats. We may refer to this niche as either 'the niche of the spotted hyaena' or 'the niche of the arctic fox'. More triplets may be added if required. For a more modern example we turn to a study of the waterflea *Daphnia* by Ranta (1979). Three species are involved *D. magna*, *D*, *pulex*, and *D longispina*. The animals are filter feeders and the size of the ingested particles is controlled by the density of the filtering combs and the width of the carapace crevice. The animals thus act as first-order modifiers in their own environment. The niche is:

<*D. magna* ; large particles ; *D. magna* >
<*D. pulex* ; medium particles ; *D. pulex* >
<*D. longispina* ; small particles ; *D. longispina*>

The niche is a first-order simple niche. Notice that in this example the habitat is the same throughout, a freshwater rock pool in an archipelago near the Gulf of Finland.

X THE FORMALIZED CONCEPTS OF ENVIRONMENT, COMMUNITY, NICHE AND SPECIES ARE LINKED AT THE FOUNDATIONAL LEVEL.

Within the developing formalized theory of ecology the biologically-based primitive terms are at the foundational level. So by looking at which of these five primitive terms are used for the various definitions we can see how important concepts which lie at the heart of ecology are linked together. Four of these primitive terms are used to define environment. A different set of four is used to define species. All five are used to define community and niche.
Figure 3 illustrates the situation.

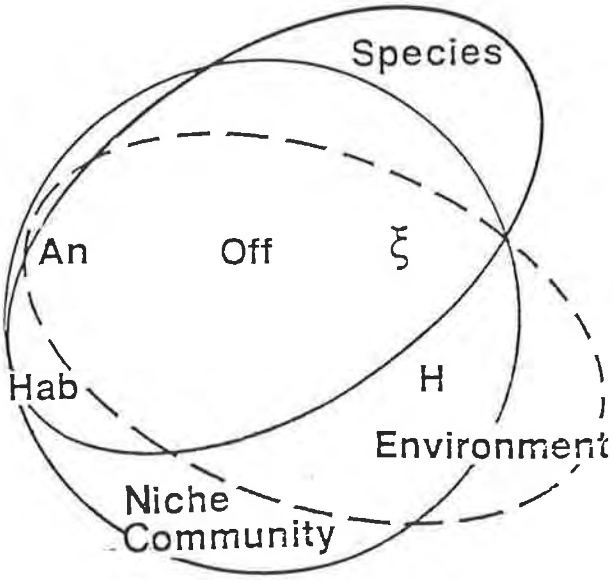

Fig.3. Linkage of 'environment', 'community', 'niche' and 'species'. All the primitive terms used to define a concept are enclosed within the appropriate boundary.

So population ecology and community ecology are seen as closely integrated. At least some field ecologists are well aware of the necessity for both points of view when working in the field. For instance Kitching (1986), on prey-predator interactions, writes ".... we should find the explanations for community structure and dynamics in processes operating at the level of the population."

XI TOWARDS THEOREMS FOR THE ECOSYSTEM: ANIMALS, PLANTS AND MODULES.

Let us return for the moment to the octopus example of communities of various orders. In the community we include only the animals named. Nevertheless it would be easy to include the octopus lair in some extension to the animal community since it is linked to the subject octopus as a modifier of predators; it is a first-order modifier in the environment of the octopus. Similarly other inanimate objects and plants may be linked to the animals of the community. In general, when we consider the plant world, it is conceivable that a series of formalized definitions could be developed for plant ecology, containing primitive terms which would be something like those used for the animal system. We may speculate that perhaps it would be appropriate to replace the primitive term 'animal' by 'plant', and 'H' and 'offspring' by some plant-related equivalents. The directed interaction primitive ξ could presumably remain much the same, with some changes in the explication. Finally 'habitat' for plants would have the same meaning as for animals.

It is often the case that animals eat only specific parts of plants, also insects which lay their eggs on plants usually choose a particular place, which is species-dependent. For this kind of reason it seems clear that when we develop new mathematics for the ecosystem we should think in terms of first a set of primary objects which are animals, plants or modules (module in the sense of Harper, 1981). Secondly we have modifier chains which act as linkages among the primary objects and may contain inanimate things (including energy) as well as animals, plants or modules. Some suggestions about a formalized definition of the ecosystem have been put forward (Niven, 1988e). However the present position is that no further work is planned along these lines due to a lack of funding.

XII THE HUMAN ANIMAL

It was realised at an early stage that humans, because of the importance of social and psychological factors and technology in their environment, cannot be adequately catered for by the scheme outlined above. Work on the formalized theory of human ecology is presently under way along the following lines:

An enlarged universe of discourse contains not just the substantive objects of the nineteenth-century physicist but *all* perceived objects. So the Taj Mahal, as an example, is a large set of perceived objects, since people will have slightly different perceptions of the edifice and some people will have more than one perception. The enlarged universe of discourse is thus an enormous, but still finite, set. It includes the universe of discourse for the animal system as a small subset. Thus the problem of perception is shifted from the observer to the subject. A basic definition within the developing formalized theory is for a 'social entity' which is defined mathematically as a set of humans ('human' is used as a primitive term) which share a set of perceptions (i.e. a subset of the universe of discourse). Every human of the social entity is itself a subset of the set of perceptions of the social entity. Use is being made of P.E. Lauer's brilliant formalization of C.I. Lewis' value theory (Lauer, 1980). The work is difficult (and totally unfunded) and is not expected to lead to a publication for several years.

XIII IS THE FORMALIZATION METHOD USEFUL IN ECOLOGY?

The proponents of the formalization method claim that it is useful in particular for clarification of ideas and for the correction of faulty notions. The first results along these lines in the formalization research outlined above concerned mistakes in the semantic definition of environment as developed by the Andrewartha school prior to 1984. In particular 'weather' was originally included as a component of environment (Andrewartha 1971, Andrewartha & Birch 1954, Browning 1963). An attempt to formalize this notion led to nonsense, which showed up clearly as nonsense in the symbolized sentences. Then the use of Venn diagrams demanded, for the sake of completeness, the extension of the notion of 'malentity'. This part of the research guaranteed the completeness of the direct environment (centrum) in the sense that all changes in the relevant values of the primitive term H were included. The original description of malentities (Andrewartha 1971) included only those objects for which H(object) did not change. However as soon as this notion was symbolized it became obvious that the set of objects for which H(object) decreased when the interaction occurred was missing from the system. It did not take long for an example of such an object to be proposed; a poisonous animal which is eaten by the subject animal is just such a case. Then the (initially very difficult) formalization of Maelzer's ideas that certain objects "only modified the value of some resource or other component of environment" (Maelzer, 1965) enabled the completion of the mathematical definition of environment by combining, symbolically, direct and indirect environments. The mathematical definition (Niven 1980, 1982) was used immediately by Andrewartha and Birch (1984) who based a new analysis of environment on the mathematics and proceeded to classify objects according to the definition. It is unfortunate that these first two formulations of the mathematical definition were difficult for biologists to use. The third attempt (Niven 1987) is far easier to use for classification work (and was, in fact, constructed for teaching an undergraduate course in ecology).

A difficulty which has been expressed about the mathematical definition of environment is that the maximum order of modifiers is not fixed. The indirect environment may be extended to suit the convenience of the ecologist. The point that the 'environment' described in a loose semantic way as "everything" is unacceptable in a formal system, for good mathematical reasons, was explained by Haskell (1940) in his great classical article on mathematical systematization of some basic ecological notions. The method used in the present system is an attempt to bypass this fundamental objection. The difficulty that the modifier chains may be extended indefinitely is not harder to deal with in practice than the analogous practical difficulty in that other great observational science, astronomy. Every time we develop new astronomical telescopes, either by extending their visual range or by extending to non-visual radiation, the number of objects in the known universe is increased. Nevertheless this does not prevent astronomers from classifying stars. The Hertzsprung-Russell diagram, which classifies stars according to their light magnitudes and spectral types, conceptually simple though it is, constitutes a major research tool. (An excellent elementary account is given by Maddison 1988)

In the past confusion has sometimes arisen in ecology when considering the effect of thermal energy on living organisms. Because temperature is easy to measure on an apparently continuous scale, one tends to forget that at a particular time only one particular energy package is interacting with the subject animal. The formalization has forced this understanding by the requirement that the object under consideration must necessarily be an element of the universe of discourse; 'temperature', in fact, is not a substantive object. The result of these considerations is the achievement of a precise classification of thermal energy in the environment. As remarked in the section on resources we cannot work with units of 'cold' and are forced into the modern physicists' attitude towards thermal energy.

A formalization is expected to facilitate the development of theory.

In science classification is of fundamental importance. The formalization research in animal ecology has produced methods of classifying environment, community and niche. It is clear that this could be done also for plants and modules, finally yielding a classification of ecosystems which will have a biological basis, which can be checked theoretically for completeness and which will enable precise comparisons among ecosystems.

The research which led to the mathematical definition of niche has thrown up a serious mathematical difficulty which militates against the future use of this concept in theoretical ecology. This is to do with the existence of an inverse within the developing system. Mathematically speaking we may deal with confidence with a branch of pure mathematics centred on the animal community, since there is a simple morphism which will send an animal back to itself, much as multiplication by the unit will send a number back to itself in ordinary arithmetic (Niven, 1988e). At the time of writing it does not seem possible to provide this feature for the niche, where the definition necessarily includes a set of animals (the species) instead of an individual animal (Niven, 1989b). Ecologists should therefore consider carefully whether the niche concept should continue to be used in future work, or discarded as yet another dead end. Speculation about the development of theorems which will be used for deeper understanding and prediction of ecosystems must remain vague until the basic formalization of plant and module ecology is completed. Nevertheless it now seems certain that such an exercise is *feasible*; strong doubts were expressed about the feasibility of the research during the three-year planning stage, during 1974-6, by a number of the world's leading logicians. Time has shown that useful results may be obtained providing that the following rules are applied:

(i) close contact is kept with field workers,
(ii) the difficult and cumbersome notation of Whitehead and Russell (1925) which was used by Woodger (1937) is replaced by more modern notation interspersed with enough natural language to

convey meaning without losing too much rigour,

(iii) intermediate results are checked immediately against data from a wide range of appropriate biological organisms.

Whether such research is useful in ecology depends on whether ecologists are willing to take the plunge into developing a precise mathematically-based science or would prefer to continue along Aristotelian lines in the sense that, as remarked above, Aristotle and his contemporaries would have little difficulty in understanding a modern ecology article. The great theoretical article of Haskell (1940) is, of course, an exception (however its message seems to have been ignored). The formalized mathematically-based science of astrophysics has required much dedication and extremely hard intellectual effort. Consider as just one example, the Russell-Vogt theorem which asserts that the structure of a star is uniquely determined by its mass and chemical composition (Chiu, 1968). The theorem involves the solution, under special conditions pertaining to stars, of four ordinary differential equations. Parameters are notions basic to physics: temperature, density, mass, opacity, electron pressure...The theorem is important in interpreting the Hertzsprung-Russell diagram, on which stars of the same composition lie along a smooth curve. It has direct consequences for our knowledge of the sun, its age and the time it will take on its path to red-gianthood and self-destruction. In fact, these four equations are intricately bound up with the physics of stars, at a fundamental level, in sharp contrast to the way similar ordinary differential equations are used in modelling as a superficial description of ecological phenomena, with no deep reference whatsoever to the basic biology of the organisms.

Finally, it should be stated with reference to the present system that definitions of animal niche and animal community and the proposed definition of ecosystem all depend largely on the definition of environment. The present mathematical definition of environment (Niven 1987) is stated in such a way that future improvements and even drastic change will be relatively easy, should future developments require it. The web can be joined to a totally different centrum, for instance, which might contain a completely different set of primitive terms.

REFERENCES

Andrewartha H G (1971) *Introduction to the Study of Animal Populations.* 2nd Edition. Chapman and Hall, London.

Andrewartha H G and Birch L C (1954) *The Distribution and Abundance of Animals.* University of Chicago Press, Chicago.

Andrewartha H G and Birch L C (1984) *The Ecological Web: More on the Distribution and Abundance of Animals.* University of Chicago Press, Chicago.

Andrewartha H G and Browning T O (1961) An analysis of the idea of "resources" in animal ecology. *Journal of Theoretical Biology* 1, 83-97.

Aristotle (Stocks, 1930). *De Caelo. Book II. Of the Heavenly Bodies.* Trans. J L Stocks. W D Ross (ed). Clarendon Press, Oxford. 296b.

Aristotle (Peck, 1965). *Historia Animalium* V, XVII-XVIII. Trans. A L Peck. William Heinemann, London. 165.

Browning T O (1963) *Animal Populations.* Hutchinson, London.

Chiu, Heng-Yee (1968) *Stellar Physics.* Blaisdell, Waltham, Mass.

Church A (1956) *Introduction to Mathematical Logic.* Princeton University Press, Princeton, New Jersey.

Elton C (1927) *Animal Ecology.* Sidgwick and Jackson Ltd, London.

Elton C (1949) Population interspersion: An essay on animal community patterns. *Journal of Ecology* 37, 1-23.

Feller W (1959) *An Introduction to Probability Theory and its Applications*. John Wiley & Sons, New York.

Harper J L (1981) The concept of population in modular organisms. In: May R M (Ed) *Theoretical Ecology*. 2nd Edition. Sinauer Associates, Mass.

Haskell E F (1940) Mathematical systematization of "environment" "organism" and "habitat". *Ecology* 21, 1-16.

Hutchinson G E (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitive Biology* 22, 415-427.

Kitching R L (1986) Prey-predator relations. In: Kikkawa J and Anderson D J (Eds) *Community Ecology*. Blackwell, Melbourne.

Kuratowski K and Mostowski A (1976) *Set Theory: With an Introduction to Descriptive Set Theory* PWN-Polish Scientific Publishers, Warszawa; North-Holland Publishing Company, Amsterdam.

Lauer P E (1980) Towards an Axiomatization of Value Theory. *Notre Dame Journal of Formal Logic* XXI, 51-77.

Levins R (1968) *Evolution in Changing Environments*. Princeton University Press, Princeton, New Jersey.

Maddison R (1988) The Hertzsprung-Russell Diagram. *Astronomy Now* 2, 6-10.

Maelzer D A (1965) A discussion of components of environment in ecology. *Journal of Theoretical Biology* 8, 141-162.

Mangold K (1983) *Octopus vulgaris*. In: *Cephalopod life cycles* P R Boyle (Ed). Academic Press, London. 335-364.

Niven B S (1967) The stochastic simulation of *Tribolium* populations. *Physiological Zoology* 40, 67-82.

Niven B S ((1969) Simulation of two interacting species of *Tribolium*. *Physiological Zoology* 42, 248-255.

Niven B S (1980) The formal definition of the environment of an animal. *Australian Journal of Ecology* 5, 37-46.

Niven B S (1982) Formalization of the basic concepts of animal ecology. *Erkenntnis* 17, 307-320.

Niven B S (1987) Logical synthesis of an animal's environment: sponges to non-human primates. I. Primitive terms and definitions. *Australian Journal of Zoology* 35, 597-606.

Niven B S (1988a) ----- III. The rat tapeworm, *Hymenolepis diminuta*. *Australian Journal of Zoology* 36, 1-14.

Niven B S (1988b) --- IV. The common octopus, *Octopus vulgaris*. *Australian Journal of Zoology* 36, 15-27.

Niven B S (1988c) --- V The cane toad, *Bufo marinus*. *Australian Journal of Zoology* 36, 169-194.

Niven B S (1988d) --- VI The chimpanzee, *Pan troglodytes*. *Australian Journal of Zoology* 36, 195-208.

Niven B S (1988e). The ecosystem as an algebraic category: a mathematical basis for theory of community and ecosystem in animal ecology. *Coenoses* 3, 83-87.

Niven B S (1989a) Formalization of the Paterson concept of an animal species. *Rivista di Biologia*, in press.

Niven B S (1989b) The animal niche: a formalized functional definition and its use in classifying niches. *Coenoses*, in press.

Niven B S and Stewart M G (1981-1983) The Precise Environment of Some well-known Animals. Vols I - XXVII. School of Australian Environmental Studies, Griffith University, Nathan, Australia 4111.

Niven B S and Stewart M G (1987) Logical synthesis of an animal's environment: sponges to non-human primates. II The freshwater sponge, *Spongilla lacustris*.
Australian Journal of Zoology 35, 607-624.

Paterson H E H (1985) The recognition concept of species. In: Vrba E S (Ed) *Species and speciation.* Transvaal Museum Monograph No. 4., Transvaal Museum,, Pretoria. 21-29.

Quine W V (1967) Truth by convention. In: *Philosophical Essays for Alfred North Whitehead.* Russell and Russell, New York. 90-124.

Ranta E (1979) Niche of *Daphnia* species in rock pools. *Archiv fur Hydrobiologie* 87, 205-223.

Whitehead A N and Russell B (1925). *Principia Mathematica*, 2nd Edition. The University Press, Cambridge, England.

Williams M B (1970). Deducing the consequences of evolution: a mathematical model. *J. theoret. Biology.* 29, 343-385.

Woodger J H (1937). *The Axiomatic Method in Biology.* Cambridge University Press, Cambridge, England.

Woodger J H (1952). From biology to mathematics. *Brit. J. Phil. Science* 31, 1-21.

APPENDIX 1

The following Booklets are available from: Division Australian Environment Studies, Griffith University, Nathan, Queensland, 4111, Australia.

The Precise Environment of Some Well-Known Animals

by B.S. Niven and M.G. Stewart (joined by J.C. Moore in Nos. X and XII; Nos. XV, XVII, XXIII, XXV, XXVI, and XXVII by B.S. Niven only)

Series No.	AES No	Title
I	9/81	General Introduction
II	10/81	The Chimpanzee (*Pan troglodytes*)
III	11/81	The Mountain Gorilla (*Gorilla gorilla beringei*)
IV	12/81	The three-spined Stickleback (*Gasterosteus aculeatus* leiurus)
V	15/81	The King Penguin (*Aptenodytes patagonica*)
VI	1/82	The Bottlenose Dolphin (*Tursiops truncatus*)
VII	3/82	The Cane Toad (*Bufo marinus*)
VIII	4/82	The Wandering Snail (*Lymnaea peregra*)
IX	5/82	The Giant African Snail (*Achatina fulica*)
X	6/82	The Leopard Frog (*Rana pipiens*)
XI	7/82	The Common Octopus (*Octopus vulgaris*)
XII	8/82	The Rottnest quokka (*Setonix brachyurus*)
XIII	1/83	The Sheep Blowfly (*Lucilia cuprina*)
XIV	10/83	The fresh-water Sponge (*Spongilla lacustris*)
XV	11/83	The Sea Gooseberry (*Pleurobrachia pileus*)

XVI	2/83	The Earthworm (*Lumbricus terrestris*)
XVII	12/83	The Waterflea (*Daphnia magna*)
XVIII	3/83	The Marine Copepod (*Calanus finmarchicus*)
XIX	4/83	The Monarch Butterfly (*Danaus plexippus*)
XX	13/83	The Yellow-fever Mosquito (*Aedes aegypti*)
XXI	5/83	The Pacific Coast Squid (*Loligo opalescens*)
XXII	6/83	The Atlantic Fulmar (*Fulmarus glacialis glacialis*)
XXIII	14/83	The Reef Coral (*Pocillopora damicornis*)
XXIV	7/83	The Rat Tapeworm (*Hymenolepis diminuta*)
XXV	15/83	The Common Honeybee (*Apis mellifera*)
XXVI	16/83	The Brachiopod (*Lingula anatina*)
XXVII	17/83	Revised version of General Introduction

APPENDIX 2

The environments of the following nine species were analysed by Andrewartha and Birch (1984) using early versions of the mathematical definition of environment in Niven (1980, 1982).

Spruce budworm	*Choristoneura fumiferana*
Queensland fruit fly	*Dacus tryoni*
Limpet	*Cellana tramoserica*
Limpet	*Patelloida latistrigata*
Australian black-backed magpie	*Gymnorhina tibicen*
Grey teal	*Anas gibberifrons*
African buffalo	*Syncerus caffer*
Moose	*Alces alces*
Rabbit	*Oryctolagus cuniculus*

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FORMALIZATION OF SOME BASIC CONCEPTS OF PLANT ECOLOGY

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Keywords: Community, Environment, Formalization, Plant ecology

Abstract. Formalization of the concepts of the 'environment' of a plant and of a 'community' of plants is given using mainly first-order logic, with some symbols and concepts taken from probability theory, modern algebra and engineering mathematics. The primitive terms from the biological sciences are those used for the analogous animal ecology definitions with two extra added to mean 'plant' and an indication of the well-being of the plant. The functional definitions may be used for classifying objects in the environment and for classifying communities. Examples are given.

1. Introduction

Research presently being carried out on the formalized theory of ecology extends over animal, plant and human ecology. The *modus operandi* is to construct a new branch of pure mathematics, using the concepts of modern formal logic. These require, in outline, first the establishment of a semantic basis, the universe of discourse. Secondly primitive terms, undefined in the system, are laid down, followed by formal definitions (usually symbolized), axioms, rules of deduction and, finally, theorems. The theorems are then used as a basis for the arithmetic necessary for management and prediction of real-life systems. For instance when we perform an analysis of variance we use formulae which stem from theorems about the normal, chi-square and F distributions. A second example comes from the physical sciences; the enormously complex calculations required to send the space probe Voyager II on the correct course to Neptune would have been impossible without the underlying theorems of dynamics and space science. So, too, the precise management of complex ecosystems will require appropriate theorems on which formulae that the ecologists will use will be based.

This article contains mathematical definitions of certain concepts basic to plant ecology. Initially, as a basis for the formalization, I have used the ideas of the population biologists H. A. Gleason (1926) and J. L. Harper (1977). Central to their theory is the individualistic concept. Gleason writes "... a logical classification of associations into larger groups, or into successional series, has not yet been achieved." Gleason's work has been greatly extended by Harper and this paper, which is based largely on Harper's work, presents one possible "logical classification" as called for by Gleason. Thus I start with the idea of an individual plant or module (for a discussion of modular organisms see Harper, 1981). The individual is surrounded by objects, both animate and inanimate. My universe of discourse is the set of substantive objects; it includes other plants or modules, animals, soil, rocks, air... and, most importantly, energy, treated in this paper as measurable energy packages. Kinetic energy in the form of light energy, thermal energy or wind, is of particular importance. My universe of discourse includes thermal energy but not temperature, which is assumed in this paper to be defined as in modern physics and thus is not a substantive object. Some of the objects near the individual plant or module will interact directly with it, others will interact only indirectly, many very indirectly indeed. Following Maelzer (1965) I distinguish sharply between those objects which directly affect the individual of interest, plant or module, from now on referred to as the 'subject' and those objects which affect the subject only indirectly. The two sets of objects are, respectively, finite and (potentially) infinite. They are then split into subsets. From this simple but powerful notion will be developed first a mathematical definition of the 'environment' of the subject and secondly a mathematical definition of a functionally related 'community' which includes the subject and also includes in a natural way the loose association of plants in the same habitat referred to by Miles (1979) as a 'patch'. The word 'habitat' here is from Elton (1949); it is used as a primitive term (see below) and means a particular place, not a class of places.

The formalization in this work is non-standard in the sense that I have not restricted myself to first-order logic as is usual in a formalization. I have used ideas and symbolism from engineering mathematics, probability theory and modern algebra, as well as set theory and first-order logic.

Animals are necessarily incorporated in the system. The analyses for animals are available in a series of published papers (see Niven, 1989).

2. Symbols and primitive terms

The following symbols from symbolic logic are used in this paper:

(i) The existential quantifier $\exists$. '$\exists$ leaf' means "there is at least one leaf".

(ii) The negation $\sim$. '$\sim$ ($\exists$ leaf)' means "it is not the case that there is at least one leaf"

(iii) The subjunctive conditional $\supset$. '$A \supset B$' means "if A then B".

(iv) The conjunction &. 'A&B' means "A and B".

(v) The disjunction V. 'AVB' means "A or B" (or both).

The symbols $>$, $<$ and $\leq$ are from ordinary arithmetic and mean "greater than", "less than" and "less than or equal to" respectively.

The 'hard' conditional $|$ is the conditional used by statisticians and probabilists for conditional events and conditional probabilities (Feller 1959). '$A|B$' means "A (occurs) given that B (occurs)".

The symbol $\rightarrow$ is from modern algebra. $A:B \rightarrow C$ means that the morphism A sends B to C.

The symbol t_ used as a subindex comes from engineering mathematics. It means "just before t". So 'the event $A_{t\_}$' means "the event A occurs at a time just before time t".

The brackets $<...>$ are used for ordered pairs, so the pair $<a,b>$ is not the same as $<b,a>$ unless a is the same object as b.

There are seven primitive (undefined) terms from biology used in the definitions. They are:

(i) 'Pl' standing for plant or plant module.

(ii) 'Off' standing for offspring.

(iii) 'An' standing for animal or animal module.

(iv) 'Hab' standing for habitat.

(v) The well-being primitive for plants, G, which is a number.

(vii) The survival and reproduction primitive for animals, H, which is a number.

(viii) The directed-interaction primitive ξ, which ensures that the system is totally interactive.

Explications of all primitives are given in the following section.

3. The explication of the primitive terms Pl, Off, An, Hab, G, H and ξ

In any formalized system such as a branch of mathematics it is necessary to include certain undefined words or phrases called 'primitive terms'. It is not possible to construct a branch of mathematics in which all terms are defined within the system. The primitive terms are then used in definitions, which are incorporated into the axioms from which the rules of inference of the system enable us to prove theorems. Choice of primitive terms which involve notions from the biological sciences results in a formalized system which has a foundation of biology, not physics, as is the case for most modern mathematics.

3.1 $Pl_t(p)$ means that the object 'p' is, at time t, a plant or modular organism which is part of a plant. 'Plant' is a blanket word in this context which is used in this paper to mean the Plantae, Fungi, Protoctista and Monera of Margulis and Schwartz (1982). A module is a "a repeated unit of multicellular structure, normally arranged in a branch system" (Harper 1981). Modules which are not arranged in a branch system are also used in this paper.

3.2 q $Off_t p$ means that the object 'q' becomes an offspring of object 'p' at time t, for the first time, *i.e.* q is 'born', becoming a separate object from p at time t.

3.3 $An_t(a)$ means that the object 'a' is, at time t, an animal or modular organism which is part of an animal. 'Animal' is used in this paper to mean the Animalia of Margulis and Schwartz (1982). 'Module' is used as explained in 3.1.

3.4 B Hab b means that the object 'b' occupies the region of physical space 'B' at time t. 'B' is called "the habitat of b". It is a specific place, not a class of places. "The boundaries of the habitat and the qualities that determine the boundaries are fixed arbitrarily by the ecologist" (Elton 1949). The object b must be either a plant or an animal, in the sense used in this paper, *i.e.* either $Pl_t(b)$ or $An_t(b)$.

3.5 The well-being primitive G is a number which expresses the general well-being of the subject plant or module. Following Harper (1977) such things as the rate of increase of dry weight, the amount of wilt and the amount of leaf-blackening are included in G. Also included in G is the probability of reproduction. The number $G_t(p)$ refers to G at time t of object p and it is obligatory that $Pl_t(p)$. Since G includes a probability it is itself probabilistic.

3.6 The survival and reproduction primitive H is a number which is a function of:

(a) The expectation of life at birth.

(b) The probability of reproduction, sexual or asexual.

Since H includes a probability it is itself probabilistic. The number $H_t(a)$ refers to H at time t of object 'a' and it is obligatory that $An_t(a)$. H is non-decreasing with respect to (a) and (b).

3.7 The directed interaction primitive $\xi_t xy$ means that an interaction occurs between the object 'x' and the object 'y' which evokes immediately in 'y' some physical, physiological or behavioural response or a change of position and no other object (other than 'x') reduces or enhances this effect of 'x' on 'y' ie 'x' affects 'y' directly. The objects 'x' and 'y' must be elements of the universe of discourse; in particular they may be plants or animals. Judgement as to whether the response is significant is to be made by the ecologist.

In all cases the subindex 't' may be replaced by δt' implying that the observation or action takes place during an interval of time instead of at an instant.

4. The direct environment

The direct environment of a plant is the set of objects which affect the subject directly. There are five subsets called resources, associates, co-reproducers, predators and malentities.

4.1 Resources

A resource of an individual subject plant is an object which is such that when it interacts with the subject in the sense of the directed interaction primitive, the G of the subject is increased. In the case that the object is itself a plant or an animal, its G or H is decreased or unchanged. The formal definition for object 'r' to be a resource of a subject plant (or module) 'm' is:

$$\{G_t(m)>G_{t\_}(m)\}\mid\xi_t rm\&[Pl(r)\supset\{G_t(r)\leq G_{t\_}(r)\}\mid\xi_t rm]$$
$$\&[An(r)\supset\{H_t(r)\leq H_{t\_}(r)\}\mid\xi_t rm]$$

This string of symbols is a (mathematical) sentence which reads, approximately: The general well-being of the subject plant (or module) at a particular time t is greater than its well-being just before t given that at time t the object acts significantly on the plant; furthermore if it is the case that the object is itself a plant then the general well-being of the object at time t is less than or equal to its well-being just before t given that at time t the object plant acts significantly on the subject plant; further to this if it is the case that the object is an animal then its survival and reproductive ability is less than or equal to its survival and reproductive ability just before t given that at time t the object animal acts significantly on the subject plant.

Objects such as a package of light energy or thermal energy, an amount of water (some specific quantity of water), an amount of oxygen, carbon dioxide or mineral nutrient are all resources. Semi-formally, when dealing with water, say, we may write, for a subject plant, say a maize plant:

G(maize) is increased $\mid\xi$ (water)(maize).

Since water is neither plant nor animal the second part of the definition is not applicable. The semi-formal sentence is a useful device which helps to check the accuracy of the classification. It is implied that:

(i) The time constraint is to be understood.

(ii) The maize referred to is a specific individual plant.

(iii) The water referred to is a specific quantity; it is a particular individual 1cc (say) of water, not the set of all possible 1cc amounts of water or a subset of that set.

Now as the subject consider a module of the brown rot fungus *Monilinia fructicola* and as the object another module which is one particular cherry (Weier *et al.* 1982). Then the cherry is a resource of the fungus, since we may write:

G(fungus) is increased and G(cherry) is decreased $\mid\xi$ (cherry)(fungus).

Now consider a case in which the resource is an animal. Suppose the subject is an individual Venus fly trap, *Dionaea muscipula* and the object some suitably-sized insect (Weier *et al.* 1982). Then we may write:

G(Venus f. t.) is increased and H(insect) is decreased $\mid\xi$ (insect)(Venus f. t.).

A plant may not be a resource of itself, since a contradiction appears in the definition if 'r' is replaced by 'm'; we have that G(m) is both increased and decreased at time t.

4.2 Associates

An associate of an individual subject plant is an individual plant or animal which is such that when it interacts with the subject in the sense of the directed interaction primitive the G of the subject is increased. In the case that the object is a plant its G is also increased. In the case that the object is an animal its H is increased. The formal definition for object 'a' to be an associate of a subject plant (or module) 'm' is:

$$\{G_t(m)>G_{t\_}(m)\}\mid\xi_t am\&[Pl(a)\supset\{G_t(a)>G_{t\_}(a)\}\mid\xi am$$
$$\&[An(a)\supset\{H_t(a)>H_{t\_}(a)\}\mid\xi am]$$

In English, this reads, approximately: The general well-being of the subject plant at a particular time t is greater than just before t given that at time t the object acts significantly on the plant; furthermore if it is the case that the object is itself a plant then its general well-being at time t is also greater than just before t given that at time t the object plant acts significantly on the subject plant; further to this if it is the case that the object is an animal then its survival and reproductive ability at time t is greater than just before t given that at time t the object animal acts significantly on the subject plant.

An example of an associate is given by Harper (1977). This is the fungus *Epichloe typhina*, described as an "intriguing... exception..." (to the normal interaction between pathogen and host). The fungus "sterilizes its grass hosts by preventing the emergence of an inflorescence. Such eunuch plants have high vegetative persistence in pastures and apparently greater vegetative vigour. It may be that some of the resources diverted from flowering are available for the more rapid production of tillers..." The fungus is an associate of the subject grass since:

G(grass) is increased and G(fungus) is increased $\mid \xi$ (fungus)(grass).

An example of a case in which the associate is an animal is not known, but has been allowed for in the mathematical definition.

Formally speaking, a plant may be an associate of itself, since no contradiction appears in the definition if 'a' is replaced by 'm' for the case of a plant as object. This does not, at present, seem to be a useful inference.

4.3 Co-reproducers

A co-reproducer of an individual subject plant is an object which is such that when the interaction in the sense of x occurs the probability is greater than zero that a new individual will come into existence. The formal definition for an object 'o' to be a co-reproducer of a plant 'm' is:

$$\mathrm{Prob}[(\exists x)(x\mathrm{Off}_{t+\beta}m \,\&\, x\mathrm{Off}_{t+\beta}o)\,\xi_t om] > o.$$

Examples of dioecious plants are asparagus, date palms and some mosses (Weier *et al.* 1982). Thus, for instance for a subject male asparagus and an individual female asparagus as object we may write, semi-formally:

The probability is greater than zero that an offspring of both male asparagus and female asparagus will appear after a time $\beta \mid \xi$(female asparagus)(male asparagus).

If 'o' is replaced by 'm' in the mathematical definition we have the case that a plant is a co-reproducer of itself. This applies to monoecious plants such as walnut, squash and some mosses (Weier *et al.*, 1982). It also applies to a subject tiller of the infected grass of section 4.2 since we have:

The probability is greater than zero that the tiller will produce an 'offspring' tiller after a time $\beta \mid \xi$(tiller)(tiller).

The expression ξ(tiller)(tiller) means that the subject tiller interacts with itself. The time β is the 'gestation' period *i.e.* the time from the start of the interaction to the time when a new individual appears, say a seed which is separate from the parent, or a new tiller or other module. β may be very short, perhaps only a few minutes, or very long, perhaps many months. The object 'o' is normally a plant, however the definition allows for 'o' to be an artefact.

4.4 Predators

A predator of an individual subject plant is an individual plant or animal which is such that when the object interacts with it in the sense of ξ the G of the subject is decreased. If the object is a plant its G is increased; if it is an animal its H is increased. Predators of plants include grazing animals and humans. The formal definition for object 'p' to be a predator of a subject plant (or module) 'm' is:

$$G_t(m)<G_{t\_}(m) \mid \xi_t pm \& [\mathrm{Pl}(p) \supset \{G_t(p)>G_{t\_}(p)\} \mid \xi_t pm]$$
$$\& [\mathrm{An}(p) \supset \{H_t(p)>H_{t\_}(p)\} \mid \xi_t pm]$$

The blight *Endothia parasitica* attacks chestnut trees in North America (Harper 1977). This parasite is formally a predator in the environment of a subject chestnut tree since we may write:

G(chestnut) is decreased and G(blight) is increased $\mid \xi$(blight)(chestnut).

Notice that once again in the semi-formal sentence the time constraint is to be understood and the blight is either a whole individual or a module. An example of an animal predator is the caterpillar of the olethreutid moth *Ecdytolopha* sp. which feeds on the Red mangrove (*Rhizophora mangle*), (Strong *et al*, 1984). The semiformal sentence is:

G(mangrove) is decreased and H(caterpillar) is increased $\mid \xi$ (caterpillar)(mangrove).

A plant may not be a predator of itself, since if we substitute 'm' for 'p' in the mathematical definition a contradiction appears, *i.e.* G(m) is required to increase and decrease, both at time t.

4.5 Malentities

A malentity of an individual subject plant is an object which is such that when it interacts with the subject in the sense of ξ, the G of the subject is decreased. In the case that the object is itself a plant its G is decreased or remains unchanged. In the case that the object is an animal its H is decreased or remains unchanged. The formal definition for object 'c' to be a malentity in the environment of a subject plant (or module) 'm' is:

$$[\{G_t(m)<G_{t\_}(m)\} \mid \xi_t cm] \& [\mathrm{Pl}(c) \supset \{G_t(c) \le G_{t\_}(c)\} \mid \xi_t cm$$
$$\& [\mathrm{An}(c) \supset \{H_t(c) \le H_{t\_}(c)\} \mid \xi_t cm].$$

Inanimate objects such as a falling rock, a violent wind (the kinetic energy is the object), a hailstone, a blast of lighting (electrical energy), fire (thermal energy) are all malentities. The semi-formal sentence for a subject plant and lightning as the malentity is:

G(plant) is decreased $\mid \xi$ (lightning)(plant).

A banyan which destroyed some small plant by forcing its roots through that plant is acting as a malentity; the small plant is destroyed, the banyan is unaffected:

G(small plant) is decreased and G(banyan) is unchanged $\mid \xi$ (small plant)(banyan).

An example of a human acting as a malentity is given by Liddle and Thyer (1986). Ramets of the grass *Entolasia stricta* were significantly harmed by human trampling. The semi-formal sentence for a subject ramet is:

G(ramet) is decreased and H(human) is unchanged $\mid \xi$ (human)(ramet).

The definition allows for both subject and malentity to be adversely affected by the encounter. An example would be a human trampler whose foot was pierced by the trampled plant (bearing thorns for instance).

Formally, a plant may be a malentity of itself. There is no logical contradiction involved if 'c' is substituted for 'm'.

5. The indirect environment

The indirect environment of a plant is the structured set of objects which affect the subject indirectly. These objects are called 'modifiers', a term due to Maelzer (1965) writing on animal ecology. First-order modifiers modify the effect on the subject of objects in the direct environment. Second-order modifiers modify first-order ones; third-order modify second-order, and so on. The formal mathematical definition is given in Section 5.3 below. Modifiers of all orders may be either negative or positive.

5.1 First-order Modifiers

These are objects which interact directly with the resources, associates, co-reproducers, predators or malentities in the environment of the subject plant. Harper (1977) records that the larvae of the cabbage white butterflies *Pieris brassicae* and *P. rapae* are attracted by mustard oil glycosides in their food plants and will eat other leaves (or even filter papers) if treated with sinigrin or sinalbin. Thus a leaf of the 'wrong' species becomes a resource if treated. For a subject leaf, say, an individual larva is a predator, since:

G(leaf) is decreased and H(larva) is increased | ξ (larva)(leaf).

The glycoside is a positive first-order modifier in the environment of the subject leaf since:

($\exists$ larva)[(larva)Pred(leaf) | ξ(glycoside)(leaf) &
$\sim$(larva)Pred(leaf) | $\sim\xi$(glycoside)(leaf)].

That is, there is at least one larva, such that the larva is a predator of the leaf given that there is significant interaction between glycoside and leaf in the sense of ξ and it is not the case that the larva is a predator of the leaf given that there is no interaction between glycoside and leaf. The interaction primitive (section 3.7) in this case should be interpreted as evoking a physiological or physical response, depending on whether the glycoside is incorporated in the structure of the leaf or merely smeared on.

Also from Harper (1977) we have that the cyanogenic glycosides protect plants of *Trifolium repens* against slugs. Without the glycoside the slug would be a predator, so the glycoside in this case is a negative first-order modifier, since we may write, for a subject *T. repens* individual:

($\exists$ slug)[(slug)Pred(T.repens) | $\sim\xi$(glycoside)(T.repens) &
$\sim$(slug)Pred(T.repens) | ξ(glycoside)(T.repens)].

That is, there is at least one slug such that it is a predator of the subject *T. repens* plant given that it is not the case that there is an interaction in the sense of ξ between glycoside and plant, and it is not the case that the slug is a predator given that there is an interaction between glycoside and plant. Notice the difference between positive and negative modifiers brought out by these two examples. The time constraint applies throughout.

Symbiosis between two organisms is often a first-order-modifier situation. An interesting example is a lichen, which consists of two plants, an alga and a fungus, in symbiosis. The fungus hyphae enmesh the alga, introducing haustoria into it which absorb food material from the alga. The fungus provides the thallus which supports the alga (Weier *et al.* 1982). Consider first a subject alga, the thallus which supports it being a resource, since:

G(alga) is increased and G(thallus) is unchanged | ξ (thallus)(alga).

The fungus which supplies the thallus is a positive first-order modifier, since:

($\exists$ thallus)[thallus)Res(alga) | ξ(fungus)(alga) &
$\sim$(thallus)Res(alga) | $\sim\xi$(fungus)(alga)].

Now consider a subject fungus. The food it gains from the alga is a resource, since:

G(fungus) is increased | ξ (food)(fungus).

The alga which supplies the food is a positive first-order modifier, since:

($\exists$ food)[(food)Res(fungus) | ξ(alga)(fungus) &
$\sim$(food)Res(fungus) | $\sim\xi$(alga)(fungus)].

Grime (1979) remarks that the treatment of productive vegetation with the growth retardant maleic hydrazide tends to suppress potential dominants and to increase species density. In the environment of a small plant as subject, the dominant is either a predator or a first-order modifier by shading the subject. If the dominant is a predator then the maleic hydrazide is a negative first-order modifier since:

($\exists$ dominant)[(dominant)Pred(small plant) | $\sim\xi$(mal. hyd.)
(dominant) &
$\sim$(dominant)Pred(small plant) | ξ(mal. hyd.)(dominant)].

The shading situation is dealt with in the following section.

Another interesting example of symbiosis is that of a mycorrhiza which associates with the roots of a higher plant (Weier *et al.* 1982). The endomycorrhizal fungi which live within individual root cells are, formally, classified as predators. More interesting, from the logical point of view, are the ectomycorrhizal fungi, the hyphae of which grow between the root cells but do not form haustoria; but contact between root and fungus is nevertheless close enough for metabolites to be transferred in both directions. In this case each plant provides resources for the other and is therefore a positive first-order modifier in the other's environment since, for a subject fungus we may write:

(∃ metabolite)[(metabolite)Res (fungus) | ξ(plant root)(metabolite) &

~(metabolite)Res(fungus) | ~ξ(plant root)(metabolite)].

Similarly, for a subject plant:

(∃ metabolite)[(metabolite)Res(plant) | ξ(fungus)(metabolite) &

~(metabolite)Res(plant) | ~ξ(fungus)(metabolite)].

The rules of construction of the semi-formal sentences allow, in the term starting with ξ, for the second individual to be either the subject or an object in the direct environment of the subject.

5.2 Second- and Third-order Modifiers

Second-order modifiers are objects in the environment of the subject which modify first-order modifiers. Third-order modifiers modify second-order modifiers. To continue with the example of the previous section from Grime (1979) suppose the dominant is shading the subject small plant and thereby interfering with the thermal energy or light energy that it requires. Some one particular package of thermal energy corresponding to a suitable temperature is a resource since:

G(small plant) is increased | ξ(thermal energy)(small plant).

The dominant is a negative first-order modifier, since:

(∃ thermal energy)[(therm. en.)Res(small plant) | ~ξ(dominant)(therm. en.) &

~(therm. en.)Res(small plant) | ξ(dominant)(them. en.)].

The maleic hydrazide is a positive second-order modifier, since:

(∃ dominant)[(dominant)Mod^1(small plant) | ξ(mal.hyd.)(dominant) &

~(dominant)Mod^1(small plant) | ~ξ(mal.hyd.)(dominant)]

If we now introduce the human who treats the vegetation with maleic hydrazide we find that the human is a third-order modifier in the environment of the small plant, since:

(∃ mal. hyd.)[(mal. hyd.)Mod^2(small plant) | ξ(human)(mal. hyd.) &

~(mal. hyd.)Mod^2(small plant) | ~ξ(human)(mal. hyd.)].

In this latter case the interaction primitive is interpreted as meaning that the response is a change of position of the maleic hydrazide. Notice that the notation Mod^1 and Mod^2 is being used here for first and second-order modifiers.

Harper (1977) writes that the jay *Garrulus glandarius* carries acorns of *Quercus* spp. up to a distance of one kilometre for burial. They search for them during the autumn and winter and eat them, but a number of seedlings survive. The burial may be vital for the viability of the acorn. The thermal energy associated with above-ground temperatures is a malentity, since:

G(acorn) is decreased | ξ(therm. en.)(acorn).

The soil which covers the acorn is a negative first-order modifier:

(∃ therm.en.)[(therm.en.)Mal(acorn) | ~ξ(soil)(therm en.)&

~(therm.en.)Mal(acorn) | ξ(soil)(therm.en.)].

In this case a physical change is induced on the thermal energy by the soil.

The jay which buries the acorn is a positive second-order modifier:

(∃ soil)[(soil)Mod^1(acorn) | ξ(jay)(acorn) &
~(soil)Mod^1(acorn) | ~ξ(jay)(acorn)].

5.3 Modifiers of all Orders

The formal definition of the set of modifiers (which is potentially infinite) is given here. First, we shall refer to objects in the direct environment of a subject plant m as 'modifiers of order zero'. A modifier is an object w. Thus for a resource, an associate, a co-reproducer, a predator or a malentity referred to as w we have $w\mathrm{Mod}^0{}_t m$. Then:

$$w\mathrm{Mod}_t^{+(n+1)}m =_{df} (\exists x)\,[\{x\mathrm{Mod}_t^{n}m \mid (\xi_t wx \vee \xi_t wy)\}\,\&$$
$$\{{}^{\sim}x\mathrm{Mod}_t^{n}m \mid \sim(\xi_t wx \vee \xi_t wy)\}]$$

$$w\mathrm{Mod}_t^{-(n+1)}m =_{df} (\exists x)[\{x\mathrm{Mod}_t^{n}m \mid \sim(\xi_t wx \vee \xi_t wy)\}\,\&$$
$$\{{}^{\sim}x\mathrm{Mod}_t^{n}m \mid (\xi_t wx \vee_t wy)\}]$$

$n=0,1,2,\ldots;$

y is either m or a modifier of order ≤ n

$$\mathrm{Mod}_t^{n}m =_{df} \mathrm{Mod}_t^{+n}m \vee \mathrm{Mod}_t^{-n}m$$

A set of objects connected by the modifier definitions, taken in order, is called a 'modifier chain'.

Notice that we have the choice of either ξwx or ξwy when writing down the justifying sentence for a modifier. Thus in second example of section 5.2 above the first-order modifier definition includes ξ(soil)(therm. en.) *i.e.* ξwy where y is a modifier of order zero. For the second-order modifier semi-formal sentence we use ξ(jay)(acorn) *i.e.* ξwm.

6. The total environment

The total environment of a plant or module m is the structured set which is the union of direct and indirect environment of m in which the structure of the five subsets of the direct environment and their attached modifier chains is preserved. The environment is total in the sense that all possible increases or decreases of G(subject) and G(object) (or H(object)) are included in the direct environment. If G(subject) does not change the object being considered does not belong to the direct environment. If it exists (*i.e.* belongs to the universe of discourse) then it must necessarily be, in this case, a modifier.

The 'environment', as mathematically defined in this paper, is an extremely complex network, since any one object may occupy many logical positions in the environment of a subject plant, all at the same instant. This occurs because of the use of the conditional |

(given that) in the definitions. In ordinary English objects in the environment would be referred to as '*potential* resources', '*potential* associates', '*potential* co-reproducers', '*potential,* predators', '*potential* malentities' and '*potential* modifiers'. The situation is similar to that in the related formalized theory of animal ecology and an example is given by Niven (1989) from a study of the environment of the three-spined stickleback (*Gasterosteus aculeatus*) in which a parasitic worm Schistocephalus solidus appears in six logical positions in the known environment --- once as a predator, three times as a first-order modifier and once as a third-order modifier. This conceptual difficulty is significantly resolved by the use of a brilliantly simple diagram called an 'envirogram', which was invented by H G Andrewartha, using the mathematical definition of the total environment of an animal given by Niven (1980). The diagram was introduced into the animal ecology literature by Kitching (1983) and used extensively by Andrewartha and Birch (1984). The envirogram opens out the complex network of the environment and projects it on to a flat surface, making it very easy to scan. Envirograms are now being constructed for plants, using the definitions in this paper. Until recently drawn by hand, these diagrams may now be computer-constructed (Abel *et al.* 1989).

7. Communities

The modifier chains which formalize the functional relations between plant and plant, or plant and animal will now be treated as the functional linkages which knit together a plant or plant-and-animal community. I now introduce a change of notation; instead of saying "plant 'q' or animal 'a' is a kth-order modifier in the environment of plant 'p'" I shall say

"Mod^k sends plant 'q' or animal 'a' to plant 'p'" and write this symbolically as:

Mod^k: q→p, or

Mod^k: a→p.

The idea of modifiers in the environment of a subject plant is thus transformed into the mathematical notion of a morphism.

We can now define an nth-order community C_n within a habitat as a structured set of plants, animals and modules a,b,c,........ such that for every ordered pair <a,b> we have Mod^k:a→b, k=0,1,2,...,n, where k is the maximum of the smallest integer for every pair. The time constraint holds as for environment, *i.e.* we allow for a change within a community from instant to instant. Thus we start with a specific habitat B, say, which is such that for every plant, animal and module, p, to be considered, B Hab p. We consider each pair in turn. Each pair is considered twice, taking the ordering into account. For the first pair, <a_1,a_2> say, we write down the modifier connection. We repeat this for <a_2,a_1>. If n is small then C_n will be a set of plants (modules, animals) which is closely knit together. Several such communities (non-overlapping) may occur in a large habitat. If n is large then Miles' (1979) idea of patch is satisfied. In some cases the functional relation between two plants in a patch will be very tenuous indeed; this is catered for in the definition since there will be at least one modifier chain, which may contain scores of objects, which connect the two.

For the definition to be helpful certain universal modifiers must be excluded. Oxygen and thermal energy are examples of universal modifiers, which will knit together, since they are resources for all, even extreme 'logical outliers' in a Miles 'patch'.

7.1 A zero-order community

Consider the example of a predator from Harper (1977) in Section 4.4. The blight *Endothia parasitica* attacks chestnut trees and is formally classified as a predator of a subject chestnut tree. We rewrite this as:

Mod^0:blight → tree. ("Mod zero sends blight to tree.")

Now take an individual blight as the subject. Then:

G(blight) is increased and G(tree) is decreased | ξ (tree)(blight).

We rewrite this as:

Mod^0: tree → blight.

The two individuals, chestnut tree and blight, constitute a zero-order community. If now we add another chestnut tree, then this second tree is a first-order modifier in the environment of the first tree; it "competes" for blight (or nutrient) and we write, semi-formally:

(∃blight)[(blight)Pred(first tree) | ~ξ(blight)(second tree)& ~(blight)Pred(first tree) | ξ(blight)(second tree)].

In other words:

Mod^1: second tree → first tree.

Thus we no longer have a zero-order community.

A zero-order community, then, is one in which the plants (modules, animals) are linked together by being in one another's direct environments; they are usually very small, with only two or three individuals. The concept is a useful one when classifying communities, but is not usually appropriate to real-life communities in the wild.

7.2 Higher-order communities

Consider the example of section 5.2 taken from Grime (1978), in which a dominant, which normally shades a small plant, is adversely affected by maleic hydrazide sprayed by a human. We have:

Mod^3: human→ small plant.

It is not clear from the example what the converse relation is. The dominant is a (negative) first-order modifier of the small plant, thus:

Mod^1: dominant → small plant.

The converse relation is not clear, but it may well be that the small plant 'shares' nutrient with the dominant, in which case:

Mod^1: small plant → dominant.

The human who sprays the maleic hydrazide on the dominant is also a first-order modifier in the environment of the dominant, so

Mod^1: human → dominant.

Finally, for this rather artificial community containing one small plant, one dominant and one human in some definite fixed habitat B we have:

Mod^3: human → small plant.

Mod^1: dominant → small plant.

Mod^1: small plant → dominant.

Mod^1: human → dominant.

The community, therefore, is classified as a third-order community within the habitat B, as far as our knowledge extends. We lack the information about the two missing morphisms small plant→human and dominant→human.

7.3 Example of an Observed Community.

Boyd (1988) studied a Searocket community as follows:

"Two species of searockets (*Cakile maritima* and *C. edentula* ssp. *edentula* var. *edentula*) have been sequentially established on the West Coast of North America since the 1880's. In California, *C. maritima* has replaced *C. edentula* in the southern 1000 km of their former sympatric distributions. This research tested the hypothesis that differential herbivory contributed to the ascendance of *C. maritima*. Choice experiments were conducted with three herbivores (two insects and a rodent) which consume *Cakile* at Point Reyes National Seashore, California, where only *C. maritima* now occurs. Larvae of the moth *Platyprepia virginalis* (Arctiidae) displayed a significant preference for foliage of *C. maritima* in a laboratory test. No evidence of any foliage preference was found for a short-horned grasshopper *Microtes occidentalis* (Acrididae) in laboratory and field experiments. Field experiments with deer mice (*Peromyscus maniculatus*) demonstrated a significant preference for *C. edentula* seedlings and fruits. Degree of preference by mice for seedlings was affected by the distance from the experimental location to patches of introduced beachgrass (*Ammophila arenaria*), which mice use for nesting sites and cover, but this distance-dependence did not occur for fruit predation. Herbivory by the two insect species was not a factor in this case of species replacement. *Peromyscus* preference for seedlings and fruits of *C. edentula* would have affected the rapidity of local species replacement at Point Reyes, but this preference does not explain the current distribution of *Cakile* on the Pacific Coast. I concluded that differential predation by mice was not the ultimate cause of *Cakile* species replacement in California."

We start the mathematical analysis by choosing the habitat, say a bounded area in the same region as that used by Boyd, but still containing both species of *Cakile*. Now consider two individual *C. maritima* and *C. edentula*. Since they compete for nutrients they are first-order modifiers of each other. Call them 'm' and 'e'. Then

Mod^1:m → e, and

Mod^1:e → m.

Now consider other plants of the same species in the habitat, m_1,m_2... and e_1, e_2,... For any pair, we have:

Mod^1:m → e,

Mod^1:m → m,

Mod^1:e → m, and

Mod^1:e → e.

Now introduce the moth larvae, l_1, l_2... say. For any larva, and m or e:

Mod^0:l → m,

Mod^0:l → e,

Mod^0:m → l, and

Mod^0:e → l.

Among larvae, since they are predators of the same plants,

Mod^1:l_1→l_2, and

Mod^1:l_2→l_1.

The same argument applies to the grasshoppers g_1,g_2,... and rodents r_1,r_2...

We now add plants of the beachgrass, b_1,b_2,... which serve as protection for the rodents (from unknown predaters or malentities). Thus for any m or b:

Mod^1:b → m.

It follows from this that the beachgrass is a second-order modifier in the environment of a Searocket:

Mod^2:b → m, and

Mod^2:b → e.

We now have to consider the Searockets as objects in the environment of the beachgrass, similarly moth larvae and grasshoppers. If the beachgrass and Searockets use the same nutrients, which seems a reasonable assumption, then we have, for any b and e or m:

Mod^1:m → b, and

Mod^1:e → b.

Since larvae and grasshoppers attack first-order modifiers of the beachgrass they are both, therefore, second-order modifiers in the environment of a subject beachgrass, thus, for any larva and grasshopper:

Mod^2:l → b, and

Mod^2:g → b.

Altogether there are three species of plants and three species of animals mentioned in this example. It is advisable when doing the analysis to consider two individuals of each species, to ensure that the analysis is complete. Thus we consider all possible ordered pairs of 12 individuals, *i.e.* 132 pairs, from which we can subtract 12 intraspecific pairs, since in this case <a,b> is equivalent to <b,a>. Thus altogether we should consider 120 ordered pairs. The work is reduced if we realise that in this particular case all 3 animal species act in much the same way. Clearly, however, the complete analysis of a complex community will require computer assistance. Work towards this goal is already under way, with a study of the use of the specification language Object Z for animal communities, following on the use of Z for animal environment (Abel and Niven 1989). The final result for Boyd's example is that the community is a second-order one, in the habitat specified.

7.4 Second Example of an Observed Community

Strong *et al.* (1984) describe a community consisting of *Spartina alterniflora*, a common grass of saltmarshes, and its associated insects. They list 3 leaf-feeders, 5 stem-borers and 4 saprovores. Larvae of 9 parasitoids attack the leaf-feeders, larval parasitoids of 10 spp,. attack the stem-borers and larval parasitoids of 2 spp. attack the saprovores.

We start the mathematical analysis by choosing the habitat. Let the habitat B be a bounded (fenced, say) saltmarsh on the Gulf coast of North America. B extends upwards for a height of, say, 10m and down into the marsh to a depth of, say, 3 m. The plants, animals and modules, p say, in the community to be analysed are all such that B Hab p. Let us choose as our time constraint some particular interval of time, say one day during a period when all plants and animals under study are active.

Now consider an individual tiller of *S. alterniflora* as the subject. The 3 leaf-feeders, 5 stem-borers and 4 saprovores are all predators, or first-order modifiers (competitors) of predators. Now if we choose an individual animal from this set as the subject then the tiller is a resource and the other animals are all first-order modifiers. To make this clear we write down the semi-formal sentences for the tiller, an individual leaf-feeder and one other animal, which is a leaf-feeder, a stem-borer or a saprovore. First, the leaf-feeder is a predator of the tiller:

G(tiller) is decreased and H(leaf-feeder) is increased | ξ (leaf-feeder)(tiller).

The other animal is a negative first-order modifier in the environment of the tiller:

(∃ leaf-feeder)[(leaf-feeder)Pred(tiller) | ~ξ(other animal)(tiller) &
~(leaf-feeder)Pred(tiller) | ξ(other animal)(tiller)].

Now take the leaf-feeder as the subject. Then the tiller is a resource, since:

H(leaf-feeder) is increased and G(tiller) is decreased
| ξ(tiller)(leaf-feeder).

The other animal is a negative first-order modifier, since:

(∃ tiller)[(tiller)Res(leaf-feeder) | ~ξ(other animal)(tiller) &
~(tiller)Res(leaf-feeder) | ξ(other animal)(tiller)].

Thus we have:

Mod^{0}:leaf-feeder→tiller,
Mod^{1}:other animal→tiller,
Mod^{0}:tiller→leaf-feeder, and
Mod^{1}:other animal→leaf-feeder.

Similarly,

Mod^{0}:tiller→other animal, and
Mod^{1}:leaf-feeder→other animal.

We have written down all 6 of the morphisms which occur when we consider 3 individuals.

A parasitoid acts as a second-order modifier in the environment of a subject tiller. Now consider as subject a larval parasitoid of a saprovore. The saprovore is a resource in the environment of the parasitoid. The tiller, a resource of a resource, is a first-order modifier. A stem-borer, which is a predator of a resource of a resource, is a second-order modifier and finally a parasitoid which attacks the stem-borer is a predator of a predator of a resource of a resource of the subject larval parasitoid; it is a third-order modifier. Thus:

Mod^{3}:stem-borer parasitoid→saprovore parasitoid.

Another stem-borer parasitoid modifies the action of the first stem-borer; it is a fourth-order modifier in the environment of the subject saprovore parasitoid. Thus:

Mod^{4}:other stem-borer parasitoid→saprovore parasitoid.

Clearly the listing of all possible functional relations between the ordered pairs of the 34 species in this example is a task for a computer analysis. There are 68x67-34=4522 ordered pairs which should be considered to complete the analysis and classify the community. From the analysis given above this is a fouth-order community in the designated habitat. A complete analysis awaits the advent of computer software.

8. Discussion

Southwood (1980) in his article entitled 'Ecology - a mixture of pattern and probabilism' wrote that ecology may be defined as "the study of living organisms at the level of the population and community". In this paper I have presented a probabilistic pattern extending from individual plant to plant community which is intended to serve as a mathematical basis for plant ecology. The system I have developed is stochastic in two ways. First, at a fundamental semantic level, the two primitive terms G, for plants, and H, for animals, both contain probabilistic ideas. G (or H) is incorporated in all definitions, explicitly in the five definitions of the direct environment and implicitly in the infinite set of definitions of the indirect environment. It is also the case that the definition of co-reproducer ('mate' in the animal equivalent) contains a probabilistic sentence. The system is also totally interactive, via the directed-interaction primitive. It is time-dependent; provision is made for the environment of an individual plant, or a community of plants, to change from instant to instant. All definitions are functional; it is the functional relations among plants (or animals) which provide both the structure of the environment and the structure of a community. By excluding the primitive term Hab (for habitat) from the definition of environment I have made the concept of environment habitat-indepenent. This enables us, for example, to include the blight *Endothia parasitica* among the predators of a chestnut tree, even in the case that the tree is growing in an area far removed from the place in which the observation was made.

In the first paper on the corresponding environment definition for animals (Niven 1980) the terms 'direct environment' and 'indirect environment' were used, as in this paper. However, Andrewartha and Birch (1984) preferred to rename these two sets of objects the 'Centrum' and the 'Web' respectively. It is for experienced plant biologists to decide whether the terms 'Centrum' and 'Web' should be used for the plant system. (To a mathematician, modifiers of order 0,1,2,3,... would seem more natural). All animal studies published by Niven and colleagues since 1984 have incorporated the names Centrum and Web.

The explication of G has been deliberately left rather vague. It is a number which expresses the general well-being of the subject plant. In this connection Harper (1977) writes "A large part of the study of mechanisms of plant interaction has concentrated on gross measurements such as life or death, or weight. The more successful attempts to understand interference have involved studying symptoms. Often the effects of a toxin or a nutrient deficiency are very specific: leaf tip blackening in *Grevillea*, potassium deficiency symptoms in *Desmodium,* sudden wilt... change in leaf area/weight ratio..." The mathematical definitions containing G are not dependent on the precise explication of G; should the explication be changed slightly, as experience in using the system is acquired, the formal definitions should remain unchanged.

In this paper I have attempted to strike a sensible balance between the amount of symbolism and explanation in ordinary English, where this can be done without losing too much precision. For example the notions that resources, co-reproducers and malentities may be both non-plant and non-animal, whereas it is obligatory that predators and associates be either plant or animal could be symbolized and added to the symbolic definitions. This seems to me to be unnecessary and I have been content to use natural language only.

The existence of the set I have called 'associates' came as a surprise to me, since the animal equivalent does not seem to exist in real life, although of course it is easy enough to write down the corresponding definition (in which the H of both subject and object animal increases). The example given by Harper (1977) is one of a fungus associate of a grass in the case that the fungus prevents seed formation, the result being a 'forced' vegetative growth by the plant. Liddle (1975) reports that trampling by humans may have the same effect and Liddle (pers. comm.) adds that the destruction of a plant's reproductive mechanism in order to stimulate its vegetative growth is not uncommon in horticulture. In these cases the human would be classified as a resource since:

G(plant) is increased and H(human) is unchanged $\mid \xi$ (human)(plant).

The choice of habitat, an essential item for the classification of a community, is of critical importance. Harper (1977) writes "The diversity of microsites within the habitat may permit different species to occupy specialized microenvironments within the community. Often this underlying heterogeneity is difficult to define..." Harper continues with a detailed example then "A statement about the floristic richness of such a pasture as a whole has no real meaning in relation to the chances of interspecific encounter." If when undertaking a mathematical analysis we find that a number of, say, non-overlapping fourth-order communities appear to exist in the same habitat, this would seem a pointer towards splitting the original habitat into several subunits.

The explication of the primitive term 'Off' (offspring) says nothing at all about whether the new separate individual is the same species as the parent, or parents. The assumption in the general system of formalized ecology, of which this paper gives a part, is that the idea of Paterson (1985) of the recognition concept of a species, is relevant. Paterson's semantic definition of species has been formalized in Niven (1989), for animals. It is confidently expected that the result will also apply to dioecious plants.

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REFERENCES

Abel, D. E., K. L. Bass, T. A. Chorvat, A. B. Gavranic, R. J. Howlett, E. Hove, B. S. Niven and M. P. Zalucki. 1989. A computer program for producing envirograms. Bull. Ecol. Soc. Aust. 19: 16-17.

Abel, D. E. and B. S. Niven. 1989. Application of a formal specification language to animal ecology I. Environment. Ecological Modelling. In Press.

Andrewartha, H. G. and L. C. Birch. 1984. *The Ecological Web. More on the Distribution and Abundance of Animals.* Chicago University Press, Chicago.

Boyd, R. S. 1988. Herbivory and species replacement in the West Coast Searockets (*Cakile*, Brassicaceae). Amer. Midland Nat. 119: 304-317.

Elton, C. 1949. Population interspersion: An essay on animal community patterns. J. Ecol. 37: 1-23.

Feller, W. 1959 *An Introduction to Probability Theory and its Applications*. Wiley, New York.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey bot. Club 53: 7-26.

Grime, J. P. 1979 *Plant Strategies and Vegetation Processes.* Wiley, Chichester.

Harper, J. L. 1977. *Population Biology of Plants.* Academic Press, London..

Harper, J. L. 1981. The concept of population in modular organisms. In: R. M. May (ed.), *Theoretical Ecology,* 2nd edn. Sinauer, Sunderland. pp. 53-77.

Kitching, R. L. 1983. *Systems Ecology.* Queensland University Press, Brisbane.

Liddle, M. J. 1975. A selective review of the ecological effects of human trampling on natural ecosystems. Biol. Conserv. 7: 17-36.

Liddle, M. J. and N. C. Thyer. 1986. Trampling and fire in a subtropical dry sclerophyll forest. Environmental Conservation 13: 33-40.

Maelzer, D. A. 1965. A discussion of components of environment in ecology. J. Theoret. Biol. 8: 141-162.

Margulis, L. and K. V. Schwartz. 1982. *Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth.* Freeman, San Francisco.

Miles, J. 1979. *Vegetation Dynamics.* Chapman and Hall, London.

Niven, B. S. 1980. The formal definition of the environment of an animal. Aust. J. Ecol. 5: 37-46.

Niven, B. S. 1989. *Towards a Mathematically-Based Theory of Ecology: A Monograph.* AES Publications, Griffith University, Nathan, Queensland.

Niven, B. S. 1989. Formalization of the Paterson concept of an animal species. Rivista di Biologica 82: 191-200.

Paterson, H. E. H. 1985. The recognition concept of species. In: E. S. Vrba (ed.), *Species and Speciation.* Transvaal Museum Monograph No 4: 21-29. Transvaal Museum, Pretoria.

Southwood, T. R. E. 1980. Ecology - a mixture of pattern and probabilism. In: E. Saarinen (ed.), *Conceptual Issues in Ecology.* Reidel, Dordrecht.

Strong, D. R., J. H. Lawton and R. Southwood. 1984. *Insects on Plants: Community Patterns and Mechanisms.* Blackwell, Oxford.

Weier, T. E., C. R. Stocking, M. G. Barbour and T. L. Rost. 1982. *Botany: An Introduction to Plant Biology.* Wiley, New York.

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THE TWENTY-FIVE ANIMAL STUDY

Introduction

(a) *Five lower invertebrates:*

Sponge
Coral
Sea Gooseberry
Tapeworm
Earthworm

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XXVII REVISED VERSION OF GENERAL INTRODUCTION

by

B.S. NIVEN

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CONTENTS

Note: Roman numbers in the text refer to the animal studies; see Appendix.

1. THE REASONS FOR FORMALIZATION

This study of the precise environment of twenty-five well-known animals is part of a larger project the aim of which is to formalize the theory of ecology. For convenience the total project is split into four areas: plant ecology, protist ecology, animal ecology, human ecology. A formalization includes specification of the individuals of the system, primitive terms, axioms, definitions, rules of inference, theorems. This part of the project employs that subset of the definitions that explicate the environment of an animal, in order to provide a basis for the establishment of the axioms and associated mathematical detail.

I have used as a starting point the theory associated with the names of H.G. Andrewartha, L.C. Birch, T.O. Browning, D.A. Maelzer and their students. Central to their theory is the classification of the environment of one typical animal. The original classification, given by Andrewartha and Birch (1954) was developed by Browning (1963), Maelzer (1965) and Andrewartha (1971). The classification in the latter publication had five components. They were: (i) resources, (ii) mates, (iii) predators, pathogens and aggressors, (iv) weather, (v) malentities. An example of (i) is an item of food. Examples of (v) are (a) an animal which accidentally treads on the animal of interest and crushes it; (b) vagaries of the weather which accidentally kill or damage the animal. The theory, as given by Andrewartha (1971) is then extended to encompass the interaction of the animal with the five components and further extended to populations of animals. Included are such concepts as the "niche" of an animal, i.e. its relations to food and enemies, and the interlocking of niches in an ecological complex.

The end product of the formalization will be a new symbolic language, that is, a calculus, which will have its own symbols and rules of manipulation, tailored precisely to the theory. There are three main reasons for undertaking the project:

(i) To facilitate the development of ecology theory.
A formalization will aid in ensuring that all the assumptions are explicitly laid down; in particular it will give an accurate way of saying explicitly what

assumptions are incorporated in a chain of deductions. The rules of deduction will enable us to arrive at the consequences of our assumptions in a systematic way: by formalizing we are less likely to omit important consequences. The use of clearcut definitions is almost essential for the exact communication of the theory to others.

(ii) To provide a basis for comparison of the theory with other theories of ecology.

(iii) To clarify the theory itself. A formalized language for a scientific theory provides an aid to intuition, a corrective to faulty thinking and a systematic method of criticising obscure ideas. On the latter point, consider the advantages of the symbolization given below; in a few lines I give an explicit account of what constitutes the environment of an animal. Even if this is deemed to be incorrect its assumptions, primitive terms and the relationships it posits are absolutely clear and anyone who disagrees can easily see the precise point(s) of contention. An explicit change can then be made.

The project has already had some impact among ecologists - witnessed by the following two examples. Perhaps more importantly, however, these two results, obtained immediately upon symbolization, will also serve to illustrate the values of formalization. First, the concept "weather" ((iv) above) had grouped together as one object a cluster of entities that had widely differing influences on the animal; difficulties with symbolization made it clear that this vague and unsatisfactory concept had to be resolved into discrete parcels of energy, water, etc. Secondly, I use a primitive term, 'H' to capture the notion of "an animal's chance to survive and reproduce" in defining the effect of an object on the subject animal (see §10.3 below). The changes in 'H' will fall into three classes: increased, unchanged, decreased. Furthermore, in one subset of cases the affecting object will be another animal which will also have "a chance to survive and reproduce", i.e. an 'H' of its own. By considering the permutations of the values of 'H', it was realized (see Niven 1980) that Andrewartha's definition of "malentity" was incomplete in that it did not include the case in which the affecting animal is also harmed (H decreased). When the discovery was made, purely by symbolic manipulation, that this category had to be included to complete the formalization an example within this apparently empty subclass was quickly found. Consider the case of an animal eating a poisonous fish, where both animal and fish suffer; clearly this accords with Andrewartha's original notion of malentity.

In addition to the above clarifications, the formalization has provided a synthesis of the ideas of Andrewartha and his colleagues with the extended notion of Maelzer's "modifiers", capturing the important idea that there are objects which only influence the animal indirectly.

Later work in the program has seen the definition of 'environment' incorporated in definitions of 'community' and 'ecosystem' (Niven, 1982). Only one new primitive term, 'habitat', is required. It is clear that a natural initial move by an ecologist who wishes to study an ecosystem is the detailed study of the environment of certain chosen animals. The infrastructure of the ecosystem, as defined, is a complex network built up from a knowledge of the relevant set of animals within the chosen habitat. We may start with any suitable animal and proceed step by step to the total community and hence to the ecosystem. These later definitions thus show precisely how population ecology and community ecology are linked.

2. THE INDIVIDUALS OF THE SYSTEM

In this study 'objects' are the familiar measurable objects of the physical sciences. They are material things and specific measured amounts of energy. An object is a lump of matter or a lump of energy.

'Temperature' is not an object. A specific measured amount of heat energy is. Examples of other objects are sticks, stones, plants, viruses, animals, humans, light energy, kinetic energy. Strictly, the energy objects should always be referred to as either potential or kinetic energy; in this study it seems more informative to refer to 'light energy', 'sound energy', 'gravitational energy' and so on.

Sometimes the use of the formal definitions leads to the consideration of objects which disappear from the system, or even objects which do not exist. Thus in the absence of kidney glue a stickleback nest cannot be made; it is not in the system, or it falls to pieces and ceases to be a proper nest. Informally, the definition of kidney glue as a second-order modifier (see §13 below and IV in the series) may be written:

$$(\exists\ \text{nest})[(\xi\ \text{glue nest} \supset \text{nest Mod stickleback})\ \&\ (\sim \xi\ \text{glue nest} \supset \sim \text{nest Mod stickleback})]$$

Since only the classification of an animal's environment is dealt with in this study objects which seem to be of little importance in the ecology of the animal are given the same weight as objects of obviously great importance. The field ecologist using an envirogram as a tool may well wish to attach numbers to some of these objects. Thus the cane toad (VII) seldom strikes at, and eats, such objects as strychnine flowers or ping-pong balls, but often eats insects; numbers attached to the names of these objects on the envirogram may be of value here; there is nothing to militate against the use of the envirogram in this way. Nevertheless there is nothing in the classification itself to tell us that an insect is 'more important' to the toad than a ping-pong ball, just as, in the Linnaean taxonomic system there is nothing to indicate that a beetle is 'more important' than a frog.

3. THE FORMAL DEFINITION OF THE ENVIRONMENT

The definition given in this section is that of Niven (1982), with two minor amendments. It is an improved version of the Niven (1980) definition.

Note that the conditional '$\supset$' should be read as given in §4 below.

The environment of animal a at time t, $E_t a$ is as follows:

Centrum, $C_t a$

$$r_i \mathrm{Res}_t a = {}_{\mathrm{Df}} \xi_t r_i a \supset \left[\{H_t(a) > H_{t-\alpha}(a)\} \;\&\; \{\mathrm{An}(r_i) \supset H_t(r_i) \leqq H_{t-\gamma}(r_i)\} \right],$$

$$m\ \mathrm{Mat}_t a = {}_{\mathrm{Df}} \xi_i m a \supset \mathrm{Prob}\{(\exists x)\ (x\ \mathrm{Off}_{t+\beta} a \;\&\; x\ \mathrm{Off}_{t+\beta} m)\} > 0,$$

$$p\ \mathrm{Pred}_t a = {}_{\mathrm{Df}} \xi_t\ p a \supset \left[\{H_t(a) < H_{t-\alpha}\ (a)\} \;\&\; \{H_t(p) \geqq H_{t-\gamma}(p)\} \right],$$

$$c\ \mathrm{Mal}_t a = {}_{\mathrm{Df}} \xi_t c a \supset \left[\{H_t(a) < H_{t-\alpha}(a)\} \;\&\; \{\mathrm{An}(c) \supset H_t(c) \leqq H_{t-\gamma}(c)\} \right]$$

Web, $W_t a$

$$w\ \mathrm{Mod}_t^{\circ} a \text{ iff } w \in C_t a$$

$$\begin{aligned} w\ \mathrm{Mod}_t^{n+1} a = {}_{\mathrm{Df}}\ (\exists x) \Big[& \{[(\xi_t w x V \xi_t w_y) \supset x\ \mathrm{Mod}_t^n a] \;\&\; [(\sim\xi_t w x V \sim\xi_t w_y) \supset \sim x \mathrm{Mod}_t^n a]\} \\ & V\{[(\sim\xi_t w x V \sim\xi_t w y) \supset x\ \mathrm{Mod}_t^n a] \;\&\; [(\xi_t w x V \xi_t w y) \supset \sim x\ \mathrm{Mod}_t^n a]\} \Big] \end{aligned}$$

n = 0,1,2, ---; y is either a or a modifier of order $\leqq (n-1)$.

Environment, $E_t a$

$$E_t a = {}_{\mathrm{Df}}\ C_t a \cup W_t a$$

List of Symbols

Logical, set theoretic and mathematical:

$>$	Greater than.
$<$	Less than.
$\leqq$	Less than or equal to.
$=_{Df}$	Definition. Read '$x =_{Df} y$' as "x is interchangeable with y" or "x is equal by definition to y".
$\sim$	Negation. Read '$\sim A$' as "not A" or "A does not occur".
$\cup$	Union. '$A \cup B$' is the set of all objects belonging to either A or B (or both).
&	Conjunction. Read 'A & B' as "A and B".
V	Disjunction. Read 'A V B' as "either A or B (or both)".
$\supset$	The conditional. Read '$A \supset B$' as "If A then B".
$\exists$	The existential quantifier. Read '$(\exists x)$' as "There exists an x (such that) ...", or "There is at least one x (such that) ..."

4. THE CONDITIONAL IN THE DEFINING EQUATIONS

The use of the conditional 'If ξ object animal then ---' in the definitions of centrum and web obviates the use of a probability statement. A malentity, for example, could be defined in terms of conditional probabilities as follows:

$$c \text{ Mal}_t a =_{Df} \text{Prob}\left[\{(H_t(a) > H_{t-\alpha}(a)) \,\middle|\, \xi_t ca\} \& \{(H_t(c) \leqq H_{t-\alpha}(c)) \,\middle|\, \xi_t ca\}\right] \geqq k$$

where $0 \leqq k \leqq 1$. $A|B$ should be read 'event A occurs given that event B occurs'. However, it is usually the case that k cannot be estimated; even if it could there would be difficulty in assigning a sensible numerical value to this probability. The case $k = 1$ is perhaps the obvious one to choose; thus immediately the statement becomes deterministic. It seems preferable, for the moment anyway, to use the simpler deterministic form as given in §3.

The symbol '$\supset$' is used with the understanding that the sentence is true and that the scientifically vacuous case of antecedent false and consequent true is disregarded (much as pure imaginary terms are disregarded when complex number theory is used in an application). A possible alternative here is to use the '>' of Daniels and Freeman (1980). These authors introduce the notion of tacit assumptions made by a speaker uttering a conditional; the conjunction of all such assumptions is represented by 'R'. Then '(RP)>Q' is read 'If it were the case that P, then it would be the case that Q'. The ideas of Daniels and Freeman seem to be relevant to the case that the speaker is an animal ecologist. If the subject animal is, say, a particular bottlenose dolphin, then 'R' is the conjunction of both a large set of propositions concerning the habitat, physiology, anatomy, biochemistry and so on of that particular dolphin and a large set of propositions concerning background information about the particular fish, say, which we ask should be classified as a resource. All these propositions need not concern the ecologist in a direct sense, but are borne in mind by the environmental taxonomist in precisely the sense used by these authors. In the scientific literature about the dolphin, for instance, it is often not even mentioned that the animal swims in the sea; after all, we all know this.

5. SYMMETRY, REFLEXIVITY, TRANSITIVITY AND CONNECTIVITY

5.1 Symmetric relations among the animals of the system

A relation is said to be symmetric if it holds in both directions. Thus 'Mate' is symmetric because, according to the formal definition given in §3 above if animal 'a' is a mate of animal 'b' then it follows that animal 'b' is a mate of 'a'. The relations 'Resource', 'Predator' and 'Malentity' are non-symmetric; if 'a' is a resource of 'b' then 'b' cannot be a resource of 'a' because $H_t(b)$ cannot be both (greater than $H_{t-\alpha}(b)$) and (less than or equal to $H_{t-\alpha}(b)$). This would be a logical contradiction which would occur also for 'Predator' and 'Malentity'.

The relation 'centrum' is often factually symmetric in a particular case. For example, the honeybee appears in the centrum of the cane toad as a resource (VII, n. 41), so the cane toad is in the centrum of the honeybee as a predator. This situation is common. However, it is not logically necessary that 'centrum' be symmetric. For instance, feral goats are in the centrum of the Giant African snail as malentities (IX, n. 33), however the snail would not appear in the centrum of a feral goat, since the encounter is essentially an accidental hazard and the goat is normally unaffected. Nevertheless, the snail is probably a modifier in the goat's environment; the relation 'environment' is almost certainly always factually symmetric if high order modifiers are taken into account.

5.2 Reflexive relations among the animals of the system

Among certain animals self-mating is possible or may be the norm as for the Wandering snail (VIII) or the tapeworm (XXIV) or may be obligatory, as for the New Mexico whiptail lizard (*Cnemidophorus neomexicanus*) (not included in this study) which has exclusively females (Mittwoch, 1978). No contradiction occurs when 'm' is replaced by 'a' in the symbolic definition of 'Mate' given in §3 above; the relation is reflexive. Relations 'Resource', 'Predator' and 'Malentity' are not reflexive; an animal may not (logically) be a resource, predator or malentity of itself. However in a vacuous sense an animal is always a modifier in its own environment; there is no logical contradiction here.

5.3 Transitive relations among the animals of the system

The relation 'modifier' is transitive because if animal 'a' is a modifier of animal 'b' and 'b' of animal 'c' then 'a' is a modifier of 'c'. The relation 'Predator' is often factually transitive, but it is not logically so. 'Mate' is non-transitive. In rare cases 'Malentity' may be factually transitive. 'Centrum' is not logically transitive but 'environment' is almost certainly factually so, providing high order modifiers are used.

5.4 Connected relations among the objects of the system

A relation is connected if any two elements are comparable. We may say that a high order modifier is 'further from' the subject animal than a low order modifier. In this sense the two objects are connected.

6. THE TREATMENT OF TIME

The real environment of an animal changes from instant to instant. This is represented in the formal definition by the use of the sub-index 't'; the environment is defined to be a function of time. Thus objects may appear or disappear from the formalized environment, depending on the numerical value of t. For instance, if the envirograms for a female chimpanzee are drawn up at regular intervals adult male chimpanzees will suddenly appear on the envirogram when the subject animal moves into oestrous; they will as suddenly disappear from the envirogram as she moves out of oestrous. Similarly, in later developments of the theory, changes in time occur in the niche, community and ecosystem; all of these are dynamic since all their theoretical bases are the notion of the formalized environment.

Kitching (1977) discusses time as a resource (XIII, n. 7). There are good reasons for doing this, however a more complex logical basis would be required to handle time in Kitching's sense.

7. ANIMALS INCLUDED IN THE STUDY

Twenty-five animals are included in this study. The complete list is given in the Appendix to this Working Paper. There are:

Five lower invertebrates: sponge, coral, sea gooseberry, tapeworm, earthworm.
Six arthropods: waterflea, copepod, butterfly, mosquito, blowfly, honeybee.
Five higher invertebrates: aquatic snail, terrestrial snail, octopus, squid, brachiopod.

Nine vertebrates: Two anurans: frog, toad.
Fish: stickleback.
Two birds: Fulmar, penguin.
Aquatic mammal: bottlenose dolphin.
Marsupial: quokka.
Two primates: chimpanzee, gorilla.

Animals were chosen not only because they were well known but because the documentation was easily available. A number of pairs were included for comparative purposes later in the work - two snails etc. Strenuous efforts were made to include a rotifer in the study, thus filling the gap in the phyla from Platyhelminth to Annelid. Unfortunately the literature on well-known rotifers was not readily available so the gap remains. Altogether, the literature on 58 well-known animals was examined; 33 were rejected for various reasons, often on the advice of colleagues in Australia and overseas.

8. THE PLACE OF HUMANS IN THE SYSTEM

It was difficult to classify humans in many of the animal studies. This was because the interpretation of the primitive term 'H' is limited to expectation of life and probability of reproduction (see §10.3 below). To ignore the sense of well-being that a human collector of animals may experience when the desired animal is caught does not seem to be very satisfactory; but should such humans be classified as predators - or malentities? Furthermore, if one is using a human as subject animal, the subject's perception of the objects in the neighbourhood is (unlike other animals) easily communicated; should one ignore this perception? While it may be true that a chimpanzee, or a sponge, perceives the universe, we do not know exactly what the non-human animal thinks about things, or even if they can be said to 'think'. One may argue that animal behaviour can be interpreted and that this interpretation can, and should, be used in the classification of that animal's environment. However, in the human case we know of gross errors of interpretation by anthropologists of the social interactions of primitive peoples - if we can make such mistakes with members of our own species are we not likely to make massive blunders in our interpretation of animal behaviour?

For these reasons it was decided to exclude humans from this particular study. An extension to the basic logical system has been made for humans as the 'subject animals' of further study. Briefly, an extra primitive term has been added to take account of our species' perception of the world. This has resulted in a large increase in the size of the centrum. The definition of the web has, to date, been used unchanged.

9. AN ANIMAL'S HABITAT

The habitat of an animal is the place where the animal lives. The word 'Habitat' is used as a primitive term in later developments of the formalized theory of ecology. It does not appear in the definition of the environment.

When drawing envirograms in this study, it was sometimes convenient to limit the objects to those observed in a relatively small area. For instance, the discussion of the stickleback environment is largely limited to the Wirral Peninsula (IV). Nevertheless, the conditional form of the definitions enables use to be made of the entire planet as a habitat. Thus, if an adult stickleback is in the correct juxtaposition in any habitat or place whatsoever to a waterflea (*Daphnia magna*) the waterflea is likely to be eaten; *D. magna* is defined as a resource no matter where in the real world the observations are made.

10. THE PRIMITIVE TERMS

Four primitive terms special to the theory of ecology appear in the formal definition of the environment (§3 above). They are:

An
Off
H
ξ

10.1 The primitive term 'An'.

'An(x)' is used to mean that x is an animal in a more limited sense than is usual among zoologists. x may belong to any of the animal phyla ranging from the Porifera to the Vertebrates, but excluding humans.

Humans are specifically excluded because of difficulties experienced in this study (§8 above). Apart from a few rare occasions it is quite clear in the field or laboratory what precisely is meant by 'the animal' of the study. Two examples in which it may not be immediately clear are the sponge (XIV) and coral (XXIII). However, when the literature is examined it soon becomes apparent that the whole mass of sponge and the entire colony of coral are the objects of interest to zoologists working in these fields; their preferences are followed in the relevant Working Papers. In the case of the sponge some detail is given in the Introductory Note regarding a possible choice of a choanocyte (collar cell) as the 'animal'. However, in both cases the necessary literature is not available for providing sufficient information to draw up envirograms for choanocyte or coral polyp.

In this series of Working Papers the organism of main interest is in all cases assumed to be an animal. All life stages of an animal are used; thus 'egg' or 'larva' may be the subject animal of the envirogram and 'second-instar larva' would have been used in a case for which the relevant information was available.

10.2 The primitive term 'Off'.

By 'x Off_ty' is meant "x is an offspring of y at time t (for the first time)". 'Off' may be interpreted as an egg (e.g. in the case of the Fulmar, XXII), pouch young (as for the quokka, XII) or larval or pupal forms, as well as offspring in the sense of everyday English.

The young of an animal do not appear as a separate class in the centrum. Young animals may compete with their parents for food, thus acting as first-order modifiers of resources. A young mammal taking milk from its mother does not appear in the centrum of the mother; the mother is a first-order modifier in the environment of the suckling; the milk is a resource.

10.3 The primitive term 'H'.

'$H_t(x)$' is a positive real number which is a non-decreasing function of:

(i) the expectation of life of x at birth or on entering its present stage of the life cycle, and

(ii) the probability that x will have an offspring.

It is assumed that it is possible to estimate (i) and (ii). This has been done for humans. Life expectation and fecundity have also been estimated for some other animals: see for example Caughley (1966) for mammals and Mertz *et al* (1965) and Park *et al* (1961) for the *Tribolium* beetle.

'H' should not be confused with "Darwinian fitness" - a totally different concept. However 'Darwinian fitness' is interpreted, it certainly involves a notion of more than one generation. The primitive term 'H', however, refers to one generation only and may well be limited quite severely to a local population only. For instance H(stickleback) (IV) in the habitat of the Wirral Peninsula differs markedly from H(stickleback) in many other regions. On the Wirral Peninsula, in the Birket River, the stickleback can live up to four years and it does not breed until into its second year; in other regions the life span is shorter and the age of maturity is less.

Humans who are collectors for zoos may well perceive their work as giving them pleasure and therefore increasing their 'H' - but see §8 above.

In the case of disease-causing organisms it is often convenient to use a loose interpretation of 'H'. This has been done in a number of these studies; it is assumed that H(organism) increases if the organism benefits from the encounter and *vice versa*. Thus 'non-animals' in the sense of §10.1 are often classified as falling within the centrum of an animal (see also §11.3 below).

10.4 The primitive term 'ξ'.

By '$\xi_t xy$' we mean that object x is brought into close physical proximity with object y at time t, evoking immediately in y some physical, physiological or behavioural response or a change of position in space, and that no other object reduces or enhances this effect of x on y, i.e. that x affects y directly. The sub-index "t" is replaced by "τ" when the action takes place during an interval of time τ. Judgement as to whether or not a (significant) response occurs is made by the ecologist, thus certain actions of the animal of interest would normally be ignored. For example, if the animal gazes at some object, this is a response of the animal to the presence of the object and doubtless some sort of physiological or biochemical process is evoked; however, normally an action of this type would be regarded by the ecologist as trivial and ignored. Also the "closeness" of x and y will depend on the situation. Among mammals contact is normally necessary for procreation. This is not necessary among fishes. Nor indeed is it necessary when a farmer uses artificial insemination to improve his livestock.

The requirement that the response be immediate is sometimes important e.g. when dealing with sex change in the male cane toad (VII, n. 45). A male toad which will at some future time change its sex cannot be classified as a mate of a male subject animal; it can be so classified only at that time in the future when the change is completed. Similarly a food object might be nutritious immediately but poisonous in the long run; however the most satisfactory way of handling this difficulty is to refer to the poisonous component as a separate object.

11. THE CENTRUM

The centrum is the set of objects which, if placed in the correct juxtaposition, affect the animal directly. There are four subsets:

Resources
Mates
Predators
Malentities

The inverse of a predator is usually a resource i.e. if object 'a' is a predator of object 'b' then 'b' is a resource of 'a'. However a vertebrate 'a' which eats a cane toad 'b' is likely to die, or at least fall ill (VII, n. 1); in this case 'b' is a malentity of 'a'. In the case of certain spiders (not dealt with in this series) the female 'a' is simultaneously a predator and a mate of the male 'b'; 'b' is simultaneously both resource and mate of 'a'.

11.1 Resources

A resource is an object in the environment of the subject animal which, as a result of a direct interaction, is of benefit to the animal (in the exact sense of §10.3) but is itself either unaffected or adversely affected. There are two main classes of resources: food and energy. Other objects which may be resources are gases (oxygen being the most important one) water and other liquids. Sometimes the place in which the animal lives should clearly be classified as a resource e.g. in the case of the Fulmar 'suitable nesting site' has been so classified (XXII, n. 4) since only certain restricted places are suitable otherwise the bird will not breed, thus H(Fulmar) will not be increased. A less usual kind of resource is the intermediate host of the tapeworm (XXIV, n. 7); the arthropod mechanically ruptures the outer capsule of the tapeworm larva thus increasing H(larva) while H(arthropod) is, as far as we know, unchanged. The intermediate host has not been classified as a 'place-to-live' kind of resource; further information on this point would be useful.

Confusion often arises when considering 'heat energy' in the environment. Because temperature is easy to measure, apparently on a continuous scale, one tends to forget that at a particular time only one particular 'lump' of heat energy is interacting with the subject animal. This one particular object may damage or kill the animal, in which case it is classified as a malentity, or it may increase H(animal) in which case it is classified as a resource. It seems possible that there may be a third case; for the sheep blowfly (XIII, n. 13) it seems that there is a range of temperature in which the animal does not breed but is not distressed - if this is so then such a particular 'lump' of heat energy is neither a resource nor a malentity - it is not in the centrum. Since energy is inanimate the second part of the definition need not be considered; an energy object does not have an 'H'.

Another object which may seem difficult to classify is a lump of poisoned food. Confusion is avoided if the constituents are treated separately - the protein (say) as a resource, the poison as a malentity (see also §10.4 above).

Shelter is nearly always a modifier of some element of the centrum. An animal may thrive when in shelter; this is invariably not a direct effect but the result of being sheltered from predators or malentities.

11.2 Mates

The definition of a mate is that it is an object which is such that the interaction with the subject animal will result in an offspring of subject animal and mate appearing in the system with probability greater than zero. Thus a mate is usually either an adult animal of the same species but opposite sex, or, in the case of hermaphrodites (see earthworm, XVI) simply another adult. In rarer cases the animal may be habitually self-mating (see tapeworm, XXIV) in which case the mate is the subject animal itself (§5.2 above).

In all cases dealt with in this study, the mate has been an animal. Nevertheless the definition is such that an esoteric gamete-producing machine would also be classed as a mate.

In the case of artificially produced parthenogenesis the instrument used to activate the ovum is a first-order modifier of the subject animal, which is then a mate of itself.

11.3 Predators

According to the formal definition a predator of an animal is necessarily itself an animal. Thus on the one hand humans and on the other such organisms as bacteria, rickettsia and fungi are eliminated from this class. However it is often convenient to include humans on the envirogram when they eat the animal e.g. in the case of the bottlenose dolphin (XI, n. 14). H(human) should be interpreted precisely as H(animal) i.e. a function of expectation of life and probability of reproduction. But in the case that dolphin leather is used (to make harness) this interpretation of H(human) is unsatisfactory (see §8 above) and H should be replaced by the 'well-being primitive, W' appropriate for humans (Niven, 1984). Thus, speaking formally, in the latter case the object 'human' is a 'perceived predator' and not a 'predator'. The cases of protista and plants are much more difficult. It has seemed sensible e.g. on the envirogram for the honebee (XXV) to list the disease-causing organisms as predators, even though a precise interpretation of 'H' is not available. In these cases, one is forced to use the rather vague notion that H(organism) increases if the organism is benefited by the interaction and decreases if the organism is adversely affected. Clarification of this point awaits further work on the formalization of theories of plant and protist ecology.

Modifier chains are often chains of predators. For example the leech *Glossiphonia* is a predator of the Wandering Snail (VIII); in turn mallard ducks are predators of the leech (and humans predators of the ducks, if we are willing to use H(human) here).

11.4 Malentities

The word 'malentity' was introduced into the ecology literature by H.G. Andrewartha in 1971. The original notion of an object in the environment which harmed the subject animal more-or-less by accident was suggested by Browning (1963) who called such an object a 'hazard'. However Browning's hazards were inanimate; Andrewartha's malentities were not necessarily so. Andrewartha insisted, at that time, that the malentity was itself undamaged by the encounter with the subject animal, however an early result of the symbolization revealed a gap in the conceptual environment (see §1 above), which led to the present extension of the notion of a malentity to include poisonous organisms which may be accidentally eaten by the subject animal (see cane toad, VII).

In many of the twenty-five animal studies 'collectors for zoos' are classified as malentities, because of the initial shock to the animal. However captive animals often live rather well; it could be argued that a collector acts as a first-order modifier of resources and mates (see also §8, §11.3).

Just as disease-causing organisms have been added to the envirograms as predators by using a loose interpretation of 'H', so this has sometimes been done for malentities e.g. the insectivorous bladderwort which accidently 'eats' cane toad tadpoles; the tadpole dies but is not of any benefit to the bladderwort, which either is unaffected by the encounter or suffers (the literature is not clear on this point) (see cane toad, VII, n. 21 on the tadpole envirogram).

The case of heat energy is discussed in §11.1.

12. THE WEB

The web is the set of modifiers defined by the infinite set of defining equations in §3 above. Maelzer (1965) observed that certain objects in the vicinity of an animal 'only modified the value of some resource or other component of environment'. Thus, a member of the centrum may be changed in some way or its availability to the subject animal may be influenced by another object. For example, a certain quantity of calcium may have no effect on an animal unless it (the calcium) is in the presence of (a certain quantity of) vitamin D - in this case the vitamin D will be a 'Maelzer Modifier' and the calcium will only become a component of the observed environment if the vitamin D is present. In turn a modifier of this first order may itself be modified (changed or made available) and so on.

The two disjuncts in the definition of the (n+1)th-order modifier may be termed 'positive' and 'negative' modifiers. A positive modifier appears in the observed (real) environment if the event symbolized by 'ξ' takes place; it is absent from the environment if the event does not occur. Thus honey becomes a resource in the environment of the queen bee if a worker provides her with the honey but if the worker does not provide honey then it is no longer available as a food-resource (see honeybee, XXV). A negative modifier appears in the observed environment if the event symbolized by 'ξ' does not take place, and *vice versa*. Thus if an animal is under shelter a malentity or predator may disappear from the observed environment.

Although modifiers are defined using only one equation we should indicate that they have a variable character. Some modifiers contribute to the animal's welfare while others detract from it. In addition, some modifiers will be necessary e.g. the vitamin D example referred to above, while others will be merely contingent e.g. in the envirogram for an adult male stickleback (III, n. 26) the parasite *Schistocephalus solidus* increases the probability that the stickleback will be taken by a fish-eating bird, but in the absence of the parasite the bird still appears as a predator. These characteristics of modifiers can apply at any stage during a chain e.g. on the same envirogram the mate, 'adult-female-distended-by-parasite' will appear only if the parasite appears as a modifier of the next highest order; this is another case of a necessary modifier.

In future work it may become necessary to incorporate the possibility of replacing an individual object which is a modifier by a set of objects. For instance in the study of the tapeworm (XXIV) a rat has been classified as a first-order modifier of a mouse-predator, the argument being (informally):

$$(\exists\ \text{mouse})\ [(\sim\xi_t \text{rat tapeworm} \supset \text{mouse is predator})\ \&\ (\xi_t \text{rat tapeworm} \supset \text{mouse is not predator})].$$

It would seem more sensible to replace 'rat' by a set of definitive hosts; one possibility is that the modifier w (rat above) should be the set {w:w is a definitive host other than a rat}.

Some objects appear to act as first-order modifiers of a very large set of objects in the centrum. For example, it is established that rain increases the activity of the frog *Rana pipiens* (X). Thus, extra food-resources become available to the animal; it is more likely to meet a mate; it is more likely to encounter certain predators and malentities.

According to the formal definition we may classify objects as modifiers of order as high as we please. In practice field ecologists do not usually work with modifiers of order higher than 5 and in many instances second- or even first-order modifiers are sufficient. In the case of lesser known animals, such as the Sea Gooseberry (XV) even work on first-order modifiers (and objects in the centrum) is sparse.

The structure of the modifier chains is of theoretical interest for the future mathematical development of ecology theory. There seem to be four main types:

(i) The chain continues indefinitely.

(ii) It ends in the sun. One could doubtless proceed to list modifiers of the sun, but this seems pointless at the present time.

(iii) After passing through several objects the chain loops back to the subject animal e.g. in the cane toad study (VII) there is a chain 'toad-fowl-eyeworm-cockroach-toad'.

(iv) The chain loops back to the subject animal almost immediately in that the animal itself is a first-order modifier in its own environment. An interesting example is the twin loop in the frog study (X) in which the animal, by making precisely the same movement, modifies both a resource (oxygen) and its predators (fish).

An interesting pattern appeared in a modifier chain for the butterfly (XIX).: 'a-b-a-b' where 'a' was the subject animal and 'b' a mate. In the case that the subject animal is an adult female which has oestrous periods, e.g. the chimpanzee (I) the modifier chains attached to the mates appear and disappear from the environment as the subject animal goes into, and out of, oestrous.

An object which adversely affects a possible mate of the subject animal by, say, upsetting its breeding ability is classified as a first-order modifier of the mate; such an object is likely to be also a malentity of the subject animal. Similarly an object which contributes to the mating ability of a suitable mate is likely also to be a resource of the subject animal. An object such as a quantity of juvenile hormone which prevents an animal from maturing is acting as a first-order modifier of a (potential) mate.

Symbionts are usually first-order modifiers in each others environments; sometimes one animal provides shelter and is thus a second-order modifier of predators and malentities; the other animal provides food and is thus a first-order modifier of a resource.

13. THE ENVIROGRAM

The realization of the formal definition of the environment is called an 'envirogram', a term due to H.G. Andrewartha, who drew up the first of these diagrams (for a rabbit) in 1978, using the definition published by Niven (1980). Each envirogram contains:

(i) A Centrum (of four parts - corresponding to the formal definitions of Resources, Mates, Predators and Malentities), being those objects that directly affect the subject animal;

(ii) A Web of 'Modifiers' of successively higher orders (again, corresponding to the definition).

The connections between objects belonging to the centrum and successively higher order modifiers are marked on the envirogram by arrows all pointing in the direction of the subject animal. A series of objects which are connected in this way is called a 'chain' or a 'modifier chain'. It is convenient to think of a modifier chain as 'acting on' the subject animal; one may use the term 'ecological action' here, not necessarily implying passage through time (although of course the system is a dynamic one) but rather some sort of influence aimed at the subject animal. Successive objects in a chain are not necessarily linked by causation in an obvious sense; they are simply placed there by virtue of the definitions of §3.

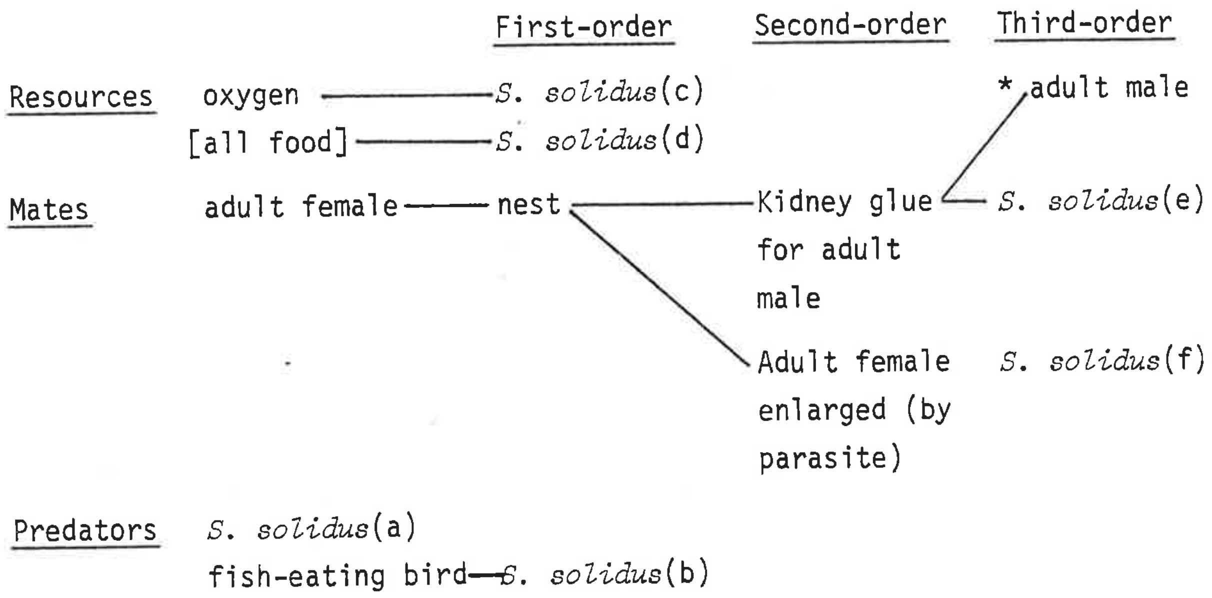
While the definitions provide a framework for an absolutely precise realization, the data available on any one animal is never complete. However the envirogram shows at a glance where extra work need be done. Although the definitions are written for a specific animal, in practice each envirogram is a concatenation of many partial realizations. Nevertheless, nothing precludes the drawing up of a <u>specific</u> envirogram in the course of field work.

Apart from its more theoretical uses an envirogram is useful in itself, more so than a review, e.g. (i) it can be easily projected as a teaching aid and (ii) the technique lends itself to convenient comparison of the environment of two or more species.

Each time an animal appears in an envirogram the whole envirogram for this new animal is generated, with the centrum of the new animal appearing as a modifier of the next highest order and so on. In practice we do not usually do this, but it is sometimes convenient to show a part of the new envirogram e.g. on the envirogram for a stickleback egg (III, see the upper chain on predators).

Any particular object may appear in more than one way in the environment of an animal. A simple example is an apple in the environment of a caterpillar living in and feeding on the apple. The apple provides food and is thus classified as a resource in the environment of the animal; it also protects the caterpillar from various malentities and predators, thus being classified also as a first order modifier. An extreme example of this kind of multiple classification is the case of the flatworm *Schistocephalus solidus* in the environment of the three-spined stickleback *Gasterosteus aculeatus* leiurus. The parasite appears six times in the envirogram (see a-f below), once in the centrum, three times as a first-order modifier and twice as a third-order modifier (see also III).

The occurrence of *S. solidus* in the envirogram of the stickleback



These six occurrences are formally justified in the following manner:

(a) In the environment of an adult stickleback, a, *S. solidus*, p, is a predator, since the stickleback will become sick or die directly from the infestation (strictly we need many animals to achieve death). Thus, the definition holds:

$$\text{p Pred } a =_{\text{Df}} \xi_t pa \supset \left[\{H_t(a)<H_{t-\alpha}(a)\} \;\&\; \{H_t(p)>H_{t-\gamma}(p)\}\right]$$

(b) In this case the predator of *a* is a fish-eating bird x. A stickleback, *a*, infected by *S. solidus*, w, will swim higher in the water than it would otherwise and thus becomes easier prey for x. So x is in the centrum; for convenience, a modifier of degree zero. The first part of the definition of a first-order modifier holds here:

$$w\ \mathrm{Mod}_t^1\ a =_{\mathrm{Df}} (\exists x)\left[(\xi_t w a \supset x\ \mathrm{Mod}_t^0\ a)\ \&\ ({\sim}\xi_t w a \supset {\sim}x\ \mathrm{Mod}_t^0 a)\right]$$

(c) In this case the resource of the adult stickleback is a quantity of oxygen which is extra to its normal consumption. Thus if the stickleback, *a*, is infected by *S. solidus*, w, w's oxygen consumption, x, is a parasitic burden on *a* at time t. So, formally, w is acting as a first-order modifier for *a* in precisely the same sense as in (b) - though modifying a resource, not a predator:

$$w_0\ \mathrm{Mod}_t^1\ a =_{\mathrm{Df}} (\exists x)\left[(\xi_t w a \supset x\ \mathrm{Mod}_t^0 a)\ \&\ ({\sim}\xi_t w a \supset {\sim}x\ \mathrm{Mod}_t^0 a)\right]$$

(d) This case is exactly analogous to (c). Only the affected resource changes, with the parasitic burden, x, placed on food rather than oxygen.

(e) According to Wootton (1976) it is possible that *S. solidus* affects the production of nest glue by the male stickleback. Here we have assumed that this effect is well established. In this case the parasite, w_3, is a third-order modifier in the environment of *a*, where *a* now is an adult <u>male</u> stickleback. The adult female, w_0, is a mate of *a*:

$$w_0\ \mathrm{Mat}_t a =_{\mathrm{Df}} \xi_t w_0 a \supset \mathrm{Prob}\{(\exists x)\ (x\ \mathrm{Off}_{t+\beta} a\ \&\ x\mathrm{Off}_{t+\beta} w_0)\} > 0,$$

where time t+β will be any time after fertilization - that is after w_0 and *a* have been in the appropriate physical circumstances.

The nest, w_1, is a first-order modifier of *a*, since without a nest *a* will not attract a mate. If we write 'x' for the female adult w_0, then:

$$w_1\ \mathrm{Mod}_t^1 a =_{\mathrm{Df}} (\exists x)\left[(\xi_t w_1 a \supset x\ \mathrm{Mod}_t^0 a)\ \&\ ({\sim}\xi_t w_1 a \supset {\sim}x\ \mathrm{Mod}_t^1 a)\right|.$$

The kidney glue, w_2, manufactured by the adult male, is necessary to hold the nest, w_1, together. The definition here, writing 'x' for the nest w_1, is:

$$w_2 \ \mathrm{Mod}^2_t a =_{\mathrm{Df}} (\exists x)\left[(\xi_t w_2 x \supset x \ \mathrm{Mod}^1_t a) \ \& \ ({\sim}\xi_t w_2 x \supset {\sim}x \ \mathrm{Mod}^1_t a)\right].$$

In this case, in the second item of the definiens, the nest disappears not only from the environment of the adult male stickleback, but totally; it ceases to exist as an object. Without glue there cannot be a nest, only a jumble of vegetation. The presence of *S. solidus*, w_3, prevents the kidney glue, w_2, from appearing in the environment of a. So when *S. solidus* is present in this particular sense there is no kidney glue: the formal statement now depends on the second part of the definition of a modifier. If we write 'x' for the kidney glue, w_2, then:

$$w_3 \ \mathrm{Mod}^3_t a =_{\mathrm{Df}} (\exists x)\left[({\sim}\xi_t w_3 a \supset x \ \mathrm{Mod}^2_t a) \ \& \ (\xi_t w_3 a \supset {\sim}x \ \mathrm{Mod}^2_t a)\right].$$

Notice that the adult male appears in the environment also as a third-order modifier in his own environment (see * on the diagram above), since he manufactures the kidney glue.

(f) Finally, *S. solidus*, w'_3, is also a third-order modifier in the environment of the adult male a. With a severe infestation the female, w'_2, may break up the nest, w_1, while spawning (because of her increased bulk, see graphic in III). In the absence of w'_3 the usual minor damage will occur but devastation is very unlikely. Thus the definitions are:

(i) Adult female, w_0; a mate as in (e).

(ii) Nest, w_1; a first-order modifier as in (e).

(iii) Adult female (distended by parasite), w'_2; a second-order modifier; if we write 'x' for the nest w_1 then:

$$w'_2 \ \mathrm{Mod}^2_t a =_{\mathrm{Df}} (\exists x)\left[({\sim}\xi_t w'_2 x \supset x \ \mathrm{Mod}^1_t a) \ \& \ (\xi_t w'_2 x \supset {\sim}x \ \mathrm{Mod}^1_t a)\right].$$

(iv) *S. solidus*, w_3', is responsible for the enlargement of the female. If w_3' is not present then the object 'Adult female (distended by parasite), w_2', will also not appear in the envirogram of a. Thus if we write 'x' for the distended female w_2' the definition is:

$$w_3' \text{ Mod}_t^3 a =_{Df} (\exists x)\left[(\xi_t w_3' x \supset x \text{ Mod}_t^2 a) \;\&\; (\sim \xi_t w_3' x \supset \sim x \text{ Mod}_t^2 a)\right]$$

Animal behaviour is shown on the envirograms by the objects involved e.g. the mating behaviour of the butterfly (XIX) is represented on the adult envirogram by objects like 'other adult male' and 'subsequent mate' which are first-order modifiers of mates and on the chimpanzee envirogram a chain acting on 'termites' (a food resource) is:

hole-leafless twig-female adult-tree

which represents the training of offspring to use a twig as a tool for handling termites.

When drawing an envirogram it is usually necessary to collate information obtained over a considerable period of time and about different subject animals. An envirogram can be split, conceptually, into a large number of separate envirograms, each arising from the formal definition applied at an instant of time.

Envirograms are best constructed as the relevant information becomes available. In the paper on the Wandering Snail (VIII), the literature on calcium was the first to hand, so on the first rough sketch made for this animal's envirogram calcium (a resource) was the first entry and was the subject of the first note. As it happened note 1 for the cane toad (VII) is about the poisonous effect of the toad when eaten, so the first entry on this preliminary sketch was made under the heading 'malentities'. This method of drawing envirograms ensures that it is simple to enlarge (indefinitely) to accommodate new results.

If an envirogram is very sparse it has been superimposed on another envirogram to save space e.g. for the copepod (XVIII) the envirograms for larva and egg (they are both quite different) are superimposed on the adult envirogram by using {---} for objects on the larva envirogram and {{---}} for objects on the egg envirogram.

The notation [---] has been used to indicate a class of objects e.g. [food], implying all or some food, or [insects], implying all or several insects. Objects which have been provisionally classified have been bracketed thus (object); this is done when the information available is uncertain, sparse or unclear.

Only references which have actually been used for the classification are given; very often these are a subset of the literature consulted.

Acknowledgements

I have received useful comments during the planning of this study from H.G. Andrewartha, T.O. Browning, I.C. Hinckfuss, R.A. Girle and G.E. Minc. The Academic Librarian of the School, W.J. Lawson, was a tower of strength; without his help I do not think it would have been possible to tackle the mass of literature involved in such a short time. My Research Assistant, Mr M.G. Stewart contributed to the study with enthusiasm. Dr R.L. Kitching not only contributed much advice on many animals but also made available to me his collection of reprints on the sheep blowfly. Dr M.M. Bryden was equally helpful with reprints on the bottlenose dolphin and R. Floyd and S. Easteal on the cane toad. M.P. Zalucki gave me a preliminary version of his doctoral thesis on the Monarch Butterfly and provided many helpful comments. Professor Pierre Tardent wrote from Zurich that most of the *Hydra attenuata* mentioned in the extensive literature on this animal are asexual descendents of 4-5 specimens collected by him in the River Limmart; I replaced this animal, with many misgivings, by the coral *Pocillopora damicornis* (XXIII).

The bulk of the typing was done by Miss J. Davies. The envirograms for VII through XXVI were drawn by R.P. Blundell and C. Broad.

References:

Andrewartha, H.G. (1971). *Introduction to the Study of Animal Populations.* 2nd Edition. (Chapman and Hall).

Andrewartha, H.G. and L.C. Birch (1954). *The Distribution and Abundance of Animals.* (University of Chicago).

Browning, T.O. (1963). *Animal Populations.* (Hutchinson).

Caughley, G. (1966). Mortality patterns in mammals. *Ecology* 47, 906-918.

Daniels, C.B. and J.B. Freeman (1980). An analysis of the subjunctive conditional. *Notre Dame J. Form. Logic* 21(4), 639-655.

Kitching, R.L. (1977). Time, resources and population dynamics in insects. *Aust. J. Ecol.* 2, 31-42.

Maelzer, D.A. (1965). A discussion of components of environment in ecology. *J. theor. Biol.* 8, 141-162.

Mertz, David B., Thomas Park and W.J. Youden (1965). Mortality patterns in eight strains of flour beetles. *Biometrics* 21, 99-114.

Mittwoch, U. (1978). Parthenogenesis. *J. Med. Genetics* 15, 165-181.

Niven, B.S. (1980). The formal definition of the environment of an animal. *Aust. J. Ecology* 5, 37-46.

Niven, B.S. (1982). Formalization of the basic concepts of animal ecology. *Erkenntnis* 17, 307-320.

Niven, B.S. (1984). Formalization of the concept of the environment of a human being. (To be published).

Park, Thomas, D.B. Mertz and K. Petrusewicz (1961). Genetic strains of *Tribolium*: their primary characteristics. *Physiol. Zool.* 34, 62-87.

Wootton, R.J. (1976). *The biology of sticklebacks.* (Academic Press).

APPENDIX

The following Working Papers are available (private circulation) from School of Australian Environmental Studies, Griffith University, Nathan, Queensland, 4111, Australia.

The Precise Environment of Some Well-Known Animals

by B.S. Niven and M.G. Stewart (joined by J.C. Moore in Nos. X and XII; Nos. XV, XVII, XXIII, XXV, XXVI and XXVII by B.S. Niven only)

SERIES NO.	TITLE
I	General Introduction
II	The Chimpanzee *(Pan troglodytes)*
III	The mountain gorilla *(Gorilla gorilla beringei)*
IV	The three-spined stickleback *(Gasterosteus aculeatus* leiurus*)*
V	The King Penguin *(Aptenodytes patagonica)*
VI	The bottlenose dolphin *(Tursiops truncatus)*
VII	The Cane Toad *(Bufo marinus)*
VIII	The Wandering Snail *(Lymnaea peregra)*
IX	The Giant African Snail *(Achatina fulica)*
X	The Leopard Frog *(Rana pipiens)*
XI	The Common Octopus *(Octopus vulgaris)*
XII	The Rottnest quokka *(Setonix brachyurus)*
XIII	The Sheep Blowfly *(Lucilia cuprina)*
XIV	The fresh-water sponge *(Spongilla lacustris)*
XV	The Sea Gooseberry *(Pleurobrachia pileus)*
XVI	The earthworm *(Lumbricus terrestris)*
XVII	The waterflea *(Daphnia magna)*
XVIII	The marine copepod *(Calanus finmarchicus)*
XIX	The Monarch butterfly *(Danaus plexippus)*
XX	The Yellow-fever mosquito *(Aëdes aegypti)*
XXI	The Pacific Coast Squid *(Loligo opalescens)*
XXII	The Atlantic Fulmar *(Fulmarus glacialis glacialis)*
XXIII	The Reef Coral *(Pocillopora damicornis)*
XXIV	The Rat Tapeworm *(Hymenolepis diminuta)*
XXV	The Common Honeybee *(Apis mellifera)*
XXVI	The brachiopod *(Lingula anatina)*
XXVII	Revised version of General Introduction

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XIV THE FRESH-WATER SPONGE *(Spongilla lacustris)*

by

B.S. NIVEN and M.G. STEWART

AES WORKING PAPER 10/83

School of Australian Environmental Studies
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ABSTRACT

The precise environment of the Fresh-water sponge (*Spongilla lacustris*) is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A. INTRODUCTORY NOTE

Sponges are sessile multi-cellulates of only slightly differentiated form. True muscle and nerve cells are absent. Variations in cell form (and function) are present but no true organs are formed.

Spongilla lacustris is a fresh-water sponge with a world-wide distribution; however, most of the information presented in this Working Paper was taken from work done in North America. A characteristic North American annual cycle for *S. lacustris* is given briefly in note 20 - sexual reproduction in the spring following the germination of over-wintering gemmules, vegetative growth until late autumn, then colonial decay and gemmulation. However, there are localities where tissue production and gemmulation occur at all times of the year.

Throughout the United States *S. lacustris* occurs commonly in both lotic and lentic habitats. Characteristically, the animal takes one of two forms: (i) the 'green' form, the colour being caused by symbiotic intra-cellular zoochlorellae and (ii) the aposymbiont 'white' form. In addition, cases have been reported in which *S. lacustris* has formed symbiotic "colonies" with bryozoans.

"What counts as a sponge individual?" is, to the naive natural historian unaquainted with the formalized languages of scientific endeavour, a tantalizingly difficult question. There are many reasons for the difficulty, for example:

(i) body morphology and size vary drastically;

(ii) newly-settled larvae - and the largest adults - can fuse together in the course of vegetative growth (see n. 12); is the resultant mass a new individual?

(iii) gemmulation can be viewed alternatively as an adaptive over-wintering mechanism or as a means of asexual reproduction;

(iv) age and natural death is extremely hard to determine; what might be termed a sponge 'death due to old age' usually has the following sequence of events: the central part thins and holes appear but the edges continue to live until they break away; such edge pieces may re-establish elsewhere on the substrate;

(v) sponge cells in many respects maintain an almost protozoan independence; nevertheless the entire cell mass combines to pump sufficient water to effect all essential exchanges;

(vi) sponge cells show remarkable mobility and a general ability to differentiate and re-differentiate to fill various functional roles;

(vii) against the last two points, which might be used to argue that a sponge individual is a single cell: a functional sponge mechanically dislocated by rubbing through a sieve shows a remarkable ability to re-assemble itself. If such an operation is performed on several species mixed together the re-assemblages remain species specific.

There have been four major theories concerning the recognition of sponge individuals. The first two have been abandoned as serious alternatives while the fourth is coming increasingly into favour:

(a) An individual is a single cell;

(b) An individual is a choanocyte (collar cell);

(c) An individual is - {an osculum, the exhalent cells draining to it, and the sector of the inhalent surface and canal system which feeds the related choanocyte chambers};

(d) An individual is all the substance bounded by a continuous pinacoderm.

While in this paper we have adopted the fourth viewpoint the formalized system we use (see Niven, 1982) to generate an envirogram is sufficiently flexible to produce an envirogram consistent with each of the theories. For cases (b) and (c) this would, fairly trivially, only involve qualifying each entry with - per cohanyte chamber or per osculum.

An envirogram for theory 1 would be radically different. We attempted to assemble such an envirogram but the available information (of a type which would usually be classed as biochemistry or physiology) was too sparse. However, to illustrate briefly, consider the following:

Let us take as our individual an archaeocyte cell in the mesohyl:

(i) It would be responsible for obtaining its own oxygen;

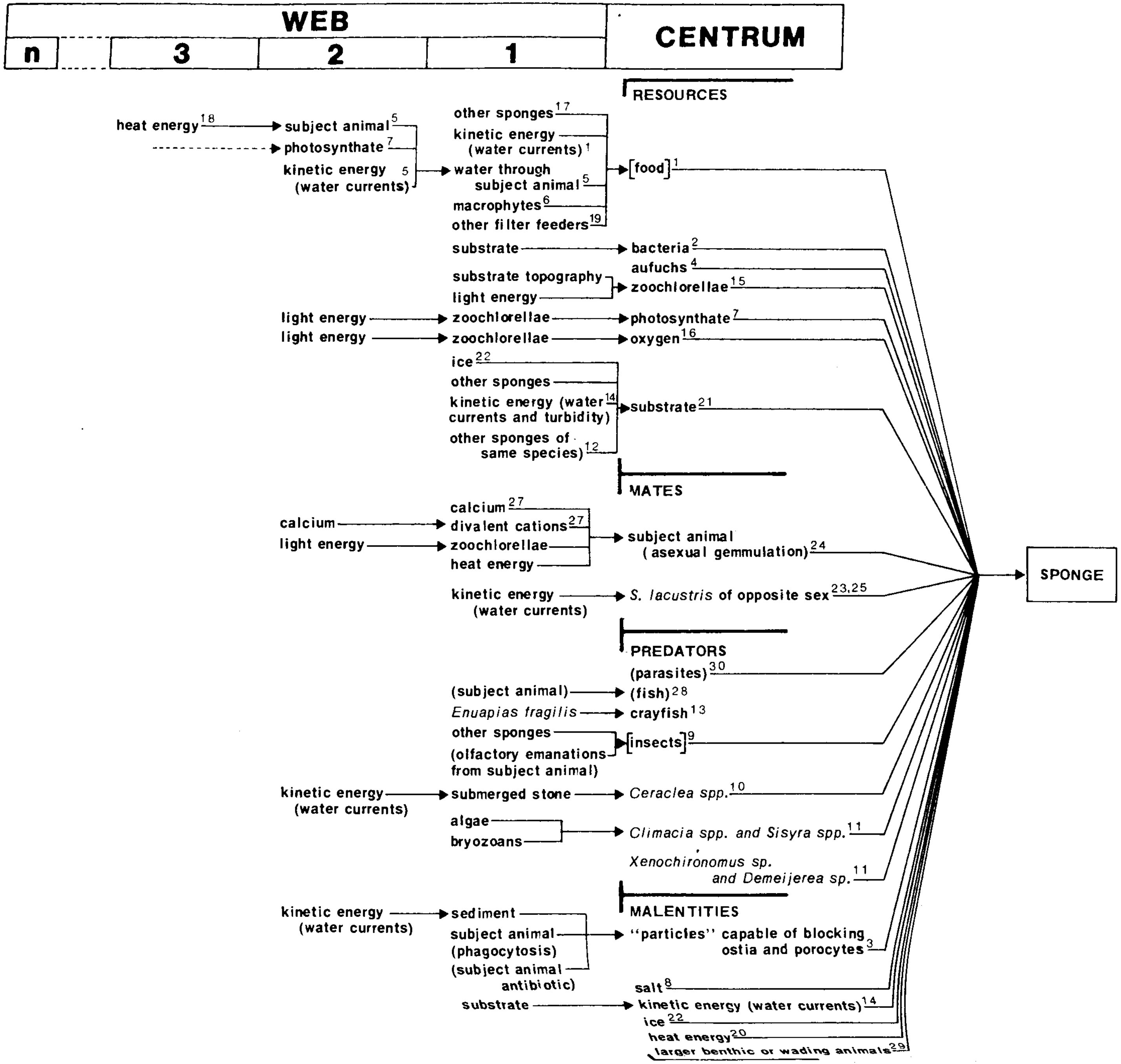
(ii) For food resources choanocytes would be first-order modifiers which would in turn be modified by all the cells from the porocytes lining the inhalent canal openings down to the choanocyte chamber.

(iii) Similarly excretory functions would be modified by spherulous cells and all the cells leading from the choanocyte chamber to the osculum.

(iv) A modifier chain in which the co-operation of other cells was required would also have the "skeleton" (spicules) and scleroblasts as modifiers.

The reason for the formalized system's flexibility in this respect is the primitive term "An" (animal). For further discussion see the General Introduction to this series, revised version, 1983.

B (i) ENVIROGRAM



C. NOTES ON THE ENVIROGRAM

1. *S. lacustris* is not a mobile animal so it depends largely on external factors to bring food resources within its limited range. The principal external factor is 'kinetic energy (water currents)' which in effect provides volumes of nutrient-containing water for the sponge to filter and removes already filtered water. Other external factors are the movements of any mobile animals or protists which the sponge consumes. (The above considerations can be generalized for all classes of the centrum).

All of the sponge's food must be suspended or dissolved in water. A current of water is set up by the flagella of the choanocytes within the sponge and "in effect, the arrangement of inhalent ostia, canals, prosopyles, choanocyte collar tentacles and inter-tentaculae mucous reticulum places a series of sieves of decreasing mesh size in the path of the water current". (Bergquist, 1978). The only selective restriction on particle intake is the passive one afforded by ostia size (see also n. 3) although individual cells are capable of distinguishing between digestible and indigestible substances. Presumably indigestible particles are ejected via the outflow ostia. It is generally agreed that *S. lacustris* can filter particles within the size range 0.1 µm to 50 µm. The sponge uses two methods to capture particles once they have entered the canal system: first, mobile archaeocytes phagocytose particles in the 2 to 5 µm range, directly; this helps to prevent canal occlusion (see n. 3); secondly, secondary capture occurs at the choanocyte collar where particles within the range 0.1 to 1.5 µm are trapped in the collar tentacles. Very little digestion takes place in the choanocytes as particles are not retained for more than 3 hours before being passed on to other cells. In the diet of three marine sponges it was found that about 80% of the particulate material utilized was of a size likely to be taken up mainly by the choanocytes.

A third method of capturing particles operates at the external surface of the sponge where exopinacocytes phagocytose larger particles. However, reports deal only with the uptake of non-nutritive particles under laboratory conditions and the importance of this method for nutrition is not known.

There are almost no 'hard' data on sponge nutrition. Bacteria, unicellulates, zooplankton, phytoplankton, yeasts and colloidal organic matter are mentioned by various authors (see n. 2). (Bergquist, 1978; Frost, 1978; Harrison and Cowden, 1976; Grzimek, 1974).

2. The best data with respect to sponge nutrition concerns bacteria. It is known that the Demospongiae extract bacteria from their aquiferous system and retain them with high efficiency - about 96%. For example, in the laboratory, Frost (1978) showed that *S. lacustris* efficiently filtered *Rhodotorula glutinis* (average diameter 3.9 μm), *Chlamydomonas reinhardti* (6.6 μm) and *Escherichia coli* (2 x 1 μm) from tanks.

The uptake of bacteria by the marginal cells of the basal pinacoderm using a method of filopodial extension and subsequent phagocytosis has been reported for the freshwater sponge *Corvomeyenia carolinensis* and also a marine species. If *S. lacustris* uses this method it could be added to the three methods of nutritional uptake mentioned in n.1.

For some sponges, living in organically rich estuaries, it has been shown that the uptake to bacteria could satisfy their entire nutritional requirements.

It is possible that *S. lacustris* supports a population of bacteria within the matrix of the sponge. The effect of the bacteria, if any, is not known.

3. Large particles (i.e. greater than 50 μm, see n. 1) in suspension are a danger to all sponges since they can block the delicate filter system for long periods - as also can very high concentrations of smaller particles.

Such blockages affect the sponge in at least the following three ways:

(i) Direct damage; for this reason we classify 'particles' as a malentity;

(ii) By causing a reduction of water-flow 'particles' will cause a proportional reduction in nutrient uptake, thus 'particles' are second-order modifiers of food (they modify water-flow);

(iii) Similarly, water-flow is prerequisite for the provision of oxygen and the removal of carbon dioxide; thus 'particles' are also second-order modifiers of 'oxygen' (see also n. 16).

For economy of space we have placed only (i) on the envirogram; all subsequent modifiers also apply to (ii) and (iii), thus extending the envirogram to modifiers of the fourth order.

Any source of 'particles' is potentially dangerous - pieces of the substrate, detritus, living organisms etc. We group these together as 'sediment', a first-order modifier. Almost invariably 'sediment' will be disturbed and carried by 'kinetic energy (water currents), a second-order modifier.

Clearly it is to the subject animal's advantage to maintain its external surface as free of 'particles' as possible. Note 1 gives details of the phagocytosis of particles; in this way, the 'subject animal' acts as a first-order modifier. A second mechanism may contribute to the maintenance of a clear aquiferous system. Frost (1976) reports a significantly smaller build-up of aufwuchs (see also n. 4) on the surface of *S. lacustris* as opposed to the surface of nearby macrophytes. It is known that some marine sponges have an antibiotic effect on organisms; this explanation is suggested though not proved for *S. lacustris*. Thus we have tentatively classified 'subject animal (antibiotic)' as a first-order modifier of 'particles' as malentities.

4. Most fresh-water sponges, including *S. lacustris*, have a relatively aufwuchs-free epithelium. The phagocytic ability of pinacocytes is almost certainly responsible, possibly aided by an antibiotic effect of the sponge on organisms (see n. 3).

The phagocytosis of aufwuchs will contribute to sponge nutrition. In general aufwuchs will include diatoms, fungi and filamentous algae. Frost (1976) reports the following filamentous algal forms collected from *S. lacustris*: *Mougeotia* sp. and *Spirogyra* sp.

were most common; *Bulbochaeta* sp., *Oedogonium* sp. and *Zygnema* sp. were also observed.

5. Given that all sponge food resources must be in suspension, in a given locality the quantity of food that becomes available to a sponge will depend on the quantity of water passing through the animal. Many authors have attempted to calculate water transport rates for *S. lacustris*; methods and conclusions vary greatly. Frost, in Harrison and Cowden (1976), regards 0.0118 ml/sec/ml as a good estimate.

Several factors can affect water transport rates. It is generally agreed that water flow through a sponge is augmented by external current flow across the osculum; however authors disagree on the magnitude of the effect. This is apparently why most sponges in a moving environment are tubular and upright, or, if not upright, are oriented perpendicular to the prevailing water current.

The subject animal is capable of regulating water flow, as evidenced by its response to certain stimuli. On mechanical or electrical stimulation or with thermal (n. 18) or light stimuli the whole body or at least a portion of it is contracted, the osculum and pores first and the canal system last. The mechanism of the response is not known.

6. It is not uncommon for *S. lacustris* to live in close association with macrophytes. The water-plants provide a good surface for aufwuchs and are thus likely to contribute to the maintenance of nutritionally rich water.

In addition, *S. lacustris* not infrequently uses macrophytes as a substrate (see n. 21). Frost (1976) reports the sponge living close to or on the following macrophytes:

Nymphea odorata, Nuphar advena and four species of *Utricularia*.

7. *S. lacustris* (and many other fresh-water sponges) may contain intracellular algae (zoochlorellae) as symbionts. Those sponges containing algae will usually be green while those without are usually white. The presence of algae depends largely on the light conditions in which the sponge lives - i.e. if in dark conditions,

under rocks etc., the sponge is less likely to contain algal symbionts. Algae may be present in a sponge from the beginning if it derives from the gemmulation of an algae-containing parent. Otherwise suitable algae can be filtered and phagocytosed but not digested.

The exact relationship between the symbionts is not known. However, studies on *S. lacustris* have indicated that algal photosynthate is transferred from the alga to the host sponge, thus potentially benefitting the sponge by augmenting its nutrition. This result is in keeping with results from other freshwater invertebrates containing unicellular algal symbionts; in general both growth rates and surfival under starvation conditions are significantly improved.

S. lacustris with algal symbionts is an active, efficient photosynthetic system with a calculated efficiency of 5.4%. Suitable light conditions are required. Gross primary productivity is linearly related to water temperature. It is suggested that the presence of algae, with the effects mentioned above, will reduce the need for active feeding and food uptake on the part of the sponge.

(see also notes 15, 16, 24).

8. *S. lacustris* is exclusively a freshwater species. Attempts to introduce the sponge to brackish water in both field and laboratory have failed. There is some evidence to suggest that the species can withstand brief exposure to salinities well above those in which it is capable of long term survival.

We have therefore classified 'salt' (i.e. dissolved in water) as a malentity.

9. *S. lacustris*, characteristically, has an abundance of commensals both on its surface and in its tissue and canal systems. There has been speculation that sponges have evolved defensive mechanisms (difficulties at spicule digestion, antiobiotic effects, metabolic poisons etc.) enabling them to be free of predators; this hypothesis is false.

The ability to feed on fresh-water sponge is exhibited by certain species in single families of three insect orders: the Trichoptera (see n. 10), the Neuroptera and the Diptera (both in n. 11). Benthic invertebrates relate to fresh-water sponges in two ways other than the predator-prey relation. First, the sponge can serve as a substrate for many aquatic insects; secondly, many organisms, including protozoans, nematodes, oligochaetes and water mites, utilize the vascular system and irregular surfaces of the sponge as suitable permanent habitats. The organisms forming these last two associations will occur as modifiers of food resources in the sponge's environment.

From available information, it appears that there is little host specificity among insect sponge predators. Thus the presence of 'other sponges' (first-order modifiers) will modify insect predators in two ways: first, the proximity of other sponges will increase the probability of predators finding the subject sponge; however, secondly, this effect may be offset by the predatory load being spread over more sponges.

In addition, it seems likely that 'olfactory emanations' (first-order modifiers) from sponges may provide the mechanism by which insect predators locate sponge hosts; this is not definitely established.

10. Resh, in Harrison and Cowden (1976), gives the following list of predacious caddis flies of fresh-water sponges. All are from the genus *Ceraclea* (Order: Trichoptera, Family: Heptoceridae):

Species	Distribution
Fulva Group:	
Ceraclea biwaensis (Tsuda and Kuwayama)	Japan
C. alces (Ross)	North America
C. resurgens (Walker)	North America
C. transversa (Hagen)	North America
C. fulva (Rambur)	Western Palearctic Region
C. albimacula (Rambur)	Western Palearctic Region
C. cama (Flint)	North America
C. vertreesi (Denning)	North America
C. latahensis (Smith)	North America
C. alboguttata (Hagan)	Western Palearctic Region

Species	Distribution
Senilis Group:	
C. senilis (Burmeister)	Western Palearctic Region
C. spongillovorax (Resh)	North America
Nigronervosa Group:	
C. nigronervosa(Retzuis)	Transcontinental Palearctic Region, North America

He also comments that atypical occurrences of caddis flies of the families Polycentropodidae and Limnephibidae have been reported in fresh-water sponges.

All members of the Fulva Group (see table above) are obligatory sponge feeders and have corresponding morphological adaptations. The Senilis Group appears to have both facultative and obligate species of sponge feeders and have less pronounced morphological adaptations. The single member of the Nigronervosa Group appears to be an obligate sponge feeder but has little in the way of morphological adaptation.

There are two basic life-history patterns exhibited by caddis flies which predate sponges. *C. resurgens* is typical of the first; it has a univoltine pattern (i.e. one generation per annual cycle). Adults emerge, mate and oviposit during a brief period in the spring. Eggs released on the water surface sink and adhere to submerged stones. After hatching the larva locates a sponge host; water currents increase the search area and possible also bear olfactory stimuli from the sponge. Following development the larva over-winters as a prepupa and emerges the following spring.

C. transversa, which is typical of the second life-history pattern, has two periods of emergence, mating and so on. The first cohort is similar to *C. resurgens*. The second cohort emerges in mid-summer through autumn. Larvae must over-winter as active detritus feeders after the colonial sponges have deteriorated in late autumn to over-winter as gemmules (see n. 24).

11. Spongillaflies of the family Sisyridae (Order: Neuroptera) are commonly found in association with fresh-water sponges. The genera *Sisyra* and *Climacia* are known predators.

Unlike the sponge-feeding caddis flies (n. 10), sysirid larvae do not ingest whole particles of sponge, rather they suck fluids from the sponge through their tubular mouthparts. Besides feeding on sponge, spongillaflies also suck fluids from Bryozoans and algae, which are thus first-order modifiers.

Two genera, *Xenochironomus* and *Demeijerea* of the sponge-feeding midges (Diptera: Chironomidae) are also known to feed on fresh-water sponges.

12. Body size within the sponges, including *S. lacustris*, is much less restricted than in any other animal group. Individual sponges growing next to each other can grow together to form a new organism. Sponges are known to produce diffusible surface-active molecules which operate to promote or prevent cell-to-cell adhesion. Such factors, which are strain- or species-specific, provide a simple system of "self"-recognition which can lead to fusion or non-fusion.

S. lacustris requires a stable substrate. Other sponges will compete for such space but fusion with other appropriately "recognised" *S. lacustris* is one way of protecting the colonized area (see n. 21).

13. In North America, Williamson (1979) reports the predation of fresh-water sponges, including *S. lacustris*, by a fresh-water crayfish *Orconectes* sp. Both sexes of the crayfish readily consumed both adult and gemmulated *S. lacustris*.

The crayfish also predated the sponge *Eunapius fragilis* which is thus classified as a first-order modifier.

14. Several authors report that strong water currents can damage, and break pieces off, sponges, particularly branched forms. The substrate and the strength and morphology of the sponge provide the only resistance. The latter in turn is influenced by the typical current flow of a locality e.g. branched forms of *S. lacustris* usually occur only in areas with very slow currents.

In addition water current and turbidity can affect the choice of substrate during the initial settling stage. *S. lacustris* is not found in areas with very rapid currents. Williamson and Williamson (1979) report congregations of *S. lacustris* on a rock-water interface where the current was well below 0.01 m/sec. However, Harrison (1977) found *S. lacustris* common in a current of 0.342 ft/sec (approximately 0.1 m/sec).

15. Note 7 gives some details of the provision of photosynthate by symbiont zoochlorellae to host sponges. The algae will live and reproduce within the host cells provided light conditions are sufficient. If for some reason a sponge with algal symbionts is kept in darkness for a few weeks it is likely that the algae will be digested; this 'zoochlorellae' appear on the envirogram as food resources.

Possible advantages to the algal symbiont from the association include: protection, carbon dioxide and other inorganic nutrients. In addition to nutrients the sponge may derive oxygen (n. 16) and an automatic removal of waste products.

16. *S. lacustris* has no special respiratory organs. A continual stream of water is required to transport oxygen into the organism and to remove carbon dioxide. Respiration is by diffusion to individual cells - along the intake canals, at the body surface and at the collar tentacles of choanocytes. Every individual needs to be self-sufficient in this respect. Because it is a sedentary animal oxygen consumption is low and no more than 20% of the available oxygen is withdrawn from the water flowing through the aquiferous system.

Szuch (1978) reports that oxygen consumption by *S. lacustris* kept in the light is lower than that for individuals kept in the dark. This difference is probably the result of algal photosynthesis - oxygen produced by endocellular algae reducing the demand on that carried through the aquiferous system. In normal summer conditions there exists the potential for the symbiotic system to produce its entire oxygen requirements.

17. Any organism which feeds by filtering water will compete for food resources with the subject animal. We have placed 'other sponges' on the envirogram as a first-order modifier of food resources to cover this class.

The class includes sponges such as: *Corvomyenia carolinensis, Heteromeyenia baileyi, Anheteromeyenia ryderi, Trochospongilla pennsylvanica* and *Eunapius fragilis* (all present in North America) and many other organisms (see n. 19).

18. Water temperature is known to affect water transport rates in *S. lacustris*. Frost, in Harrison and Cowden, 1976 gives the following table:

TABLE 2: Filtering rates of *Spongilla lacustris*

SPONGE VOLUME ml	FILTERING RATE ml/sec/ml
	1 October, 13.2^{0}C
1.6	0.027
2.8	0.023
3.0	0.011
	17 October, 9.2^{0}C
8.6	0.010
9.8	0.010
7.9	0.009

19. Many filter feeders other than sponges will compete with *S. lacustris* for food resources. The following are just a few exmaples: the mollusc *(Dreissenia polymorpha)*, the waterfleas *(Bosmina longirostrus* and *Daphnia* spp.), the copepod *(Diaptomus oregonensis)*.

20. Throughout most of North America *S. lacustris* exhibits the following annual cycle. The change from the over-wintering gemmule stage to the definite colonial form of the sponge begins in the spring, with peak abundance and size of the colonies occurring in late summer and early autumn. Lower water temperatures in autumn cause deterioration of the colonial sponge until only gemmules remain.

Clearly, there is a range of heat energies which are harmful to the sponge; we classify these as malentities.

Heat energy also affects reproduction by gemmulation; it is known that gemmules will remain dormant when water temperature is below 4°C.

21. As individuals, all sponges, including *S. lacustris*, must find attachment space. On the species level there must be sufficient space to allow development of a sufficient number of individuals, of large enough body size, to sustain reproduction in the population at a viable level. In aquatic habitats this resource is more frequently limiting than food. Once the resource has been gained it has to be protected from encroachment by other species (see n. 12 re fusion).

Settling larvae of *S. lacustris* prefer a surface which has been pre-coated with bacterial or algal film. Rock or macrophyte substrates (see n. 6) are also preferred, nevertheless the orientation of the particular surface to the prevailing currents is at least as important.

22. Cases have been reported in which ice scour has removed a sponge species from a location. We classify 'ice' as both a malentity and a modifier of the resource 'substrate'.

23. *S. lacustris*, like all other sponges, can reproduce sexually. Again, like other sponges, *S. lacustris* is hermaphroditic though in a unique way which ensures that in any one breeding season each individual will be either female or male but not both (see n. 25).

During the annual cycle outlined in n. 20, oocyte and sperm production commences shortly after the gemmules are released from dormancy in the early spring. Williamson and Williamson (1979) report a case in which sperm production lasted about 6 weeks. It seems likely that both sperm and oocytes are produced by the re-differentiation of choanocyte cells.

Sperm arereleased into the exhalent stream and water currents are necessary to carry the sperm ot a position where they will be sucked into the inhalent stream of a female. The sperm are trapped by choanocytes and transferred to eggs in the mesohyl.

Embryos develop into larvae and when ready for release move to an exhalent canal. At this stage we regard the parents as having reproduced successfully.

24. Some authors refer to gemmulation directly as a method of asexual reproduction, while others write in a way which seems to imply that this is merely an adaptive stage in the life of an individual. Once again, we encounter difficulty with what is to count as an individual sponge (see Introductory Note).

Gemmules are complex armoured structures coated in a thick layer of spongin embedded with microscleres. These small spherical structures are produced at the onset of winter (when the colonial sponge dies back) and are capable of withstanding freezing and desiccation. When environmental conditions are again favourable the gemmule hatches and grows quickly.

With respect to algal symbionts, *S. lacustris* has two forms: the characteristically 'green' symbiotic form containing intracellular zoochlorellae; and the 'white' aposymbiotic form. The two forms show slight but significant differences in the gemmulation process. The 'white' form gemmulates a few weeks before the 'green' (in late autumn) and produces significantly smaller gemmules; for the 'white' form the former point confers the disadvantage of a shorter growing season which "could potentially decrease their ability to reproduce vegetatively and procure food for winter dormancy". Both forms hatch at the same time in the spring. It is cautiously suggested that the larger 'green' gemmules are "more viable in nature" - i.e. the hatching rate is larger.

Light (photoperiod), both in combination with intracellular zoochlorellae and without, is also suggested as an important triggering mechanism for gemmulation in *S. lacustris*.

S. lacustris gemmules will remain dormant indefinitely if kept at temperatures below 4°C.

(The quotations above are from Williamson and Williamson, 1979).

25. *S. lacustris* are hermaphroditic but in a rather unusual way. It has been shown that in any given reproductive season an individual sponge will be strictly either male or female. However, of five individuals, tagged so that they could be reliably identified after their period of winter dormancy, three had changed sex by the following reproductive season, one male becoming a female and two females becoming male; the sex of the other two was unchanged.

"While it is only theorizing to guess at the significance of this behaviour it is possible to see advantages for a sessile organism which disperses by free larvae. An isolated larva can produce an individual which will produce gemmules. Next spring when those gemmules germinate some may change sex. This enables successful fertilization and ensures the spread of the species". (Bergquist, 1978).

In their work on 'white' and 'green' forms of *S. lacustris*, Williamson and Williamson (1979) observed male sexual elements in twice as many 'white' sponges as in 'green'; one explanation involves the possibility of antibiosis in zoochlorellae.

26. All fresh-water sponges, including *S. lacustris*, are characterized by silica (silicon dioxide) skeleton needles or spicules. Spicules are formed by a cell type called the scleroblast which deposits silica on an organic 'axial thread'. Such spicules consist of about 92% silicon dioxide, 7% water and traces of magnesium, potassium and sodium. Because of the contribution of the skeleton to sponge growth all of these materials will be resources. To obtain silica *S. lacustris* can only utilize dissolved silicic acid and not solid quartz.

Several authors suggest that the sharpness of the spicules and their difficulty of digestion affords the sponge protection from some potential predators.

27. Calcium and divalent cations can play a significant role in the gemmulation process for *S. lacustris* and other fresh-water sponges.

If kept in pure water gemmules will hatch, demonstrating that all essential factors, including any essential ions, are contained within the gemmule. Results establish that calcium at concentrations of 5mM and higher foster germination; however the presence of sufficient amounts of strontium, barium, zinc, or manganese results in an inhibition of germination. Nevertheless, in the latter case, if a sufficient concentration of calcium is also present any inhibition will be overcome (Ostrom and Simpson, 1978).

28. Pieces of fresh-water sponge have occasionally been found in the stomachs of fish; whether the fish were directly predatory is doubtful but not known. The sharp, indigestible silica skeleton and noxious chemicals have been given as reasons for the sponge's relative freedom from larger predators.

Thus, we tentatively classify 'fish' as predators, modified by 'subject animal' (skeleton and poisons).

29. Snails and other crawling or browsing animals have been reported as occasionally damaging sponges as an accidental adjunct of their normal activities. Presumably the same sort of damage can be done by wading animals. We group these animals together and classify them as malentities.

30. In note 9 a few of the many animals frequently associated with fresh-water sponges, including *S. lacustris*, were mentioned. In the absence of better information it was suggested that many of this group would function in the sponge's environment as, at least, some modifier of food. Still without hard data some authors suggest a parasite-host relationship. Thus we tentatively group the animals mentioned below as 'parasites' on the envirogram:

(i) Larvae from eggs of water mites, including *Unionicula crassipes*, which frequently oviposit on fresh-water sponges.
(ii) Annelids (round worms) of the genera *Aelosoma* and *Naïs*.
(iii) Certain predatory ciliates.
(iv) Fresh-water gammarids (sand fleas) of the family Leucothoidae.

E. REFERENCES

Bergquist, P.R. (1978). *Sponges.* (Hutchinson, London).

Fjerdingstad, E.J. (1970). Ultrastructure of the spicules of *Spongilla lacustris* (L.), in Fry, W.G. (Ed.).

Frost, T.M. (1976). Sponge feeding: A review with a discussion of some continuing research, in Harrison, F.W. and R.R. Cowden (Eds.), 283-298.

Frost, T.M. (1976). Investigations of the Aufwuchs of freshwater sponges. I. A quantitative comparison between the surfaces of *Spongilla lacustris* and three acquatic macrophytes. *Hydrobiologia* 50 (2), 145-149.

Frost, T.M. (1978). In situ measurements of clearance rates for the freshwater sponge *Spongilla lacustris*. *Limnol. Oceanogr.* 23(5), 1034-1039.

Fry, W.G. (Ed.) (1970). *The Biology of the Porifera, Symp. Zool. Soc. London.* (1970) No. 25 (Academic Press).

Grzimek, B. (Ed.) (1974). *Grzimek's Animal Life Encyclopedia,* Vol. 1 (van Nostrand Reinhold).

Harrison, F.W. (1977). The taxonomic and ecological states of the environmentally restricted Spongillid species of North America. III. *Corvomeyenia carolinensis* Harrison 1971, *Hydrobiologia* 56(2), 187-190.

Harrison, F.W. and R.R. Cowden (Eds.) (1976). *Aspects of Sponge Biology,* (Academic Press).

Niven, B.S. (1982). Formalization of the Basic Concepts of Animal Ecology. *Erkenntnis* 17, 307-320.

Ostrom, K.M. and T.L. Simpson (1978). Calcium and the release from dormancy of freshwater sponge gemmules. *Dev. Biol.* 64(2), 332-338.

Poirrier, M.A. (1976). A taxonomic study of the *Spongilla alba, S. cenota, S. wagneri* species group (Porifera: Spongillidae) with ecological observations of *S. alba*, in Harrison, F.W. and R.R. Cowden (Eds.), 203-214.

Resh, V.H. (1976). Life cycles of invertebrate predators of freshwater sponge, in Harrison, F.W. and R.R. Cowden (1976).

Sara, M. (1970). Competition and cooperation in sponge populations, in Fry, W.G. (Ed.) (1970).

Simpson, T.L., L.M. Refold and M.E. Kaby (1979). Effects of germanium on the morphology of silica deposition in a freshwater sponge. *J. Morphol.* 159(3), 343-354.

Szuch, E.J., E.H. Studier and R.B. Sullivan, Jr. (1978). The relationship of light duration to oxygen consumption in the green, freshwater sponge *Spongilla lacustris*. *Comp. Biochem. Physiol. a Comp. Physiol.* 60(2), 221-224.

Williamson, C.E. (1977). Fluorescence identification of Zoochlorellae: A rapid method for investigating Algae-Invertebrate symbioses. *J. Exp. Zool.* 202(2), 187-194.

Williamson, C.E. (1979). Crayfish predation in freshwater sponges. *Am. Midl. Nat.* 101(1), 245-246.

Willaimson, C.E. and G.L. Williamson (1979). Life-cycles of lotic populations of *Spongilla lacustris* and *Eunapius fragilis* (Porifera: Spongillidae). *Freshwater Biol.* 9, 543-553.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS
XXIII THE REEF CORAL *(Pocillopora damicornis)*

by

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ABSTRACT

The precise environment of the Reef Coral *(Pocillopora damicornis)* is given, using as a basis for the classification the defining equations of Niven *(Erkenntnis,* 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A INTRODUCTORY NOTE

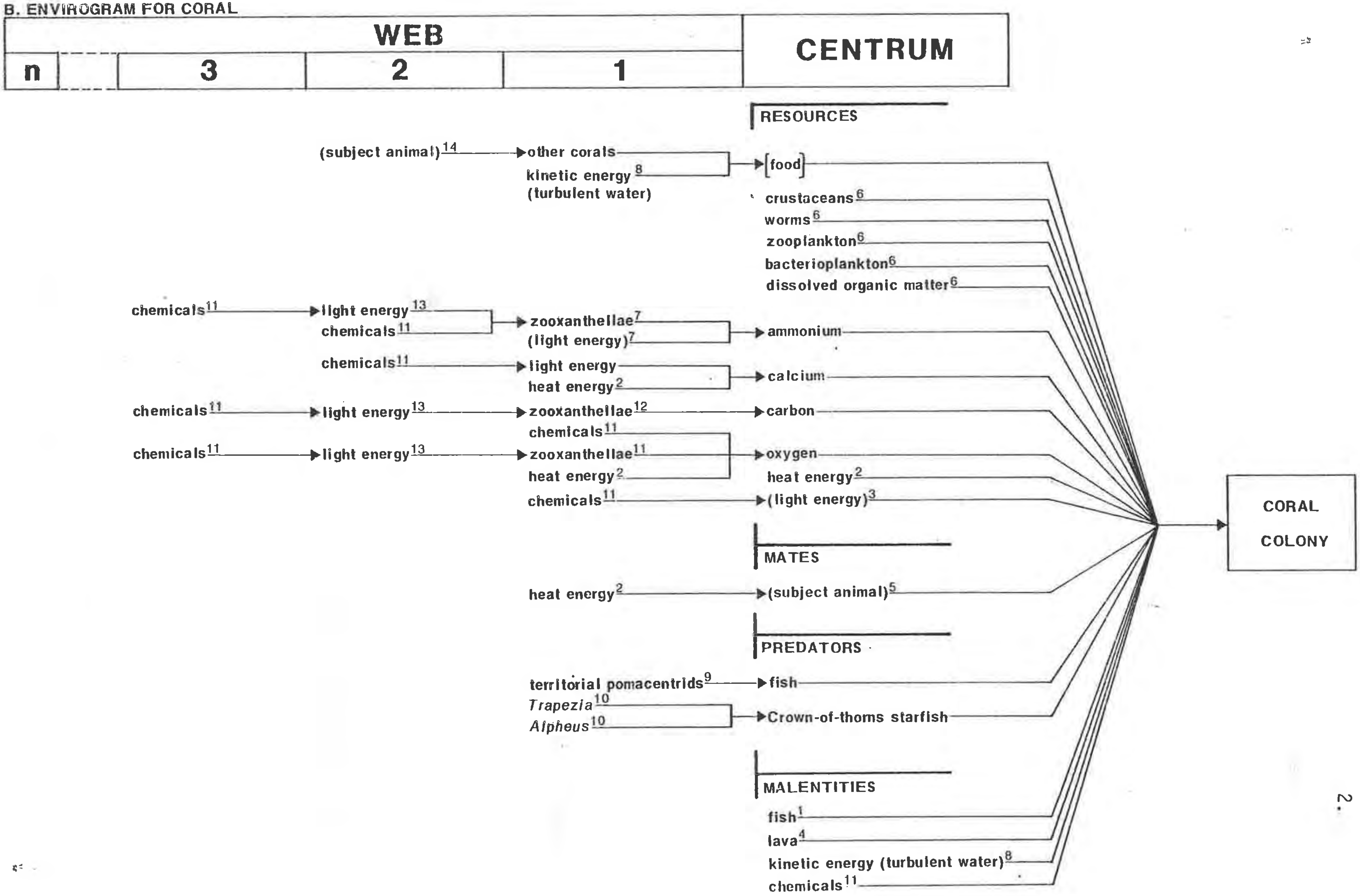
Pocillopora damicornis is one of the most common of the branching reef corals. It is widespread in tropical and subtropical waters and has been studied in the waters off Panama, the West Indies, Hawaii, Guam and Australia.

In this Working Paper the primitive term 'animal' is taken to mean a coral colony, not a single polyp. This is in accordance with the literature quoted in section E; authors are interested in the colony as a whole and there is little information available about the individual polyp.

The animal is often studied almost as a by-product of studies of the communities living within or near the coral branches. Authors such as Castro (1978) observed in particular the crab *Trapezia ferruginea*, the pontoniid shrimps *Harpiliapsis depressa* (Stimpson) and *H. spinigera* (Ortmann) and the alpheid shrimp *Alpheus lottini* (Guerin), and Lassig (1977) reports on behavioural interactions among fish, crabs and shrimps associated with *P. damicornis*. These "coral symbionts" are often host-specific; Abele (1976), studying the relation between environmental constancy and species richness, found that the porcellanid crab *Pisidia magdalenensis* was the most abundant species on *P. damicornis* in the Pearl Islands (Pacific coast of Panama) whereas not a single individual was found on *P. damicornis* at Uva Island (also on the Pacific coast of Panama). It is not always clear exactly what is the relation between commensal and coral. (However, see notes 9 and 10). Patton (1974) studied community structure among animals in *P. damicornis* at Heron Island (Australia) and gives an interesting diagrammatic cross-section of the coral showing the more common associates. A list taken from Patton's article is included in section D.

Excellent photographs of the coral are to be found on Sisson (1973).

B. ENVIROGRAM FOR CORAL



C NOTES ON THE ENVIROGRAM

1. Castro (1978) quotes Glynn *et al* (1972) as observing a tetradontid fish *Arthron meleagris* breaking the tip of coral branches, perhaps in order to expose crabs to predation.

2. *P. damicornis* "... Flourish and breed best within the range 25 - 29°C" (Wells, 1957, quoted by Glynn, 1977).

   Jokiel and Coles (1977) found, in laboratory experiments, that temperatures of about 32°C produce death within days. Prolonged exposure to temperatures of approximately 30°C eventually causes loss of photosynthetic pigment, increased mortality and reduced calcification. The corals live only one to two weeks at 18°C. They show greater initial resistance at the lower lethal limit, but ultimately low temperature is more deleterious than high temperatures.

   Glynn (1977) reports that mean annual growth of *P. damicornis* at Saboga Island (Gulf of Panama) is 3.1cm/yr as against 3.9cm/yr at Secas (Gulf of Chiriquí). The major hydrographic difference between the two study sites is seasonal upwelling which occurs in the Gulf of Panama but not in the Gulf of Chiriquí; it is a local, wind-induced up welling which results in a fall of 3 to 4°C below a wet season mean of about 28°C, with extreme low temperatures of 16 to 20°C. Glynn reports that coral growth and water temperature are significantly correlated at Saboga Island but not on the Secas reef, and suggests that the poor relationship at Secas is due to the nearly constant temperature conditions.

   According to Jokiel and Guinther (1978) the ability of *P. damicornis* to reproduce is curtailed under suboptimal conditions far more severely than is growth rate. Successful reproduction was found to diminish by an order of magnitude with a 1°C temperature change from the 26 to 27°C optimum. The growth rate of adult colonies of the animal is relatively high throughout a range of 24 to 29°C and generally changes by less than 10% with a 1°C temperature shift.

Although the coral can produce planulae throughout the year in Hawaii significant recruitment of new colonies probably is restricted to the summer months, when the water temperature exceeds 26°C.

Clausen and Roth (1975) studied the effect of temperature on the calcification rate of *P. damicornis*. They found that the effect varies depending on the "temperature history" of the coral, i.e. that the animal adapts to the temperature regime. Both 27°C and 31°C are optimal depending on the temperature to which the coral is adapted. (They suggest a biochemical mechanism to account for this result). They also suggest that corals may be able to adapt sufficiently to be able to survive short-term high temperatures.

Coles and Jokiel (1977) found significant regression between photosynthetic rates and temperature, and respiration and temperature. The ratio photosynthesis/respiration is significantly and negatively related with temperature between 18°C and 31°C for all Hawaiian corals; at Enewetak this ratio has a curvilinear relationship with temperature.

3. Glynn (1977) reports that when coral growth and cloud cover are compared under relatively constant temperature conditions a significant inverse correlation is found. Calcification proceeds more intensively in the shade than in the light according to Mashanskii *et al* (1979).

   The effect may, however, be due to the increased concentration of zooxanthellae in shaded corals.
   (See also notes 11 and 13).

4. Lava flows in the Hawaiian Islands have been recorded since 1801. Grigg and Maragos (1974) have compared coral communities on successively older flows, in order to reconstruct patterns of community succession. They report that *P. meandrina* is a pioneer species in the area. *(P. damicornis* is not mentioned).

5. *P. damicornis,* like other reef corals, reproduces by releasing planula larvae which are dispersed by currents to new regions. Under favourable conditions the larvae settle and grow into new colonies. (Jokiel and Guinther, 1978).

It does not seem to be known whether this particular species is dioecious or hermaphroditic. Nevertheless Grzimek (1974) states that (for scleractinian corals in general) the ova are fertilized in the enteron of the female or the hermaphroditic enteron and the planula larvae develop there.

Harrigan (1972) found that planulae may settle at an age of less than 4 hours or up to 212 days post-hatching. Newly-hatched planulae are positively phototactic; older planulae become photonegative or indifferent to light. The preferred substrate for settlement is a dark surface covered with a thin living film of green filamentous algae, diatoms and bacteria.

Stimson (1978) found that *P. damicornis* planulated in captivity all the year round.

6. The tentacles and cilia of the animal bring small planktonic organisms towards the mouth. Corals are purely carnivorous and digest their food extremely rapidly. Indigestible remains are extruded through the mouth. The enterons of coral polyps have been found to contain plankton, bottom-living crustaceans and worms. The polyps usually emerge to feed as darkness falls and retract into their calcareous calyxes at sunrise (Grzimek, 1974).

Sorokin (1980) remarks that dissolved organic matter and bacterioplankton are important as a source of nutrients; energy is provided by the photosynthesis of associated zooxanthellae (n.12).

7. Muscatine and D'Elia (1978) report that *P. damicornis*, like other reef corals with zooxanthellae, take up and retain NH_4^+. Uptake and retention are enhanced by light; this may occur because of the effect of light on the zooxanthellae rather than directly on the coral.

8. Jokiel (1978) reports that *P. damicornis* is most abundant on semi-protected reefs. The influence of water motion on the growth, mortality and reproductive rate varies among different species of coral. Jokiel suggests that the water motion influences corals by controlling the rate of exchange of material across the interface between the sea water and the coral tissue.

9. Neudecker (1977) reports that fish predation on living corals can be an important bioerosive agent, e.g. *Arothron meleagris* (Lacepede), a tetradontid fish, can consume 10 gr of *P. damicornis* per day in aquaria (Glynn, Stewart and McCosker, 1972, quoted by Neudecker) and Chaetodons will graze corals in aquaria to death. Neudecker also reports that grazing of *P. damicornis* can be prohibited by certain fish species e.g. the presence of territorial pomacentrids. Fish in the families Balistidae, Canthigasteridae, Chaetodontidae, Monacanthidae and Tetradontidae are known to feed on corals. *P. damicornis* can be excluded from certain habitats by fish predation. The following table is from Neudecker (1977):

Table 2. Fish species actually observed: Feeding on the transplanted *P. damicornis**always at the transplant site° or known to occur in the area ʃ

Mode of Feeding	Species observed feeding* always at transplant site° or known to occur in the area ʃ
Feeders on Branching coral tips and/or polyps	Ballistidae
	*Balistipus undulatus
	ʃBalistoides viridescens (Block & Schneider)
	°Rhinecanthus aculeatus (L.)
	Canthigasteridae
	°Canthigaster solandri (Richardson)
	Chaetodontidae
	*Chaetodon reticulatus Cuvier
	*C. mertensi Cuvier
	Labridae
	*Labroides sp.
	Pomacentridae
	°Plectroglyphidon lacrymatus (Quoy and Gaimard)
Coral Polyp Feeders	Chaetodontidae
	*Megaprotodon trifascialis (Quoy and Gaimard)
	°Chaetodon auriga Forskal
	°C. citrinellus Cuvier and Valenciennes
	°C. lunula (Lacepede)
	°C. reticulatus Cuvier
	*C. tifasciatus Mungo Park
	°C. ephippium Cuvier and Valenciennes

Neudecker (1979) used controlled coral transplant experiments to determine the effect of piscine corallivores on growth, zonation and distribution of *P. damicornis* in Guam. All transplanted colonies were heavily fed upon and branch tips removed primarily by chaetodontid and balistid fishes, but none of the colonies was killed. Polyp and mucus browsing by species which do not physically damage the coral skeleton was also substantial. In one experiment fish were found to discriminate between *P. damicornis* and other corals. The coral can survive and grow well in deeper habitats than normal when enclosed in a fish-exclusion cage.

10. Abele and Patton (1976) report that the 55 decapod species associated with *P. damicornis* (see §D) at least two, *Trapezia ferruginea* and *Alpheus lottini* feed on the coral mucus and are involved in protecting the coral against predation by the Crown-of-Thorns starfish *Acanthaster*.

11. Vandermeulen *et al* (1972) report that the selective photosynthesis inhibitors Monuron (CMU) and Divron (DCMU) inhibit photosynthesis by zooxanthellae both in intact branches of the coral and in suspensions of isolated zooxanthellae. Methyl viologen was ineffective in inhibiting photosynthesis in intact *P. damicornis* at low concentrations and lethal to the tissues at high concentrations. DCMU (in concentrations high enough to inhibit photosynthesis) probably acts only on the zooxanthellae and not on the animal's metabolic apparatus. DCMU also inhibits light-enhanced ^{45}Ca incorporated by *P. damicornis* in the light. Calcification levels in the light when DCMU is present is similar to those obtained in the dark with sea water only.

12. Zooxanthellae associated with *P. damicornis* contribute carbon to the coral animal respiration. According to Muscatine *et al* (1981) the algae in the shallow-water Hawaiian (USA) reef corals, including *P. damicornis*, can supply up to 69% of the daily respiratory carbon demands of their hosts. Sorokin (1980) reports that the daily photosynthesis production of corals with zooxanthellae reaches approximately 0.3mg C/g and compensates all metabolic expenditures of the corals. Abundance of zooxanthellae per polyp is about 2000; their biomass is approximately 2% of the polyps.

13. Mashanskii *et al* (1979) report that concentrations of zooxanthellae increase in shaded corals. (See also n.3, n.11).

14. Wellington (1980) found that *P. damicornis* was dominant over certain other species of coral, i.e. it had apparently caused tissue damage to the other species. The suggested mechanism is the induced development of sweeper tentacles by the relatively fast-growing *P. damicornis*.

D DETAIL

The following table is from Abele and Patton (1976).

Table 1. The species of decapod crustacea associated with *Pocillopora damicornis* in the Pearl Islands, Panama

Species	Number of Individuals	Size range of corals heads on which species occurred (cm^3)		Frequency of occurrence on coral heads (n=35)	
		min (960)	max (22 500)	n	%
Pisidia magdalenensis	180	1200	22500	27	77.1
Harpiliopsis depressus	109	1500	22500	31	88.6
Trapezia ferruginea	91	960	22500	35	100
Fennera chacei	89	1500	22500	20	57.1
Alpheus lottini	83	960	22500	32	91.4
Petrolisthes haigae	71	1200	22500	23	65.7
Palaemonella cf. *asymmetrica*	58	1200	18000	19	54.3
Heteractaea lunata	43	1200	22500	21	60
Petrolisthes agassizii	40	1500	22500	14	40
Mithrax pygmaeus	31	1500	22500	13	37.1
Synalpheus digueti	29	1920	22500	13	37.1
Pagurus cf. *lepidus*	26	1920	18000	12	34.3
Teleophrys cristulipes	22	960	13125	12	34.3
Cycloxanthus vittatus	22	2400	11250	9	25.7
Synalpheus sp. 1	21	2340	18000	6	17.1
Thor amboinensis	17	1200	13125	6	17.1
Harpiliopsis spinigerus	17	1920	13125	4	11.4
Synalpheus sp. 5	16	3600	22500	3	8.6
Lysmata californica	13	1920	22500	2	5.7
Stenorynchus debilis	11	2340	22500	5	14.3
Cataleptodius sp. 1	11	2520	5000	3	8.6
Pilumnus sp. 1	9	4320	18000	2	5.7
Lophoxanthus lamellipes	8	1920	6400	3	8.6
Hapalocarcinus marsupialis	7	11592	-	1	2.8
Alpheus sp. 6	7	11250	22500	3	8.6
Thor cf. *maldivensis*	7	1920	10800	2	5.7
Petrolisthes edwardsii	6	10800	22500	2	5.7
Alpheus panamensis	6	5000	18000	4	11.4
Synalpheus charon	4	6400	11592	2	5.7
Gnathophyllum panamense	4	7500	18000	3	8.6
Pilumnus reticulatus	4	4800	22500	4	11.4
Petrolisthes galathinus	3	6400	7500	2	5.7
Pilumnus stimpsonii	3	11250	-	1	2.8
Megalobrachium smithii	3	22500	-	1	2.8
Xanthidae sp. 2	3	4320	-	1	2.8
Herbstia tumida	3	9000	22500	3	8.6
Calcinus obscurus	3	3600	-	1	2.8
Pachycheles biocellatus	2	18000	-	1	2.8
Synalpheus sp. 2	2	2340	4800	2	5.7
Petrolisthes polymitus	2	1500	22500	2	5.7
Synalpheus cf. *mexicanus*	2	9000	18000	2	5.7
Megalobracium erosum	2	22500	-	1	2.8
Synalpheus anlucasei	2	2520	-	2	5.7
Alpheus sp. 2	2	4800	18000	2	5.7
Pelia pacifica	2	1920	9000	2	5.7
Megalobrachium tuberculipes	2	3600	7500	2	5.7
Ulloaia percusica	1	3600	-	1	2.8
Uhlias ellipicus	1	11250	-	1	2.8
Pagurus sp. 2	1	4320	-	1	2.8
Synalpheus biunguiculatus	1	22500	-	1	2.8
Typton sp. 1	1	2520	-	1	2.8

Pilumnus sp. 2	1	11250	-	1	2.8
Xanthidae sp. 1	1	2340	-	1	2.8
Cycloxanthus bocki	1	6400	-	1	2.8
Pachycheles vicarius	1	9000	-	1	2.8
TOTAL 55	1107				

The following list of species found in *P. damicornis* is from Table 1 of Patton (1974).

Agile shrimp

Periclimenes amymone
Periclimenes madreporae
Periclimenes spiniferus
Thor amboinensis

Sedentary shrimp

Periclimenes sp.
Harpiliopsis breaupressi
Alpheus ventrosus

Crabs

Chlorodiella nigra
Phymodius ungulatus
Cymo andreossyi
Domecia hispida
Trapezia cymodoce
Trapezia ferruginea
Trapezia ferruginea
form *areolata*
Trapezia ferruginea
form *guttata*

Fish

Paragobiodon
echinocephalus

E. REFERENCES

Abele, L.G. (1976). Comparative species richness in fluctuating and constant environments: coral associated decapod crustaceans. *Science*, N.Y., 192, 461-463.

Abele, L.G. and W.K. Patton (1976). The size of coral heads and the community biology of associated decapod crustaceans. *Journal Biogeogr.* 3(1), 35-47.

Castro, P. (1978). Movements between coral colonies in *Trapezia ferruginea* (Crustacea: Brachyura), an obligate symbiont of scleractinian corals. *Marine Biology* 46, 237-245.

Clausen, C.D. and A.A. Roth (1975). Effect of temperature and temperature adaptation on calcification rate in the hermatypic coral *Pocillopora damicornis. Marine Biol. Berlin* 33(2), 93-100.

Coles, S.L. and P.L. Jokiel (1977). Effects of temperature on photosynthesis and respiration in hermatypic corals. *Marine Biol. Berlin* 43(3), 209-216.

Glynn, P.W. (1977). Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama. *J. Marine Research*, 35(3), 568-585.

Grigg, R.W. and J.E. Maragos (1974). Recolonization of hermatypic corals in submerged lava flows in Hawaii. *Ecology*, 387-395.

Grzimek, B. (Ed.-in-Chief) (1974). *Grzimek"s Animal Life Encyclopedia* Vol. 1. (van Nostrand Reinhold).

Harrigan, J.F. (1972). Behavior of the planula larva of the scleractinian coral *Pocillopora damicornis* (L.) Ph.D. thesis, University of Hawaii. 303 pp.

Jokiel, P.L. (1978). Effects of water motion on reef corals. *J. exp. mar. Biol. Ecol.* 35(1), 87-97.

Jokiel, P.L. and S.L. Coles (1977). Effects of temperature on the mortality and growth of Hawaiianreef corals. *Marine Biol., Berlin.* 43(3), 201-208.

Jokiel, P.L. and E.B. Guinther (1978). Effects of temperature on reproduction in the hermatypic coral *Pocillopora damicornis. Bull. Mar. Sc.* 28(4), 786-789.

Lassig, B.R. (1977). Communication and coexistence in a coral community. *Marine Biology* 42, 85-92.

Mashanskii, V.F., S.E. Li, E.A. Titlyanov and B.V. Preobrazhenskii (1979). Morphofunctional correlations of the ultrastructure of calciferous cells of corals with respect to illumination. *Biol. Morya (Vladivost.)* 0(4), 80-82.

Muscatine, L. and C.F. d'Elia (1978). The uptake, retention and release of ammonium by reef corals. *Limnology Oceanogr.* 23(4), 725-734.

Muscatine, L., L.R. McCloskey and R.E. Marian (1981). Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnol. Oceanogr.* 26(4), 601-611.

Neudecker, S. (1977). Transplant experiments to test the effect of fish grazing on coral distribution. *Proc. third int. Coral Reef Symp.* 3(1), 317-323.

Neudecker, S. (1979). Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology.* 60(4), 666-672.

Patton, W.K. (1974). Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. In *Symbiosis in the Sea,* pp. 219-244. (Ed) W.B. Vernberg (Columbia, S.C.: University of South Carolina Press).

Sisson, R.F. (1973). First color record of the life cycle of a coral. *National geogr. Mag.* 143(6), 780-793.

Sorokin, Y.I. (1980). Physiological characteristics of 2 common species of coral, *Pocillopora. Zh. obshch. Biol.* 41(4), 547-556.

Stimson, J.S. (1978). Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. *Mar. Biol. (Berl.)* 48(2), 173-184.

Vandermeulen, J.H., N.D. Davis and L. Muscatine (1972). The effect of inhibitors of photosynthesis on zooxanthellae in corals and other marine invertebrates. *Marine Biol. Berl.* 16(3), 185-191.

Wellington, G.M. (1980). Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. *Oecologia (Berl).* 47, 340-343.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XV THE SEA GOOSEBERRY *(PLEUROBRACHIA PILEUS)*

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ABSTRACT

The precise environment of the Sea Gooseberry *(Pleurobrachia pileus)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the enivrogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A. INTRODUCTORY NOTE

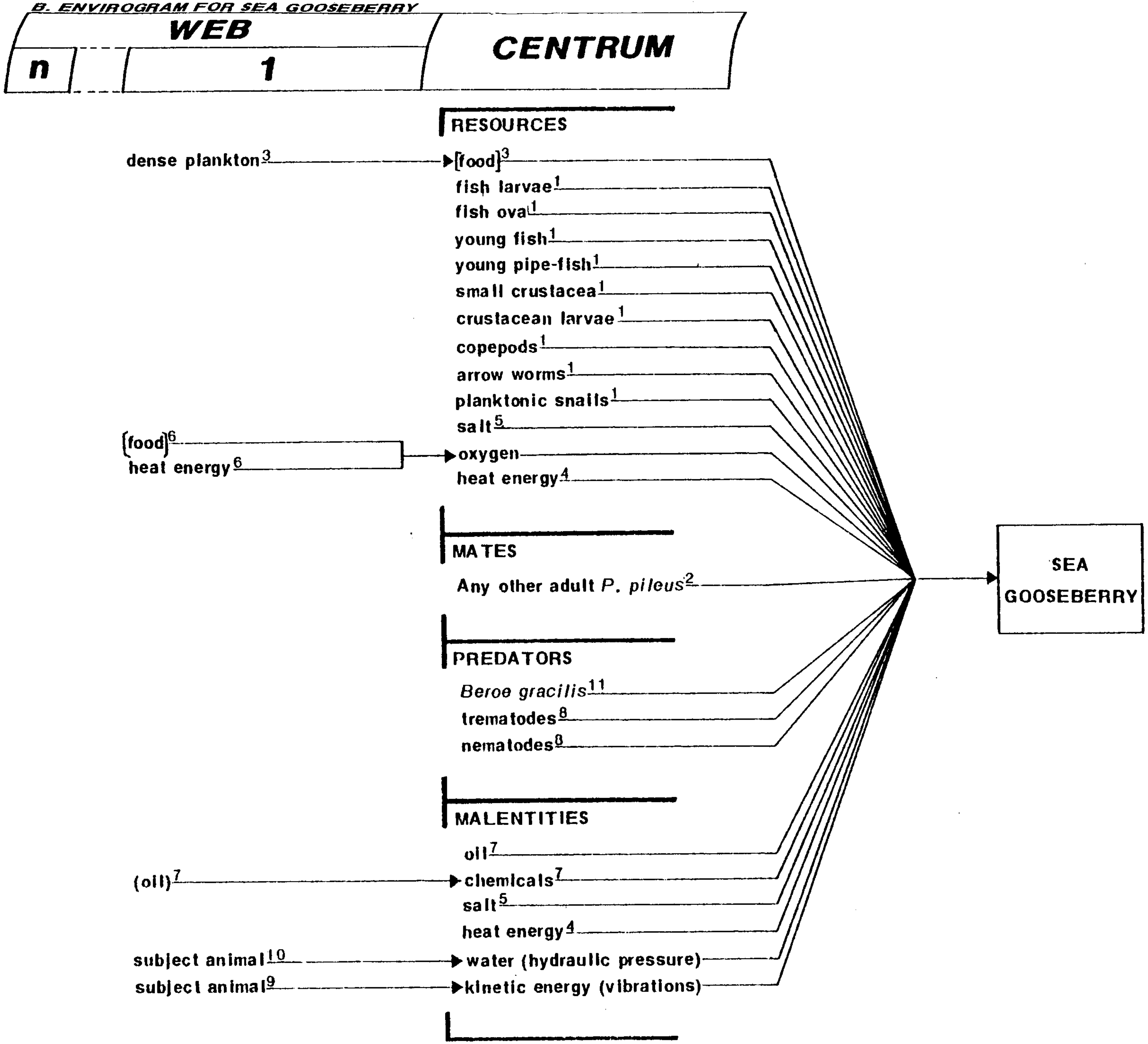
The Sea Gooseberry, *Pleurobrachia pileus* is about the size and shape of a large gooseberry; adults are from 15mm to 30mm in length. The animal is a Ctenophore, or 'comb-bearer'; it has rows of 'comb-plates' and a pair of tentacles which stretch out to about ten times the length of the body. Ctenophora form part of the plankton and are among the most voracious of the planktonic organisms (see n. 1). *P. pileus* has a mouth at the lower pole and an organ of balance at the upper pole. Down the meridians, at equal distances apart, are eight rows of beating comb-plates, each looking like a comb, made up of a line of cilia fused together at their bases but free at their outer ends. The comb-plates beat rhythmically one after the other and so propel the animal forwards. The tentacles have an immense number of smaller branches hanging at right angles from them; these have large number of very sticky lasso-cells - as the tentacles sweep out through the water they collect food for the animal.

An excellent photograph is to be found in Harder (1968).

P. pileus is often found in shallow tidal waters and may sometimes be seen in abundance in calm weather floating buoyantly at the surface, with its tentacles trailing below. (Knight-Jones and Morgan, 1966). It is cosmopolitan. There are reports of it being stranded off the South-West Lancashire Coast (Longwood, 1976), off British Columbia (Arai, 1976), in the North Pacific (Ikeda, 1976), near Valparaiso, Chile (Palma *et al*, 1977), in Loch Fyne, Scotland (Fraser and Adams, 1970), in Wellington Harbour, New Zealand (Boyle, 1966), in the Ribble Estuary, England (Popham, 1966) and the North Sea (Fraser, 1967). Haertel and Osterberg (1967) report *Pleurobrachia* present in saline water in the Columbia River Estuary (U.S.A.) all the year round. Grzimek (1974) reports that the animal is present in enormous numbers in the North Sea and can penetrate the Baltic, Atlantic and Arctic. Boyle (1966) writes of *P. pileus* in Wellington Harvour, New Zealand " ... during autumn ... the numbers of this animal are such that the net clogs to such an extent that most other species are excluded from the catch".

Pleurobrachia appears to be somewhat insensitive to light, but it reacts very readily to touch, turbulence and pressure changes (Knight-Jones and Morgan, 1966). (See also n. 9, n. 10).

B. ENVIROGRAM FOR SEA GOOSEBERRY



C. NOTES ON THE ENVIROGRAM

1. *P. pileus* spends long periods of inactivity fishing with extended tentacles. (Knight-Jones and Morgan, 1966).

   The sticky lasso-cells on the innumerable small branches of the two main tentacles sweep out through the water and continually collect small crustacea, young fish (including herring) and other members of the plankton. The tentacle contracts so that the food is delivered to the animal's mouth. The Sea Gooseberry "has been observed to 'play' a young pipe-fish, much as an angler plays his catch". A young goby more than twice the ctenophore's length has been observed to be caught and partially digested, although it was too large to be put entirely into the Sea Gooseberry's mouth (Hardy, 1958).

   Arai (1976) fed *P. pileus* in the laboratory on young stages of *Artemia salina* and Ikeda (1976) fed it on freshly collected copepods, mainly *Calanus pacificus*; Ikeda reports that they "fed very well on the copepods".

   Grzimek (1974) reports that a variety of planktonic organisms are eaten, such as copepods, crustacean larvae, arrow worms, planktonic snails, fish ova and fish larvae. It is believed that the herring catch may depend on the number of herring ova and larvae which are eaten by exceptionally large swarms of *P. pileus*.

2. The animal is hermaphroditic. A minute individual, 0.5 to 1.5mm long, develops directly from the fertilized egg. It can reproduce immediately after hatching. The gonads then regress and the animal becomes reproductively mature again only when fully grown. The ova formed the second time are, however, twice as large as the first ones (Grzimek, 1974).

3. Reeve, Walter and Ikeda (1978) report that ctenophore ingestion rates are linearly related to food density up to concentrations much higher than is usual in the natural habitat.

At high food concentrations, daily rations of newly-hatched ctenophores can exceed well over 10 times their body C. and even adults can consume these extremely large rations (Reeve, 1980).

4. Arai (1976) collected *P. pileus* from Departure Bay and Ladysmith Harbour (British Columbia, Canada) in water at 17 to 18°C.

Arai (1973, 1976) has recorded that discontinuities in temperature attract *P. pileus*, so that they tend to aggregate in these regions. The effect is enhanced by associated discontinuities in salt content (see n. 5). The aggregation of the animals is an active response rather than passive flotation in a density barrier.

Palma *et al* (1977) observed that *P. pileus* were more numerous at the beginning of spring and in the middle of summer. The greater densities were present in the neritic stations, in contrast with scarcity in the offshore station. Body size was greater at higher temperatures.

5. Arai (1976) noted surface salinities of 23.5 to 27 °/oo in the waters of Departure Bay and Ladysmith Harbour (British Columbia, Canada) from which *P. pileus* was collected. A series of experiments were run in which animals acclimated to 25 °/oo 10°C water were placed in columns in which the lower half contained 25 °/oo water and the upper half various dilutions with distilled water. No avoidance reactions were found. At dilutions above 15 °/oo the animals aggregated around the discontinuity. As the salt concentration decreased further (to approximately 10 °/oo and less) the animals became concentrated just below the discontinuity level.

In a homogeneous column *P. pileus* tend to aggregate at the top and bottom (Arai, 1973).

When temperature was combined with a salinity discontinuity small enough to cause only partial aggregation at the interface by itself, the two factors supplemented one another, so that all animals were aggregated around the discontinuity level (Arai, 1976).

Harder (1968) also noted that *P. pileus* reacts to salinity discontinuities and suggested that temperature gradients have the same effect.

6. Ikeda (1976) showed that the respiration of *P. pileus* increased 1.3 to 1.5 times after feeding.

   Gyllenberg and Greve (1979) report that (as is generally true) oxygen consumption bears an exponential relation to body weight i.e. consumption per unit weight is proportionally higher for young individuals than for adults. They report also a reduced rate of oxygen consumption during starvation and for individuals without comb plates. Oxygen consumption increases linearly over a temperature range of 2 to 24°C.

7. Latiff (1969) records that the oil counteracting agent Esso corexit 7664 is less toxic to *P. pileus* than Oil-Ex, Anti-Oil, TS 5, Sillarit, Vecom B24, Struktal J502, PS 777, Gamlen, Elimax, Slix, Peroklean and Moltoklar.

   The addition of crude oil reinforced the toxicity of Corexit.

   The lethal limits for *P. pileus* without Iraq crude oil was 0.667 Ml/l sea water; after the addition of crude oil the lethal limit was reduced to 0.222 ml/l sea water.

8. Boyle (1966) has recorded larvae of three trematodes, *Tergestia agnostomi* Manter 1954, *Lecith ocladium excisum* (Rud. 1819) and *?Pseudocreadium* Layman 1930, also larvae of the nematode *Contracaecum* Raillet and Henry, 1912.

   Boyle remarks that records of parasites of *P. pileus* are few; this may be a reflection of the small number of parasites in ctenophores or simply that they are of such small size that they are often overlooked or disregarded.

9. Horridge (1966) reports that *P. pileus* responds to strong vibrations in the water (strong enough to shake the animal) by contracting its tentacles, changing the rate of its comb-plates on one side relative to the other and turning over to swim downwards.

According to Grzimek (1974) stormy seas can be a great danger. After a storm undamaged animals are rarely found for a long time.

10. Knight-Jones and Morgan (1966) report that *P. pileus* responds to increased pressure by swimming upwards and to decreased pressure by swimming downwards. Some individuals are sensitive to changes of only 50 millibars. The animal usually rises buoyantly when inactive and spends its active periods swimming downwards.

Singarajah (1979) remarks that perhaps buoyancy mechanisms rely almost exclusively upon the exclusion of heavy sulfate ions, the animal being at only 32% of their concentration in sea water.

11. The ctenophore *Beroe gracilis* Kunne feeds on *P. pileus*. (Greve, quoted by Gyllenberg and Greve, 1979).

E. REFERENCES

Arai, M.N. (1973). Behaviour of the planktonic coelenterates, *Sarsia tubulosa*, *Phialidium gregarium*, and *Pleurobrachia pileus* in salinity discontinuity layers. *J. Fish. Res. Board Can.*, 30, 1105-1110.

Arai, M.N. (1976). Behaviour of planktonic coelenterates in temperature and salinity discontinuity layers. In Mackie, G.O. (Ed.) *Coelenterate ecology and behaviour*. (Plenum Press, New York and London, 1976), 221-218.

Boyle, M.S. (1966). Trematode and nematode parasites of *Pleurobrachia pileus* O.F. Muller in New Zealand waters. *Trans. roy. Soc. N.Z. Zool.* 8(6), 51-62.

Fraser, J.H. (1967). Zooplankton investigations from Aberdeen in 1967, Northern North Sea. *Annals biol. Copenh.* 24, 80-81.

Fraser, J.H. and J.A. Adams (1970). Deep-water plankton observations in Loch Fyne. *Rep. nat. Envion. Res. Coun.* 2, 9-10.

Grzimek, Bernhard (Ed. in Chief) (1974). *Grzimek's Animal Life Encyclopedia*, Vol. 1. (van Nostrand Reinhold).

Gyllenberg, G. and W. Greve (1979). Studies on oxygen uptake in ctenophores. *Ann. Zool. Fennici* 16, 44-49.

Haertel, L. and C. Osterberg (1967). Ecology of zooplankton, benthos and fishes in the Columbia River estuary. *Ecology* 48, 459-472.

Harder, W. (1968). Reactions of plankton organisms to water stratification. *Limnol. Oceanogr.* 13, 156-158.

Hardy, A. (1958). *The Open Sea*. Vol. I. (Collins).

Horridge, G.A. (1966). Some recently discovered underwater vibration receptors in invertebrates. In *Some Contemporary Studies in Marine Science*, Ed. H. Barnes, (George Allen and Unwin, London), 395-406.

Ikeda, T. (1976). The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton. I. Effect of feeding condition on the respiration rate. *Bull. Plankton Soc. Japan* 23(2), 1-10.

Knight-Jones, E.W. and E. Morgan (1966). Responses of marine animals to changes in hydrostatic pressure. *Oceanogr. Mar. Biol. Ann. Rev.* 4, 267-299.

Latiff, S.A. (1969). Preliminary results of the experiments on the toxicity of oil counteracting agent (Esso corexit 7664), with and without Iraq Crude Oil, for selected members of marine plankton. *Archiv fuer Fischereiwissenschaft* 20, 182-185.

Lingwood, P.F. (1976). Moribund macrofauna of the south-west Lancashire coast - 1971-1975. *Publication Lancs. Cheshire Fauna Soc.* No. 69, 6-7.

Palma, G., Sergio and Jaime Meruane, Z. (1975(1977)). Ecological aspects and growth of *Pleurobrachia pileus* (Ctenophora) in the Valparaiso region. *Invest. Mar. Univ. Catol. Valparaiso* 6(2/3), 25-40.

Popham, E.J. (1966). Studies on the littoral fauna of the Ribble estuary. *Naturalist Hull* No 897, 37-48.

Reeve, M.R. (1980). Comparative experimental studies on the feeding of chaetognaths and ctenophores. *J. Plankton Res.* 2(4), 381-394.

Reeve, M.R., M.A. Walter and T. Ikeda (1978). Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. *Limnology Oceanogr.* 23(4), 740-751.

Singarajah, K.V. (1979). Ionic regulation as buoyancy mechanism in *Noctiluca miliaris* and *Pleurobrachia pileus*. *Rev. Bras. Biol.* 39(1), 53-66.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XXIV THE RAT TAPEWORM *(Hymenolepis diminuta)*

by

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ABSTRACT

The precise environment of the Rat Tapeworm *Hymenolepis diminuta* is given, using as a basis for the classification the defining equations of Niven (*Erkeentnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equation, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A. INTRODUCTORY NOTE

Hymenolepis diminuta, the Rat Tapeworm, is widely dispersed over the whole world.

The definitive hosts are many and varied. Burt (1980) lists 99 species which act as definitive hosts, ranging through Canidae, Insectivora, Primates and in particular the Rodentia. In the latter he includes 5 species of *Microtus*, 6 species of *Apodemus*, 10 species of *Mus* and 9 species of *Rattus*. *R. norvegicus* and *R. rattus* seem to be the most common definitive hosts. Infections of *Homo sapiens* are considered to be accidental and no serious health hazard.

Intermediate hosts of *H. diminuta* are Coleoptera, Lepidoptera, Orthoptera, Siphonaptera and other arthropods. Burt (1980) lists 66 species of which 29 are beetles.

Fully developed cysticercoid larva of *H. diminuta* enters a definitive host when the intermediate host is eaten.

The top end, or 'head', of the adult tapeworm is called the 'scolex'. It is followed by a long chain of proglottids (segments), produced by segmentation from the 'neck' region of the animal. Thus as each proglottid ages it is found further down the length of the tapeworm; it becomes engorged with fertilized eggs which develop into oncospheres, may rupture and finally break off and is excreted by the host. The adult worm thus maintains a more-or-less constant length of about 70cm. However the size varies with the species of definitive host and the number of worms present.

The larva (oncosphere) is passed in the faeces of the definitive host and may be found in the gravid proglottids or free in the faecal material. An oncosphere has six hooks and is surrounded by a hardened outer envelope called a 'capsule'. Already at this early stage the larva has some of the features of the adult tapeworm, e.g., a scolex. When the capsule is pierced upon ingestion by the intermediate host (see n. 7) the oncosphere migrates to a new site; it then undergoes a metamorphosis and enters the cysticercoid (metacestode) stage, which matures steadily to adulthood; it is during the cysticercoid stage that the intermediate host is eaten by the definitive host.

Roberts (1980) writes that the growth rate after infection of the rat (i.e. at the cysticercoid stage) is "explosive" - it must "rival or surpass that of any other metazoan tissue, including embryonic and neoplastic. Within 15 days after infection of the rat, a normal *H. diminuta* will have produced up to 2200 proglottids and will have increased its length by up to 3400 times and its weight by up to 1.8 million times".

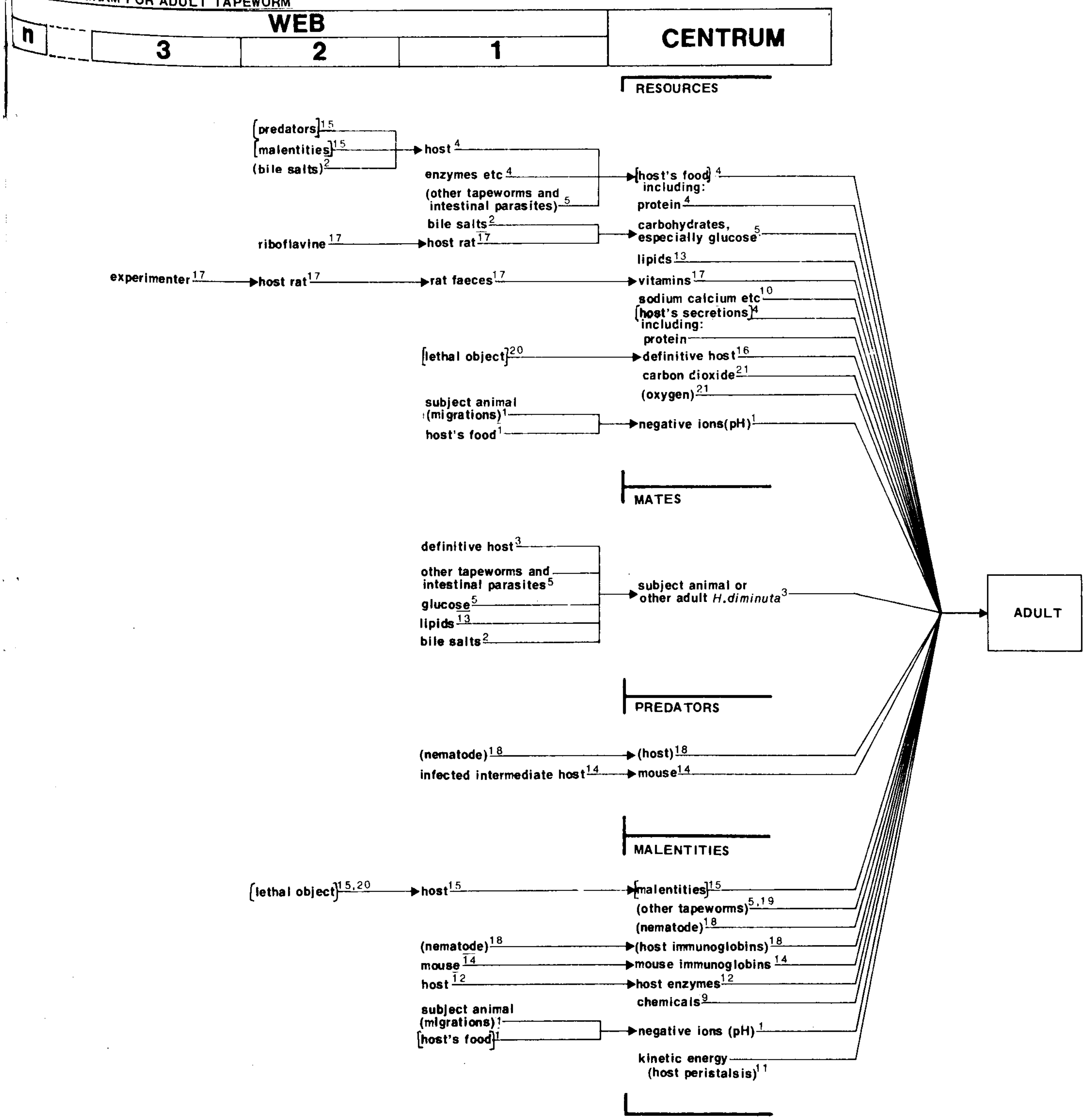
The adult tapeworm usually occupies a site in the small intestine of the rat host. There is evidence that it occupies different regions of the intestine at different times. These migrations appear to be a response to the host's feeding habits (Kennedy, 1976).

Under natural conditions the life-span of adult *H. diminuta* is probably as long as the host that harbours it. By artificial passage to successive hosts an adult tapeworm has been kept alive for 14 years - and may well live longer (Burt, 1980). The oncospheres can remain viable for about six months after having been excreted in the faeces of the definitive host.

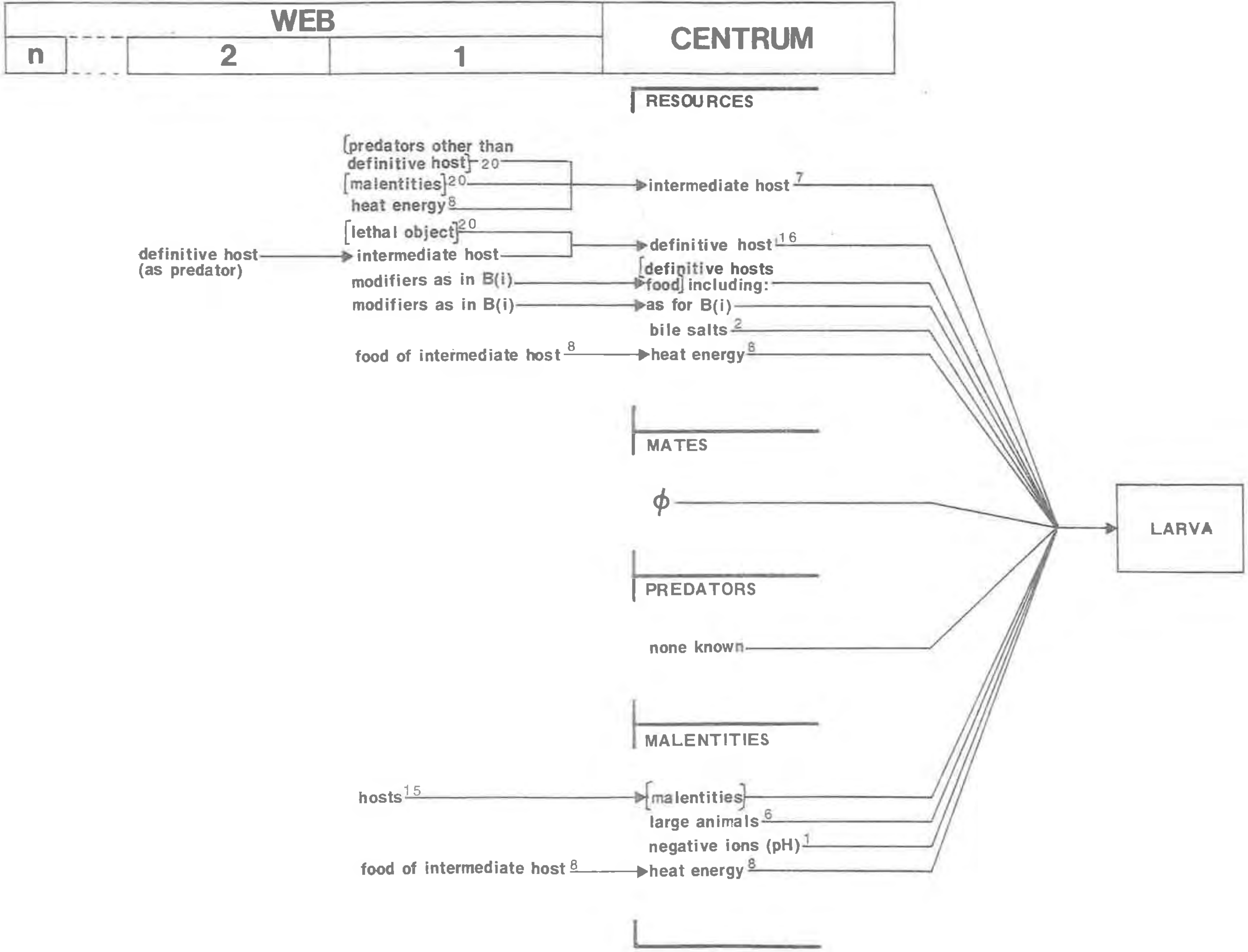
The way of life of this remarkable animal is described in the article by Lumsden and Specian (1980), quoting Dr H W Stunkard, as follows:

> " . . . As archaic as the Palaeozoic, they (tapeworms) are as modern as tomorrow. They have attained the ideal welfare state with all its beneficience; absolute security with an abundance of predigested food, and with a minimum of effort or exertion. . . . digestive, respiratory and circulatory organs have been discarded as superfluous, (since) every essential is provided in abundance with no concern for cost or other responsibility. With no need to expend energy for food or shelter, the cestode can get down seriously to the business of reproduction . . . "

B(I) ENVIROGRAM FOR ADULT TAPEWORM



B(ii) ENVIROGRAM FOR TAPEWORM LARVA



C. NOTES ON THE ENVIROGRAM

1. Following ingestion by the definitive host, the animal is protected from stomach acids by the outer layers of the cysticercoid during its passage through the host's stomach. If worms in the oncosphere stage are introduced into the stomach of the definitive host they will be destroyed, but they can establish themselves if introduced directly into the small intestine.

According to Mettrick (1980) pH is known to affect the migrations of *H. diminuta* and the region of the intestine with the lowest pH usually has the highest biomass of the tapeworm. The cestode is, however, capable of inhabiting any part of the intestine.

The principal determinants of the pH of the contents of the host's gut are the type of food and the time of ingestion.

2. Activation and excystment of the larva in the definitive host requires the presence of bile salts. Experiments in which a host rat was made bileless showed that *H. diminuta* either failed to establish itself in the gut or was severely stunted.

Egg production and carbohydrate absorption by the adult tapeworm from bileless hosts are also greatly reduced. Thus 'bile salts' will be a resource for the larva and both a modifier of mates and a modifier of carbohydrate ('glucose etc.') food resources for the adult.

Nevertheless, it is possible that the effect of the absence of bile salts may be indirect - i.e. *via* an effect on the digestion of the host.

3. *H. diminuta* is hermaphroditic; each proglottid contains both female and male reproductive organs. Like other tapeworms self-reproduction seems to be the norm, however cross-fertilization is not ruled out. Lumsden and Specian (1980) report that during copulation a male protusile organ is inserted into a genital chamber of an "appropriate" (it is not clear to us what is meant by "appropriate") proglottid of the same or another tapeworm. Self-insemination within the same proglottid is "not uncommon". The proportion of cross-fertilizations is unknown.

In any case reproduction can take place only within the definitive host which is therefore a modifier of mates.

4. Tapeworms have no mouth or digestive tract. Under normal circumstances in both definitive and intermediate hosts, they do not feed on the host itself but soak up nutrients, competing with the host for food which has already been processed. This is generally true of both protein and carbohydrate in *H. dimuta's* diet. However, Mettrick (1980) reports that depriving the host of protein has little effect because the small amount of protein secreted in the digestive juices of the host will still be sufficient for the cestode's growth.

Lumsden and Specian (1980) write that, roughly speaking, the body plan of *H. diminuta* may be conceived as "a gut turned inside out" ... "While the skin of most organisms serves as insulation from the environment, that of *H. diminuta*" ... "promotes nearly all forms of chemical interchange between the environment and the internal tissues, especially the absorption of nutriments". The success of *H. diminuta* in competing with the host mucosa for available nutrients is explained by the fact that, per unit weight, the effective surface area of the tapeworm is greater than that of the intestine by a factor of 3 or 4.

The food eaten by the host is processed and made acidic in the host's stomach; the acid chyme entering the duodenum is a mixture of semi-emulsified fat, protein, polypeptides, carbohydrates including non-hydrolized starch and water. Enzymes, water and various secretions from the host's pancreas, liver and intestinal walls are mixed with the chyme, the composition of which varies greatly from time to time, the host contributing the appropriate secretion to facilitate the digestive process. These enzymes (and other secretions) thus act as modifiers of the tapeworm's food; without the presence of the enzymes etc. the class of objects '[host's food]' would not enter the environment of the tapeworm as resources. Note that 'host' occurs as a first-order modifier of the tapeworm's resource 'host's food' both because it provides the food and because it is a competitor for it.

5. *H. diminuta* does not utilize all carbohydrates. Di- and poly-saccharides are not absorbed. The most useful of the carbohydrates is glucose. Galactose is used to a limited extent but "*H. diminuta* could not be supported on a galactose diet and sucrose, dextrin and maltose were

all inferior to glucose in promoting worm growth". (Mettrick, 1980). Kennedy (1976) reports that the tapeworm is impervious to fructose. Younger worms can take up glucose against steeper concentration gradientsthan older worms.

The rate of development and maturation within the definitive host depends particularly on the carbohydrate (and especially glucose) contents of the host's diet. The presence of other *H. diminuta*, and other parasitic larvae, is also known to affect these rates. It is certain that these co-parasites will compete with the subject animal for available carbohydrate (i.e. they will be first-order modifiers). In addition there may be an 'overcrowding effect', which, irrespective of mechanism, allows them to be classified as malentities.

Roberts (1980) reports that the presence of the acanthocephalan *Monoliformis dubius* has an 'overcrowding' effect similar to the effect observed when additional tapeworms are present (see also n. 19). Roberts reports also that while the 'overcrowding' effect is not well understood competition for host dietary carbohydrates probably plays some role and that foods other than carbohydrates are probably also involved.

6. The oncosphere (early larval stage) has a stiff outer shell which protects it from damage when it is excreted in the faeces of the definitive host. Anything crushingthe oncosphere will be a malentity; we have tentatively classified 'large animals' as malentities since we think this kind of accident must be not uncommon, even though not reported.

   Unless damaged an oncosphere can remain viable for about 6 months after having been excreted.

7. The intermediate host, an arthropod, mechanically ruptures (with its mouthparts) the outer capsule of the oncosphere, thus acting as a resource for the early larval stage of the tapeworm. The oncospherical hooks, in conjunction with the penetration glands, enable the larva to pass through the gut wall of the arthropod and establish itself.

   For some intermediate hosts the metacestodes develop more rapidly in females. The reason for this is unknown. The age of the intermediate host is also important; Ubelaker (1980) reports that older female intermediate hosts are less frequently infected than young or middle-aged females, while among males those of middle age were infected most often.

8. The development of the larva is dependent on temperature; within limits the higher the temperature the quicker the development. Ubelaker (1980) reports that 30°C is the most favourable temperature for the development of the metacestode, mature metacestodes being produced in 8 days. At 20°C the time is increased to 23 days. While temperatures above 30°C result in more rapid development, Ubelaker reports that they also result in a higher incidence of abnormalities; thus the range of heat energies corresponding to temperatures above 30°C constitute malentities Abnormalities due to heat stress can be reduced by changing the diet of the intermediate host (in this case a beetle) to pure sugar instead of whole wheat flour. Thus 'food of intermediate host' is a modifier of the malentity 'heat energy'.

The population of larval *H. diminuta* in beetles is increased at higher temperatures, the suggestion being that:

(i) The activity of certain enzymes in the oncospheres is increased, enabling them to increase their penetration and success, thus 'heat energy' acts here as a resource.

(ii) The beetles eat more at higher temperatures and therefore ingest more oncospheres. Here 'heat energy' is a modifier of 'host' which in turn is a modifier of the class of resources '[host's food]' (partially digested, see n. 4).

9. Ubelaker (1980) reports that mebendazde at a concentration of 0.1 gm/10 flour (the medium in which the beetles are kept) retards the development of the metacestodes within their hosts, while "one gram or higher concentrations were lethal to some, but not all, cysticercoids". Triethylene-thiophoramide kills some metacestodes if the beetle host walks on blotting paper which has been soaked in it for 3 hours.

10. While the skin of most organisms insulates them from the environment that of *H. diminuta* promotes nearly all forms of chemical interchange between the environment and the internal tissues. In addition to protein and carbohydrate absorption the tapeworm has a sodium transport system and calcium is required for the activation of muscle tissue (Lumsden and Specian, 1980). Presumably other elements are also required.

11. The peristaltic contractions of the definitive host's intestine are a constant threat to the tapeworm, which resists expulsion by maintaining continuous moderate contraction (tonus) of its muscles. The animal attaches itself to the host by using the two pairs of suckers on its scolex.

12. It is necessary for the tapeworm to protect itself against the digestive action of the enzymes of its host; the mechanism for doing this is unknown (although frequently discussed in the literature); we have entered 'host enzymes' as malentities modified by 'subject animal', on the envirogram since the potential danger to the tapeworm is so apparent.

13. *H. diminuta* absorbs fatty acids, modifies and stores them. At least some is used in egg production. Rat intestines infected with *H. diminuta* have been shown to contain approximately 30% less lipids than uninfested intestines. (However the lipid gradient down the intestine is generally the same).

14. Although *H. diminuta* in a rat host can survive until the host itself dies, the tapeworm is rejected within 9 to 14 days by a mouse host. The mechanism for this difference is not completely understood (Hopkins, 1980). Formally, we have two alternatives:

(i) The mouse can be classified as a predator;

OR

(ii) From a biochemical perspective, we can classify 'host immunoglobulins' as malentities.

In both cases we are talking about an immune response of the mouse.

(i) We can classify the mouse as a predator, since there is some evidence that the ejection of the tapeworm causes an increase in H(mouse) (and certainly there is a decrease in H(tapeworm)). The increase in H(mouse) will occur, for example, because the mouse will no longer lose the protein secreted during digestion (see n. 4); note that the loss of ingested protein is insufficient grounds for classifying the mouse as a predator because in this case the tapeworm is acting as a first-order modifier of the mouse's food i.e. it is causing only indirect harm and therefore the excreting of the tapeworm does not directly cause an increase in H(mouse). Of course the mouse will be a predator only if it becomes a host of *H. diminuta* - i.e. after eating an infected intermediate host. The latter is thus a first-order modifier.

(ii) Mouse immunoglobulins have been observed bound to the outer tegument of the tapeworm; it is possible that the tegumental surface is damaged when this occurs and facilitates ejection. From this point of view we can classify 'mouse immunoglobulins' as malentities. The mouse will be a first-order modifier.

Though formally incorrect, we have included both cases on the envirogram.

15. Both the definitive and intermediate host provide protection to the tapeworm against a large class of malentities. However the sword is double-edged as the tapeworm will almost certainly die if its host is killed (see note 20).

16. Because the tapeworm is unable to reproduce unless it is living in a definitive host, the definitive host is a resource (because that part of H(tapeworm) dealing with the probability of reproducing is directly increased).

17. Establishment and growth of *H. diminuta* is severely inhibited when the host rat is fed a diet deficient in all B vitamins, providing the host is prevented by the experimenter from eating its own faeces. If the rat is allowed to do this (as it is its normal behaviour) the lack of B vitamins in the diet has no effect on the cestode (Roberts 1980). The mechanism here is not clear to us.

When the host rat is fed a diet lacking riboflavine the tapeworm grows larger, whether or not the host is allowed to eat its faeces. Roberts (1980) suggests that this may be because more glucose is available to the cestode, since the host's glucose absorption is reduced when it is fed on a riboflavine-deficient diet. Riboflavine is thus a modifier of the host rat, which is in turn a modifier of glucose as a resource in the tapeworm's environment.

18. The presence of the nematode *Nippostrongylus brasiliensis* adversely affects *H. diminuta*. We have classified the nematode as a malentity since "it would appear that the effects are" either "inhospitable conditions induced by the pathogenic effects of the nematode", or "stimulation by the nematode of the immune response of the host, or both" (Roberts 1980). If the first of these alternatives is correct then the nematode can be tentatively classified as a malentity because while H(tapeworm) is decreased there is no clear evidence that H(nematode) is increased. (If there were clear evidence for the latter the nematode would be classified as a predator). The situation with the second alternative is more complicated (similar to the mouse-mouse immunoglobulin case of n. 14). Because of the stimulated immune response we can classify the nematode as a first-order modifier either of the host as predator or of host immunoglobulins as malentities.

We have put all of the above alternatives on the envirogram; all are bracketed to indicate tentativeness.

19. Other tapeworms may sometimes act as malentities in the environment of the subject animal; the mechanism causing the so-called "crowding effect" (Roberts, 1980) is unknown; Roberts writes "The important developmental implication of the crowding effect is that worms in the host's intestine are, by whatever means, influencing growth, cell division, DNA synthesis and numerous other physiological parameters of other worms".

20. Under natural conditions the life-span of adult *H. diminuta* is probably as long as the host that harbours it. Thus any object, animate and inanimate, which leads to the demise of the host will also kill the subject unless, of course, it is possible for the tapeworm to survive the ingestion of one definitive host by another. Burt (1980) reports that by artificial passage to successive hosts,

an adult tapeworm has been kept alive for 14 years - and may well live longer.

It is also possible that an object lethal to an intermediate host may kill the cysticercoid.

Nevertheless there would seem to be a real possibility of the cysticercoid surviving and the dead intermediate host being eaten by a definitive host.

21. *H. diminuta's* energy metabolism is usually anaerobic; this involves the breakdown of glucose and the fixation of CO_2. Nevertheless aerobic energy metabolism is not precluded (Fioravanti and Saz, 1980). Carbon dioxide is the gas most abundant in the intestinal lumen, reaching partial pressures as high as 680mm Hg. Reports on the oxygen content of the rat gut differ but according to Mettrick (1980) it is probably about 40 to 50mm Hg in places. The partial pressures of both gases are higher in parasitized than in unparasitized guts.

E. REFERENCES

Arai, Hisao P. (Ed.) 1980. *Biology of the Tapeworm Hymenolepis diminuta* (Academic Press).

Including:

Arai, Hisao P. Migratory Activity and Related Phenomena in *Hymenolepis diminuta*. 615-637.

Burt, M.D.B. Aspects of the Life History and Systematics of *Hymenolepis diminuta*. 1-57.

Fioravanti, Carmen F. and Howard J. Saz. Energy Metabolism of Adult *Hymenolepis diminuta*. 463-504.

Hopkins, C.A. Immunity and *Hymenolepis diminuta*. 551-614.

Lumsden, Richard Dick and Robert Specian. The Morphology, Histology, and Fine Structure of the Adult Stage of the Cyclophyllidean Tapeworm *Hymenolepis diminuta*. 157-280.

Mettrick, D.F. The Intestine as an Environment for *Hymenolepis diminuta*. 281-356.

Roberts, Larry S. Development of *Hymenolepis diminuta* in Its Definitive Host. 357-423.

Ubelaker, John E. Structure and Ultrastructure of the Larvae and Metacestodes of *Hymenolepis diminuta*. 59-156.

Kennedy, C.R. (ed.) (1976). *Ecological Aspects of Parasitology.* (North-Holland).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS
XVI THE EARTHWORM *(Lumbricus terrestris)*

by

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ABSTRACT

The precise environment of the earthworm (*Lumbricus terrestris*) is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis, 1982*). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

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A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A INTRODUCTORY NOTE

Lumbricus terrestris is an hermaphroditic segmented worm. It produces cocoons roughly 6mm long by 4.5 to 6mm in diameter which hatch into immature worms similar to adults except for the lack of genital organs.

The animal is usually pigmented red, brown or a combination or occasionally even greenish. It has epidermal sense cells sensitive to touch and primitive 'eyes' which are sensitive to light. It is photopositive to very weak sources of light (i.e. it moves towards such a source) but photonegative to stronger sources. The worm has high-speed nerve impulse transmission (600m/sec). Most respiration is through the body surface which is kept moist by mucous glands in the epidermis. Oxygen is taken up by haemoglobin in the blood.

The worm has fewer segments as it ages, even though it continues to increase in size. In culture the animal increased in weight for about 3 years. The increase occurred almost entirely during the autumn and spring; sometimes a little weight was lost in winter or summer.

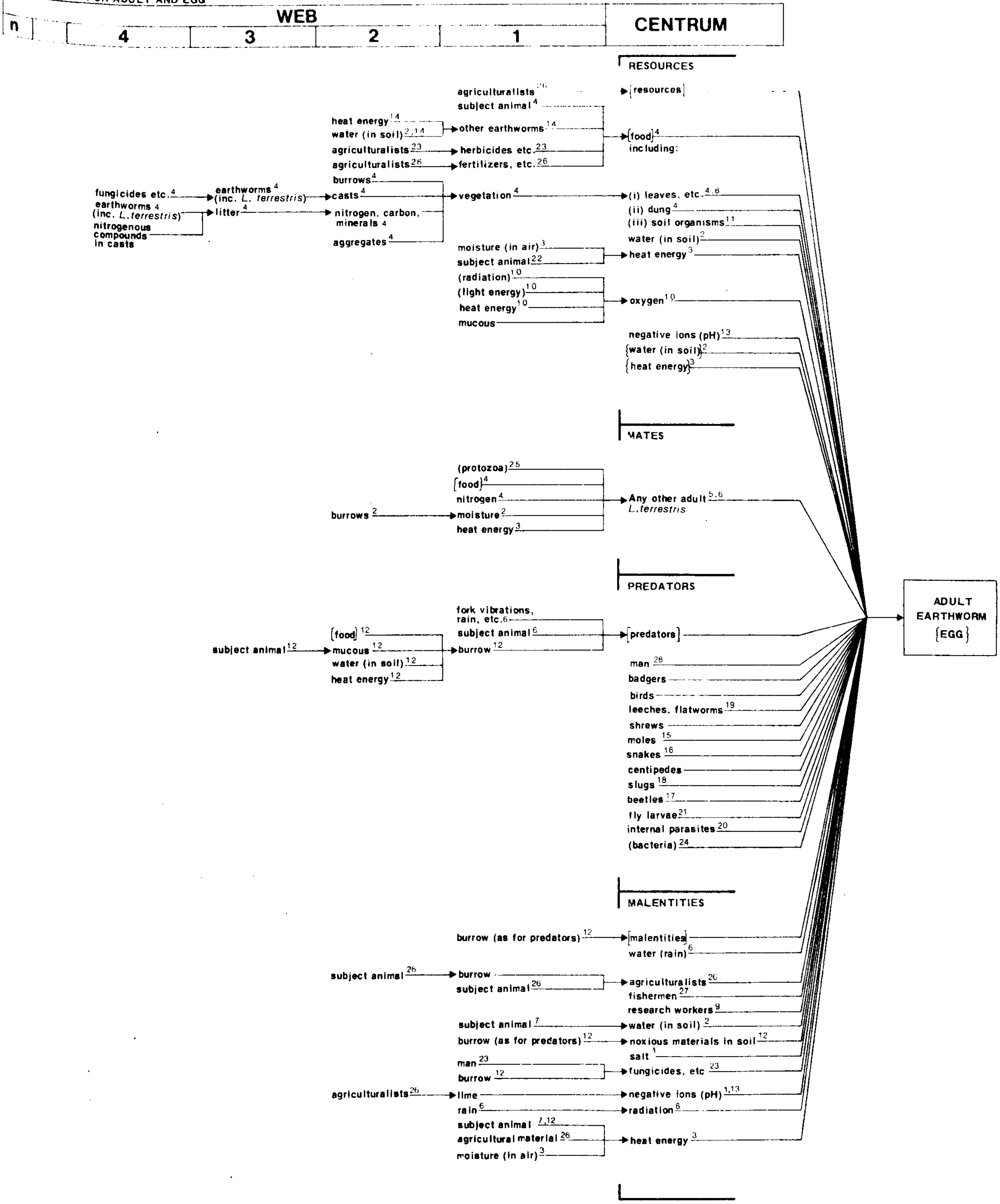
The breeding period for this species is unknown, however for another lumbricid the breeding period lasted about half the adult life span. The number of fertilized ova per cocoon ranges from 1 to 20 for lumbricids but often only 1 or 2 survive to hatch. In the field *L.terrestris* may take a year to reach maturity; it is thought that this period will vary greatly according to temperature - the higher the temperature (within limits) the faster the development. The field life span of mature lumbricids is estimated to be no more than a few months because of hazardous conditions; the potential longevity has been calculated to be 4-8 years. In protected cultures *L.terrestris* has been kept for up to 6 years.

L.terrestris creates permanent deep burrows. It can easily move to deeper soil in order to escape adverse conditions (see n.12).

The animal is probably dispersed by the cocoons being carried in soil on agricultural equipment, hooves of animals and streams. Earthworms are most abundant near populated areas, with dense populations in some places; as many as 640 earthworms per square metre have been collected (in New South Wales). The natural distribution of *L.terrestris* is Siberia, Europe, Iceland and North America, but it has been transported throughout the world. It is rarely found in deserts, mountains, rocky areas and areas under constant snow and ice. If conditions are suitable the number of earthworms usually increases until food becomes the limiting factor.

In this Working Paper we have made use of the information contained in the book on earthworms by Edwards and Lofty (1972). Much of this information is not specifically about *L. terrestris*, but more general information usually at the family level.

B. ENVIROGRAM FOR ADULT AND EGG



C NOTES ON THE ENVIROGRAM

1. Most earthworms cannot tolerate salt water even for short periods, thus the oceans have acted as a natural barrier to its dispersion.

2. Prolonged droughts markedly decrease numbers of earthworms and it may take as long as 2 years for populations to recover when conditions become favourable again - earthworm fecundity is greatly influenced by moisture. However *L.terrestris* is better at surviving dry conditions than most other earthworms, probably because of its deep burrows (see n.12).

The normal adult earthworm is 75 to 90% water by weight. It is often not fully hydrated and may increase its weight by 15% if placed in water.

Neither the thin permeable cuticle nor the mucus-secreting epidermis can do much to prevent water loss and earthworms face considerable risks of dehydration, however 70 to 75% of the body weight of *L.terrestris* can be lost without killing the animal.

Earthworms are much more active in moist soils than in dry ones (see also n.14). During periods of much rain individual adult *L.terrestris* come out onto the soil surface at night.

L.terrestris has never been recorded in flooded soils even though it has survived under water for several months in the laboratory (see n.10)

The cocoons survive dry conditions better than adults, and hatch when conditions become favourable.

Cocoons can also hatch below water and the young worms feed and grow even though totally immersed.

If the soil is very moist cocoons are deposited virtually on the surface; if it is dry the cocoons will be placed much deeper.

3. Temperature affects activity, metabolism, growth, respiration and reproduction of earthworms.

In general the most suitable conditions for activity of earthworms on the surface are nights when the soil temperature does not exceed 10.5°C., the air temperature is above 2°C and there has been some rain in the previous 4 days.

L. terrestris has been shown to prefer a temperature of about 10°C (although it develops faster at higher temperatures). The adult worms are most active during spring and autumn.

It has been suggested that earthworms, particularly in arable soils, may be destroyed by frost; in pasture and woodland it is unlikely that the soil would freeze deep enough to kill the animals.

The upper lethal temperature for *L. terrestris* is 28°C. They may however survive in high temperatures because they can maintain their bodies at a temperature lower than the ambient by evaporating water from the surface of their bodies. Earthworms in general can survive higher temperatures better in moist air.

The fecundity of some lumbricid spp. is quadrupled as the temperature rises from 6°C to 16°C.

In tests on 2 species of *Lumbricus* it was found that below 3°C no cocoons are produced. Thus in the wild the majority of eggs tend to be produced during the summer months. The higher temperatures are also necessary for hatching; there is a tendency for an accumulation of cocoons over the colder months and thus relatively higher numbers hatch during late winter and early spring. This aids the survival of the species since the young worms cannot withstand cold. The cocoons survive extremes of temperature better than adult worms and hatch when conditions become more favourable.

4. *L. terrestris* scavenges for food on the soil surface. Usually it keeps its tail in its burrow and if touched withdraws wholly therein.

Earthworms consume large amounts of food. It has been calculated that earthworms in general eat as much as 80mg of food per day per gram body weight. *L.terrestris* is estimated to pass 100-120mg per gram body weight per day through the gut.

Organically poor soils do not usually support many earthworms. Conversely if there are few earthworms the decaying organic matter usually lies in a thick mat on the surface. Protein-rich litter is taken more readily than protein-poor.

Casts (faeces) are often left on the surface of the soil. These casts contain organic matter in a form available to plants, thus the worms are useful in aiding plant growth. Darwin, in 1881, estimated that the annual production of worm casts in English pastures was 18.7 to 40.3 tonnes per hectare (7.5 to 16.1 tons per acre) which is equivalent to a soil layer, 5mm deep being deposited annually.

L.terrestris seems to be responsible for a large proportion of the fragmentation of litter in woodlands of the temperature zone, e.g. in one particular apple orchard the animal removed more than 60% of the autumn leaf during the course of the winter; in a comparable orchard from which *L.terrestris* had been virtually eliminated by spraying with a copper-based fungicide the soil had a relatively extremely poor crumb structure.

The major factor affecting the amount of litter consumed and turned over by earthworms seems to be the amount of litter available.

Part of the earthworm contribution to soil fertility is making mineralized nitrogen available to plants by:

(i) excreting nitrogen products, the nitrogen being obtained from plants in a form unsuitable for other plants,

(ii) returning it to the soil in a suitable form for plant uptake.

The resulting nitrogen contributes significantly to plant growth.

Another important contribution by earthworms towards plant growth is the adjustment of the carbon/nitrogen ratio achieved jointly by the worms' respiration and digestion.

Soils with earthworms generally have a higher base-exchange capacity and more exchangable calcium, magnesium and potassium and available phosphor than soils without. The following tables are from Edwards and Lofty (1972).

Table 15

Comparison of the available mineral elements in the casts of earthworms and in the upper layers of a ploughed soil in Connecticut, U.S.A.

	Earthworm Excreta	Depth of soil layer	
		(0-15 cm)	(20-40 cm)
Loss by ignition (%)	13.1	9.8	4.9
Carbon nitrogen ratio	14.7	13.8	13.8
Nitrate nitrogen (ppm)	21.9	4.7	1.7
Calcium:			
Total (%)	1.19	0.88	0.91
Exchangeable (ppm)	2,793	1,993	481
Exchangeable calcium/total calcium (%)	25.6	24.4	6.1
Magnesium:			
Total (%)	0.545	0.511	0.548
Exchangeable (ppm)	492	162	69
Exchangeable magnesium/total magnesium (%)	9.19	3.24	1.29
Phosphorus available (ppm)	150	20.8	8.3
Potassium available (ppm)	358	32.0	27.0
pH	7.00	6.36	6.05

(From Lunt and acobson, 1944)

TABLE 16

Mineral elements in soil and worm casts
(mg per 100g dry weight)

	Casts	Soil
C	8 550	3 925
N	536	350
C : N ratio	16	11
P(aqua regia)	102	68
P(lactate-soluble)	13.7	2.2
K(soda extract)	1 097	799
K(lactate-soluble)	44.6	7.0
pH(H_2O)	5.8	5.0
pH(KCl)	5.4	4.0

(From Graff, 1972)

The decomposition of organic material in soil is speeded up by the addition of nitrogenous compounds via earthworm casts.

The burrowing activities and turnover of material assist in keeping the soil well-drained and aerated. Aggregates of mineral granule are also necessary for well-drained and aerated soil and the presence of earthworms raises the number of these aggregates.

Many experiments with earthworms, including *L.terrestris*, have shown that crop yields increase when worms are added to the soil.

5. *L.terrestris* is hermaphroditic. An adult will mate with another adult on the surface of the soil, lying in close contact head-to-tail. Unlike some other segmented worms it seems unlikely that it can produce cocoons parthenogenetically.

L.castaneus and *L.rubellus* have been cross-bred but it is not known whether this is possible for *L.terrestris*.

The breeding period for this species is unknown, however for another lubricid the breeding period lasted about half the adult life span. The number of fertilized ova per cocoon ranges from 1 to 20 for lumbricids but often only 1 or 2 survive to hatch. In the field *L.terrestris* may take a year to reach maturity; it is thought that this period will vary greatly according to temperature - the higher the temperature (within limits) the faster the development. The field life span of mature lumbricids is estimated to be no more than a few months because of hazardous conditions; the potential longevity has been calculated to be 4 - 8 years. In protected cultures *L.terrestris* has been kept for up to 6 years.

It produces cocoon roughly 6mm long by 4.5 to 6mm in diameter which hatch into immature worms similar to adults except for the lack of genital organs. In at least some species of earthworm more cocoons are produced by those worms fed on decaying animal organic matter than those fed on plant material. Nitrogen-rich diets also result in the animals producing more cocoons. Worms fed on sewage sludge, straw or farmyard manure produce less than one-tenth of the cocoons of worms fed on bullock and horse droppings.

6. When mating, the two worms lie in close contact head-to-tail, and do not readily respond to external stimuli such as touch and light. Presumably this makes the animals easy prey for its macroscopic predators. We have classified the animal itself as a modifer of all predators for this reason.

Another way in which *L. terrestris*, by its own beahviour, modifies a potential predator is by resisting the pull if it is grasped when partly out of its burrow; the worms expands its posterior segments so as to grip the walls of the burrow and completely fill its exit - making it very difficult to pull it right out, particularly if it is a large individual - in fact, it may break in two rather than relinquish the grip. After such an attack the animal usually retreats deep into the burrow and may remain there for a long period.

Many kinds of stimuli can cause earthworms to come to the surface of the soil, where they are more accessible to predators:

(i) vibrations from a fork inserted in the soil;
(ii) stamping;
(iii) electrical stimulus i.e., electric current applied to the soil;
(iv) chemical stimuli, from e.g., formaldehyde or dilute potassium permanganate;
(v) rain.

"Often large numbers of worms appear on the surface of the soil after rain and many of these die, probably due to exposure to ultra-violet or radiation. No adequate explanation of this behaviour has yet been offered." (Edwards and Lofty, 1972).

All earthworms can regenerate either the anterior or posterior portions of their bodies if necessary, providing not too many segments are lost and the nervious system of the remaining section is intact. Sufficient (but not too much) oxygen is necessary, and temperature is also a factor.

7. It has been claimed that no *Lumbricus* spp. enter diapause, nevertheless *L. terrestris* may still become quiescent in deeper soil during adverse periods, becoming active again when conditions improve. Earthworms can tolerate cold wet conditions better than hot dry ones and this may explain why more worms are quiescent in summer than in winter. Quiescence may amount to living off reserves when little food is available or when conditions do not favour food gathering.

8. *L.terrestris* feeds on leaf and other plant material and fungi obtained on the soil surface. It eats all parts of a leaf, including veins and ribs. The worm does not actually eat the material at the surface to any great extent but first pulls it into the mouth of the burrow to a depth of about 2.5 to 7.5cm so forming a plug which may protrude from the burrow.

> "There have been several suggestions as to why they do this. it may be in order to camouflage the entrance to the burrow, although the plug often makes the burrow more obvious (Plate 6a and b). Alternatively, it may be to prevent the entry of water into the burrow during heavy rain or to keep out cold air. Whatever the reason, these earthworms never leave the mouths of their burrows exposed, and will replug them very quickly if the original plug is removed. If the mouth of the burrow is in an area where there is insufficient organic material to form a plug, they will use inorganic material, commonly small piles of stones termed 'worm cairns' which may be seen in gravel paths, blocking the mouths of burrows. Individuals of *L.terristris* normally feed on food material only within their burrows, and as far more material is stored than can be used between normal foragings, there is adequate food when inclement conditions on the soil surface prevent them from foraging, or when the local food supply is temporarily exhausted.
>
> *L.terrestris* carefully selects its food material and pulls most kinds of leaves into the burrows by the tip of the laminae, leaving the non-palatable petioles projecting from the burrow. Darwin (1818) reported that when earthworms were offered paper triangles they were always grasped by the sharpest corner, usually without any attempt to seize any other corner, and this was confirmed by Hanel (1904) although she also found conflicting evidence that if leaves of lime trees were cut so as to round of the pointed apex, worms still grasped them at this point. The general tendencey seems to be for the worms to grip the pointed tips of leaves, for instance, Darwin (1881) reported that of 227 leaves of various types, 181 had been drawn in by the tips of the leaves and only 26 had been pulled in by the base of the petioles. In some unexplained way, worms can discern the best way to drag leaves

> into their burrows with minimum effort. Darwin also described other behavioural patterns shown by individuals of this species during their foraging activities. Baldwin (1971) demonstrated experimentally that *L.terrestris* is much more active when food is available than when it is not." (Edwards and Lofty, 1972)

Thus the animal, by its behaviour, acts as a modifier for all food (see also n.4 and n.11). *L.terrestris* shows preference for particular species and conditions of leaves. The palatibility of leaves to earthworms depends largely on their polyphenol content. Alkaloid concentration above a certain level makes leaves unpalatible to earthworms. Acids such as phosphoric, tartaric, citric, oxalic and malic acid are acceptable in low concentrations but not in high. The order of preference for earthworms in general for a range of leaves has been found to be: lettuce, Kale, beet, elm, maize, lime, birch, oak, beech. Litter becomes more palatable after a few weeks of weathering which leaches out unpalatable polyphenols. For *L.terrestris* there is an inverse correlation with the amount of soluble carbohydrates.

9. Many experiments have been done to measure the learning behaviour of the animal. These mostly involve applying electric shocks or other unpleasant stimuli to the worm. It is difficult to see how such experiments can be of benefit to *Homo sapiens* so we have classified 'research workers' as malentities in this case - however see General Introduction, revised version 1983, for a discussion of this point.

10. Respiration rates for *L.terrestris* range from $38.7 - 45.2\text{mm}^{-3}O_2$ per hour per gram body weight at 10°C to $31 - 71\text{mm}^{-3}O_2$ at 16 - 17°C. Higher rates have been recorded by other workers. The animal can respire when completely submerged and so survive for long periods, dependent on the partial pressure of the dissolved oxygen. It has survived from 31 to 50 weeks in soils totally submerged beneath aerated water - even then the factor limiting survival was probably lack of food rather than lack of oxygen.

There is some experimental evidence of a diurnal rhythm in oxygen consumption and activity, with maximal rates at about 6a.m. and 7p.m.

It has been suggested that respiration decreases in response to ultra-violet light (see also n.6)

Oxygen is necessary for regeneration (n.6)

Most respiration is through the body surface which is kept moist by mucous glands in the epidermis. Oxygen is taken up by haemoglobin in the blood.

11. In addition to plant material and fungi *L. terrestris* derives its nutrition from nematodes, living protozoa, rotifers, bacteria, other micro-organisms and the decomposing remains of large and small animals, most of which are extracted from the soil as it passes through the gut. A high percentage of mineral matter is also passed through the gut as the animal burrows.

L. terrestris shows a strong preference for soils containing dung. In experiments in grassland plots at Rothamsted (England) and average of 13.1 animals preferred unmanured plots, against 22.5 which preferred plots with dung. In arable land the figures were 0.23 and 10.8.

12. Earthworms form burrows by literally eating their way through the soil and by pushing through crevices. Ejected soil in pressed into soil interspaces.

In the laboratory *L. terrestris* has been observed to take 4 to 6 weeks to form an extensive burrow system. The texture of the soil is important; the time taken in clay could be 4 or 5 times longer than in light loam.

If adequate food is available at the surface *Lumbricus* spp. do not burrow extensively, but a shortage of food greatly increases burrowing activity.

L. terrestris has burrows which are vertical for most of their depth but branch extensively near the surface. The diameter is from 3mm to 12mm depending on the size of the animal. It is not known if the original burrows are widened with growth or if new burrows are dug. The permanent burrow extends commonly to about 1 metre below the surface but can penetrate to a depth of 2.5 metres. Very cold and very dry soil seem to be the main factors in causing movement to depth.

The burrow serves to protect the animal against predators and malentities. The animal itself secretes a mucus which lines the walls and forms a protective coating against noxious materials. Pesticides are often markedly reduced in concentration by the time they reach the animal.

13. pH can be detected by *L.terrestris*. The animal will not burrow into soil with a pH below 4.1 according to some workers, however others consider that *L.terrestris* is not very sensitive to pH and have reported it as existing within a wide range down to a pH of about 3.3.

Some workers have reported that earthworm casts are usually more nuetral than the soils in which they live.

14. The following earthworms may be found living near *L.terrestris* and thus (potentially) competing for food: *Allolopophora caliginosa, A.nocturna, A.chlorotica, A.longa, A.rosea, L.castaneus, L.rubellus, Octolasium lacteum, O.cyaneum.*

In one study these other earthworms become quiescent in both summer and mid-winter when *L.terrestris* did not. Thus seasonal changes (temperature, moisture) act as modifiers of the competitors of *L. terrestris*. Also other *L.terrestris* individuals are more active in moist conditions and become increasingly competitors of the subject animal.

15. Moles are particularly common predators. They are reported to 'store' catches until required, ensuring that the worms do not escape by biting 3 to 5 segments from their anterior ends.

16. In South Africa the night adder *Causus rhombeatus* is reported to attack and devour giant micro chaetid worms. It seems likely, although there are no reports, that snakes will also attack *L.terrestris*.

17. Many carabid and staphylinid beetles and their larvae eat earthworms.

18. Three species of carnivorous slug are known to eat earthworms at a rate of 1 worm per week: *Testacella scutulum, T.haliotidea, T.maugei.*

19. A few species of leech eat earthworms e.g. *Trocheta subviridis.*

The flatworm *Bipalum kewensis* is also a predator, particularly in greenhouse soils. It is probably more important in warmer climates.

20. Earthworms have many internal parasites, including bacteria, protozoa, platyhelminthes, rotifers, nematodes and dipteroid larvae. See D, also notes 19, 21, 24.

21. The larvae of muscoid flies parasitize earthworms e.g. the cluster fly *Pollenia rudis* is a major parasite in the U.S.A. A worm may harbour 1 to 4 larvae; only 1 will mature, progressively destroying the worm and eventually killing it. Other parasitic flies are *Onesia subalpina, O.sepulchralis, Sarcophaga haemorrhoidalis* and *S.carnaria.*

22. Earthworms in general show some ability to migrate away from unsuitably high temperatures.

23. Spraying with a copper-based fungicide and treating with ammonium sulphate have been found to eliminate, or almost eliminate *L. terrestris* and other earthworms.

At least some of the herbicides, insecticides and fungicides applied to soil to kill pests are broad spectrum biocides and also kill earthworms. Arsenic compounds, particularly lead arsenate, and copper sulphate are toxic to earthworms in the high concentrations that are sometimes used in orchards cultivated soils. Fumigants such as D-D, methan sodium and methyl bromide used to control soil pathogens and nematodes permeate the soil as vapours and kill most worms, even in the deep burrows. Chloropictin is highly toxic to earthworms.

Her icides can affect the animal either directly or by killing the vegetation thus acting as a first-order modifier of food. DNOC at high concentrations kills worms directly and NNOC, chlorpropham and propham affect worms slightly, as also do triazine herbicides e.g. atriazine and simazine.

Among insecticides aldrin, dieldrin, endrin and telodrin have an effect only at high levels, BHC is only slightly toxic, chlordane and heptachlor are both extremely toxic.

The following are reported as only slightly toxic: chlorfenrinphos, disul foton, malathion, dyfonate, 'Dursban', fenitrothion, zinophos. Phorate is reported as extremely toxic and may eliminate earthworm populations even at normal rates of application. Of the three carbamate insecticides tested on earthworms carbaryl is toxic at low concentrations but aldicarb and carbofuran have only a slight affect.

Earthworms are on the whole not very susceptible to pesticides, however they may possibly concentrate some of these substances e.g. DDT in their tissues, thus harming their predators. (These earthworms would then act as malentities in the environment of worm-eating birds etc). The evidence for this is not strong.

24. At least 50 bacteria isolated from *L. terrestris* have also been found in the surrounding soil. It seems likely that the majority of bacteria found in the casts are not harmful to the animal but simply multiply in its gut and continue to increase in the casts. Some of the bacteria are nitrogen-fixers. The following table is from Edwards and Lofty (1972):

TABLE 17

Numbers of micro-organisms in different parts of the intestine of *L. terrestris*

	($x\ 10^4$)		
	Fore Gut	Mid Gut	Hind Gut
Actinomycetes	26	358	15 000
Bacteria	475	32 900	440 700

(From Parle, 1959)

Earthworms have been incriminated in transmitting many parasites and diseases of animals and plants, the spores of many pathogenic fungi, in particular dwarf bunt (*Telletia controversa*), *Fusarium* and *Pythium*, also cysts of the potato root of eelworm i.e. the nematode *Heterodera rostochiensis*, all of which are more infective, productive and viable following passage through an earthworm. The animal has also been suspected to be a vector of animal viruses e.g. that which causes 'foot-and-mouth' disease of domestic animals.

Earthworms are known to be essential intermediate hosts for various animal parasites: protozoa, cestodes (tapeworms) and nematodes. They can also be passive vectors of the eggs of various parasites.

It has been suggested that *L. terrestris* can infest human beings; the animal has been reported from human faeces and the vagina.

25. For the earthworm *Eisenia foetida* certain mobile protozoa have been found to be an essential item of the worm's diet for it to reach sexual maturity. A corresponding system for *L. terrestris* is not known.

26. Ploughing is unlikely to affect *L. terrestris* because of its deep burrow (see n.12), however preparation of seed beds with rotary cultivation, harrowing, disking etc. could be expected to cause some damage, most of which is likely to be repaired by the animal itself (see n.6)

Indeed moderate cultivation with careful selection of machinery may increase worm numbers, thus agriculturalists may act as modifiers of the animal's resources in this sense.

In cold areas the spreading of crop remains by agriculturalists can assist insulation and so modify the effects of low temperatures on the worm.

The type of crop grown generally affects earthworm abundance; continual row cropping is particularly disadvantageous. A regime of row cropping every third year results in markedly more worms than more frequent now cropping; a regime of winter grain and summer legume is markedly better than a number of other types of culture.

The addition of fertilizers (e.g. superphosphate, lime) may cause an increase in, say, clover, which has been known to result in a fourfold increase in the weight of earthworms in the soil. Lime also seems beneficial particularly in acidic soils presumably because the pH becomes more neutral.

27. Many earthworms are used as fish bait. *L. terrestris* seems to be the

most common and is bred for this purpose in the U.S.A..

28. In various parts of the world earthworms have been used as human food.

They can also be used for testing pregnancy and are used in a variety of laboratories for various purposes such as testing carcinogenic agents.

D. DETAIL

Bacteria reported from earthworms include *Spirochaeta* and *Bacillus botulinus*. Little is known of the effect on the worm.

The most numerous and probably the most inportant protozoan parasites of earthworms are the Gregarina, which are to be found in most parts of the worm's body. The following genera have been reported:

Disticopus, Rhyncocystis, Echnicoystis, Grayallia, Craterocystis, Monocystis, Nematocystis, Aikinetocystis, Nellocystis and *Pleurocystis*

A number of ciliate protozoa also infest the bodies of earthworms although few cause any serious harm. The genera include:

Anoplophrya, Maupasella, Parabursaria, Hoplitophrya, Plagiotoma and *Metaradiophrya.*

Other protozoa include *Myxocystis, Sphaeractinomyzon* and *Thelohania.*

Among platyhelminths the larvae of *Polycercus* is found in *L.terrestri* also the cysticercoid stage of *Taenia cuneata* is found in some other earthwroms.

Many nematodes occur in earthworms, few causing serious damage. In most cases the earthworm is an intermediate host. Genera include:

Rhabditis, Heterakes, Syngamus, Dicelis, Stephanurus, Metastrongylus, Spiroptera, Synoecnema and *Diporochaeta.*

The larvae of muscoid flies parasitize earthworms e.g. the cluster fly *Pollenia rudis.* Other flies include: *Onesia subalpina, O.sepulchralis, Sarcophaga haemorrhoidalis, S.carnaria.*

E. REFERENCE

Edwards, C.A. and Lofty, J.R. (1972) *Biology of Earthworms*. (Chapman and Hall, London).

THE TWENTY-FIVE ANIMAL STUDY

(b) *Six arthropods:*

Copepod
Waterflea
Mosquito
Honeybee
Blowfly
Butterfly

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XVIII THE MARINE COPEPOD *(Calanus finmarchicus)*

by

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ABSTRACT

The precise environment of the Marine Copepod *(Calanus finmarchicus)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the envirogram. Details of the environment not included in the envirogram are listed separately.

* * * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four pirmitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A INTRODUCTORY NOTE

"*Calanus finmarchicus* is one of the most important members of the zooplankton because of its enormous numbers and the part it plays in the conversion of the phytoplankton into protein and fat suitable as food for shoaling fishes, whales and many other animals" (Marshall and Orr, 1972).

In temperate northern waters *Calanus* is the dominant organism (by biomass). In arctic waters it is the numerically dominant zooplankton but is probably itself dominated in biomass by *Meganyetiphanes* and *Thysanoessa*.

The northernmost record for *C. finmarchicus* is 79°N, but the animal is widespread, excluding the Baltic. (Also it is rarely found in the Kattegut.) North of the English Channel it occurs in immense swarms (though in recognisably smaller groupings) and is found at all depths down to 4000 m, although most frequently in the top 200-300m.

There is confusion in the taxonomy; for this reason we have considered only the work carried out in the North Atlantic; and because of the greater body of information available, we have taken our subject animal to be a resident of the Clyde sea area.

The recognised stages of development are: eggs; 6 stages of nauplius (early larval form); 5 stages of copepodite (more advanced larval form); female and male adults. The nauplius stages are short-lived and our references to 'Stage x', x = I, II, ..., V, refer to copepodite stages unless qualified. In all larval stages the sexes are indistinguishable. Between each of the stages mentioned a moult must occur.

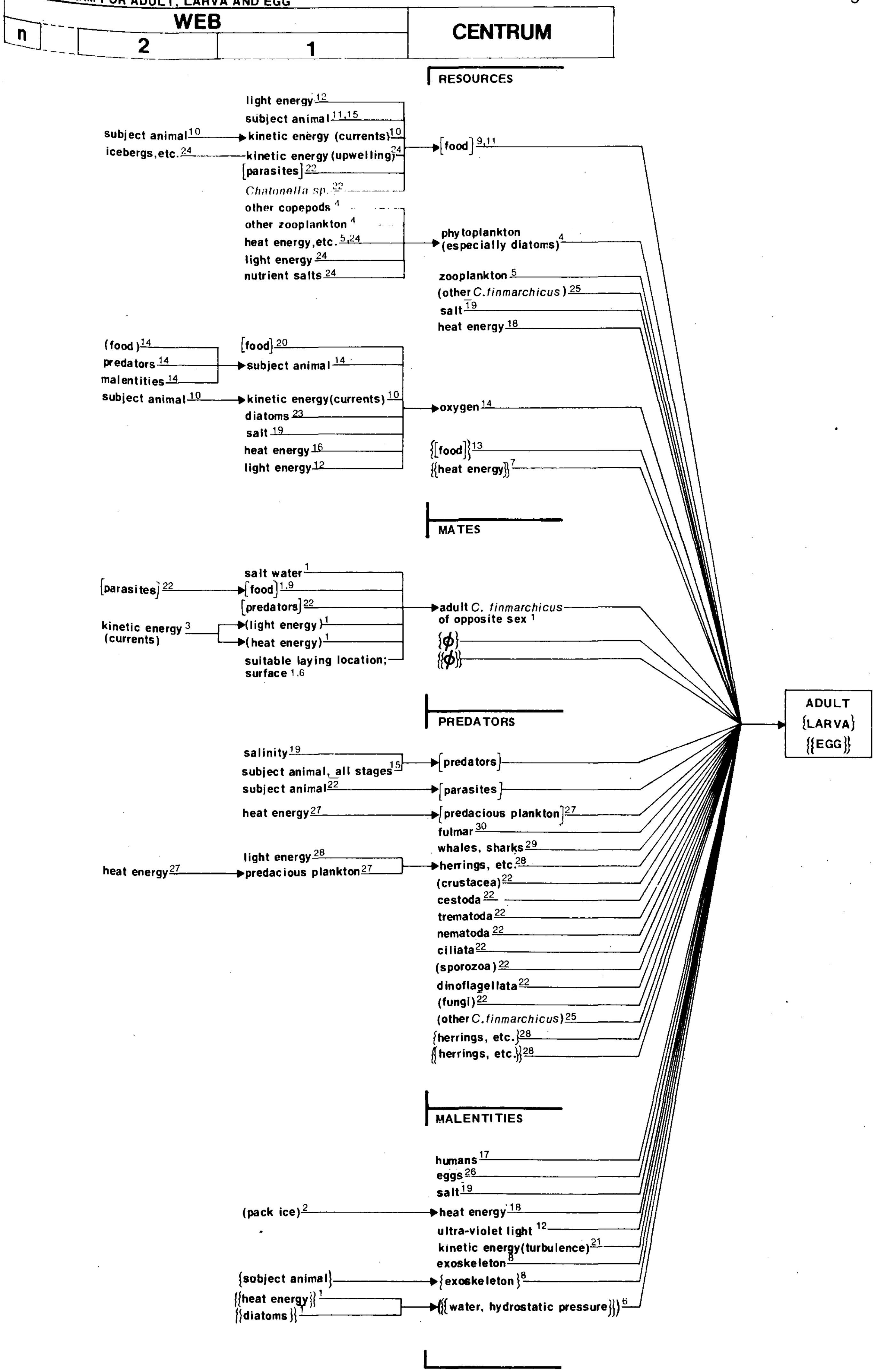
The time taken for the whole cycle depends, at least partly, on temperature; the life-span will determine the number of populations which will occur in any sea area. In the English Channel and Clyde sea area, the minimum cycle length (in summer) may be as short as two months: one month for egg-to-adult development and one month for maturing of eggs. In these areas up to four generations per annum may occur with the overwintering generation living up to six months. However, in the far North (East Greenland) a generation will characteristically live a year but on occasions some *C. finmarchicus* which have reached only copepodite stage III at the onset of winter will spend a second winter as late stage copepodites.

C. finmarchicus females have an average length of 3.1mm., males 3.0mm.

Males are shorter-lived than females; even in the highest latitudes the maximum life-span for a male probably never exceeds 7 months. However in the far north females live for a little over a year. In temperate waters the greatest life-span is found in the over-wintering populations. Females will probably live 7-8 months, males less. For between-winter populations in temperate waters the total female life-span may be as little as 60-70 days.

Over short periods, say about 2 minutes, *Calanus* can swim upward at 66 m/hr or downwards at 107 m/hr. Over longer periods (1 hour) the comparable figures are 15 m/hr and 47 m/hr.

B. ENVIROGRAM FOR ADULT, LARVA AND EGG



C. NOTES ON THE ENVIROGRAM

1. *C. finmarchicus* does not reproduce to any extent during the winter months. It is not clear whether this is due to the low temperatures or the lack of light so we have entered both heat and light energy on the envirogram as first-order modifiers of mates.

The overwintering population is made up largely of Stage V and they moult into adults, beginning in December or January. This date for the recommencement of development does not vary with latitude; in all areas from the Clyde to East Greenland adults are observed in January and February. Males appear first, predominate for a time and then the females appear and copulation takes place. There follows a period during which the female matures the eggs, then spawning takes place, the new generation grows up and the cycle is complete. The shortest period from egg to adult observed in a laboratory was 31 days.

The majority of eggs are not laid until March. However, the time of copulation is not important; females whose ovaries are quite undeveloped can carry spermatophores for several months. Females rise to the surface to lay their eggs, generally at night.

The spring egg-laying corresponds roughly in time with the spring increase in the phytoplankton, especially diatoms, which forms the bulk of the copepods' food. (see notes 5 and 9). There is some evidence to suggest that females are able to hold on to their eggs until conditions in the sea are favourable.

The adults which mature in the sea during April and May spend most of their time, day and night, at the surface, and lay their eggs at any time during a 24-hour period. This implies that surface, not night, is the operative factor (see n. 6). The next generation, which again retreats to deep water, also rises to the surface for laying eggs. The egg of *C. finmarchicus* is denser than sea-water and will begin to sink as soon as it has been laid. At 13°C it will sink about 2.5 cm/min. At this temperature the egg will take about 24 hours to develop and if laid at the surface it will hatch at about 36m depth (see also no. 6). The rate of sinking decreases markedly as the temperature drops; it is also affected by the presence of diatoms.

Males attach spermatophores to the females' genital segments; occasionally the spermatophores are misplaced. Copulation has not been observed in *Calanus*, but it is known that salt water is required to gel the "core substance" of the spermatophore, to form a channel through which sperm are pushed into the spermathecal sacs of the female. Usually a female has only one spermatophore attached, however occasionally more than one has been seen; one case was reported in which a female was carrying 15 spermatophores.

A female may lay up to 150 eggs in 24 hours. Total egg production is very variable (many factors are important; see note 9 for food); one female in a laboratory produced 586 eggs over a 74-day period however towards the end the eggs were less healthy.

None of the virgin females kept in a laboratory were able to lay parthenogenetic eggs.

2. Winter populations are usually found in deep water; an implication from Marshall and Orr (1972) is that the animal is not found near pack ice. The lower lethal temperature limit for *Calanus* is very near freezing point.

3. Kinetic energy incorporated into ocean currents may modify (second-order) the mates of the subject animal in a number of ways:

   i. It seems likely that around Greenland reproduction starts only when currents from the south raise the temperature.

   ii. The animal may be carried by the current to either a warmer or colder region.

   (iii) Light may also be a determinant of mating (see n. 1) and currents can also carry the animal into regions with different photoperiods.

4. Other copepods also eat phytoplankton and almost certainly compete with *C. finmarchicus*, e.g., *Pseudocalanus, Microcalanus, Centropages, Temora, Acartia, Oithona*. They would be expected to compete at all stages, i.e. the nauplii would compete with *Calanus* nauplii of the same size, copepodites with *Calanus* copepodites and so on.

Large numbers of zooplankton larvae, including *C. finmarchicus*, appearing in the ocean lead to a decrease in the numbers of diatoms.

5. There is evidence that all species of copepod depend greatly on the spring diatom increase. From this time until the autumn approximately 60% of captured *Calanus* contain recognisable remains (hard parts or skeletons) of, for example, diatom frustules, radiolarian spines, peridinian cases or parts of crustacean exoskeletons. Another 30 - 40% contain unrecognisable greenish or brownish debris.

In particular the diatom *Rhizosolenia fragillima* is commonly eaten by *C. finmarchicus*.

Calanus has also been seen eating flagellates e.g., *Phaeocystis*, *Gymnodinium* spp. and *Polykrikos*.

Observations made near Millport (Scotland) in 1923 showed that overwhelmingly the most common food consisted of diatoms. Other organisms eaten were crustaceans, radiolarians, dinoflagellates, silicoflagellates and coccolithophores. A small number of animals were found to have eaten algal threads, tintinnids and naked flagellates.

The following table is from Marshall and Orr (1972):

				Percentage of feeding *Calanus* whose guts contain							
Month	Guts empty	Debris only	Recognizable food	Diatoms	Dinoflagellates	Silicoflagellates	Coccolithophores	Radiolaria	Crustacea	No. of *Calanus* examined	Diatoms most common
	%	%	%								
1923											
Jan	38	43	19	38	0	6	0	54	27	179	Cosinodiscus
Feb	24	30	46	36	0	1	0	58	48	328	Coscinodiscus
March	27	15	58	57	1	3	0	43	39	135	Coscinodiscus Biddulphia, Naviculids
April	28	7	65	99	4	0	4	1	7	268	Skeletonema Thalassiosira, pennate
May	27	7	66	96	7	0	1	1	9	256	Skeletonema, Thalassiosira, pennate
June	28	9	63	95	5	0	12	0	25	241	Skeletonema Thalassiosira, pennate
July	21	13	66	80	43	1	17	0	28	141	Rhizosolenia
August	22	16	62	68	42	8	3	0	22	120	Chaetoceros Rhizosolenia
Sept	21	10	69	91	21	30	0	0	13	130	Thalassiosira Skeletonema, Chaetoceros
Oct	28	2	70	100	3	7	0	0	12	155	Skeletonema Thalassiosira
Nov	31	19	50	91	5	6	0	17	16	257	Thalassiosira Skeletonema
Dec	41	29	30	73	3	6	0	35	16	336	Thalassiosira
1924											
Jan	31	36	33	67	2	10	0	33	13	188	Thalassiosira Coscinodiscus
Feb	24	32	44	72	3	7	0	27	18	169	Thalassiosira Coscinodiscus
March	34	7	59	91	0	5	0	13	18	91	Skeletonema Thalassiosira
April	20	2	78	93	2	2	0	0	12	54	Skeletonema Thalassiosira

The 'μ-flagellates' (nanoplankton flagellates only a few microns in diameter) were not studied in the work summarised in the table above. It is suggested that *Calanus* is capable of filtering off particles as small as 1 μ. (There must also be an upper limit, but this is not given by the authors). The abundance of such small organisms in the ocean is unknown. Workers have noticed that larger diatoms, radiolarians and crustacea cannot be taken in whole and are broken up, presumably by the labral teeth and mandibles.

In rich food concentrations *Calanus* may produce a faecal pellet every 20 minutes. At 'room' temperatures (probably about 16°C in England) the time for a new food organism to appear for the first time in pellets ranges from 15 to 37 minutes.

In the laboratory a concentration of 200,000 *Nitzschia* cells is sufficient for successful growth and moulting (and good for egg-production - see n.9). However, this figure is well above concentrations recorded in the ocean.

It is clear that *Calanus* does not, or cannot, utilise the whole of the phytoplankton; while the utilization of diatoms and some flagellates is very high, for *Chlorella, Ceratom* and some other species it is very low.

6. Eggs, nauplii and young copepodites are found mainly in the top 30m of the ocean. At all times of the year females lay near the surface and this may be an adaptation to allow the eggs to hatch as near the surface as possible, either because deeper water acts as a malentity to the egg or because more food will be available to the nauplius.

7. If all the eggs in a clutch are kept at the one temperature their development is remarkably synchronized.

At 18°C, development will take place about 2½ times faster than at 8°C.

The following table is from Marshall and Orr (1972):

TABLE II

TIME OF DEVELOPMENT IN HOURS

	0	5	10	15	20
2 cells	2½		1⅓	1	¾
Segmentation cavity	10-25	10-18		2-3	2-3
Gastrula mouth visible	25-50	16,20-27	12	8-11	-
No structure visible	50-70	25-40		14-20	12
Clear nauplius form	90	27,48		16-20	14-18
Hatching	116-120	40*,59-65	25-30	20-26	19-22

* One set of eggs hatched after 40 hours, eleven sets took 59-65 hours.

8. When a *Calanus* larva moults the exoskelton splits and the animal slips out. Usually this process occurs very rapidly. *Calanus* which take a long time over it or are found swimming with the exoskelton attached are almost certain to die. In this case it is not clear whether the discarded exoskelton is a malentity or modifies food or some other object resulting in the animal's death.

Occasionally animals have been found in which the tip of the antennule has obviously been damaged during a moult (when the previous exoskeleton has been shed) and has regenerated. In this case the exoskeleton is clearly a malentity.

Factors causally connected with moulting seem to be food, warmth and light. Experiments give some indication that each of these factors may have some positive effect in speeding the transitions but no very definite results have been obtained.

9. The newly-moulted female often has a small ovary, however a late stage copepodite can moult into a female which may be in any state between immaturity and ripeness. The state of development depends very largely on the amount of food present.

Experimental evidence shows the well-fed *C. finmarchicus* lay considerably more eggs than animals which are starved, or starved for a time then fed. Also experiments have shown that feeding *Calanus* with increasing concentrations of *Chlamydomonas* cells results in an increasing number of eggs laid, up to an asymptotically-approached limit. In experiments in which *Chlamydomonas* was compared with *Lauderia*, *Gymnodinium* and *Ditylum* the three latter organisms were superior food for egg-production

The following diatoms have been found good for egg production: *Coscinodiscus centralis*, *Lauderia borealis*, *Skeletonema costatum*, *Rhizosolenia delicatula*, *Ditylum brightwelli*, *Chaetoceros pseudocrinitus* *Nitzschia closterium* var. *minutissima* (now identified as *Phaeodactylum tricornutum*).

The following organisms were also good: *Syracosphaera carterae*, *Peridinium trochoideum*, *Gymnodinium* sp., *Chlamydomonas* sp., and a Chrysomonad flagellate B11 (Raymont and Gross, 1942).

Experiments in feeding 'ripe' females with radio-actively marked cells indicated that metabolism was so rapid that food intake was used almost immediately for egg production. Half the radioactive material retained was concentrated in the ovary and oviducts and strongly radio-active eggs were laid after 8 hours of such feeding.

10. It seems likely that by moving various limbs in various ways the animal sets up water currents which help to bring particles into its filter chambers. We have tentatively classified the animal itself as a first-order modifier in its own environment of a large class (possibly all) food.

These currents also serve, perhaps primarily, to aid respiration (see n. 14).

11. Some workers are of the opinion that *Calanus* is not an automatic filter feeder, rather that it is mainly a selective feeder. However it is certain that at least some of the time *Calanus* is an automatic filter feeder. In fact:

(i) food in the gut during the year is a fairly accurate representative sample of the microplankton in the surrounding ocean and

(ii) filtering rates for this animal are largely independent of the concentration of food in the medium.

From (i) and (ii) it may be inferred that automatic filter feeding does take place. However :

(iii) crustacean remains are often an important part of the gut content indicating that the animal can capture active organisms (possibly by using its 'leap' reaction, although this has not been observed in feeding - see n. 15). Also, experiments with diatoms, particularly *Ceratium*, which the copepod rarely eats, may indicate that the animal exerts some selection.

Not all *Calanus* captured in townets contain food; the number varies with season, sex and time of day. Males eat much less than females; even in high food concentrations many males will go days without eating. Males are, however, more efficient at digesting their intake in that unattacked cells never occur in their faecal pellets.

Using oxygen consumption as a guide to food requirements, it is estimated *Calanus* needs between 1.3% and 3.6% of its dry body weight in food per day in winter and between 1.7% and 4.5% in summer.

See also n. 5.

12. Exposure to strong diffuse 'natural' light is lethal to *Calanus*; artificial light has no effect. It has been shown that the lethal effect is caused mainly by the ultra-violet componnet, which probably explains why artificial light has no effect.

When it is exposed to light the animal's respiration increases dramatically. In bright diffuse light or sunshine respiration may be double what it is in the dark. Even low light intensities have a marked effect as compared to darkness. *Calanus* which have been exposed to light then returned to darkness have higher respiration rates than control groups, suggesting that *Calanus* is permanently injured by the exposure.

In the Clyde sea area in winter *Calanus* has been found to feed almost exclusively during the hours of darkness, even bright moonlight having a deterrent effect. However, during summer there is little difference in the animal's feeding habits between night and day.

It seems likely that the diurnal vertical migrations have light as an immediate stimulus, perhaps modified in extreme cases by temperature. However the whole question of seasonal and diurnal migrations is not yet well understood.

(see also n. 20).

13. There is a possibility that the animal in the first two nauplius stages does not eat at all. However, in the last three copepodite stages the animal eats the same food as the adults. The following is from Marshall and Orr (1972):

TABLE X

AVERAGE LENGTH OF FAECAL PELLETS
OF *Calanus* FED ON *Chlamydomas* CULTURE

	Nauplius	Copepodite						
Stage	V and VI	I	II	III	IV	V	F	M
Size in	70	85	173	227	370	520	470*	240*

This may be an under-estimate for some of the large pellets were broken

In the faecal pellets of the earlier stages the organisms actually identified were as follows:

Nauplius III to V, *Skeletonema costatum* (cells 5µ diameter) *Syracosphaera* sp. (Millport strain 62, 20µ long).

Nauplius VI (and V). *Prorocentrum triestimum* (20 x 14µ); *Peridinium trochoideum* (25 x 19µ).

Copepodite I. In addition ot the above, *Prorocentrum micans* (43 x 27µ), *Syracosphaera carterae*, *Nitzschia closterium*, Naviculid sp. 26µ long.

Copepodite II. In addition to the above, *Cosinodiscus centralis* (about 100µ in diameter), *Ditylum brightwelli* (25-60µ broad, length 2-3 times greater).

Late stage nauplii possibly confine themselves to the phytoplankton less than 25μ in diameter but this would still leave them with a large number of available food species. Early stage nauplii will be able to eat organisms up to perhaps 10μ in diameter; this will include the smaller diatoms and many flagellates.

(see also notes 5, 11).

14. Oxygen intake in copepods is by diffusion through the cuticle wherever the blood sinuses lie close to the surface, i.e., in the antennules and the lateral sinuses.

The activity of the subject animal greatly affects its oxygen consumption. An increase in activity like the diurnal migration (see n. 1) or escape movements (see n. 15) has a marked effect.

Lower food concentrations also probably cause the animal to increase its movements.

In experiments at 15°C high concentrations of oxygen, up to 16 ml/l had no effect on oxygen consumption. At the other end of the scale there was a rapid fall in respiration from concentrations of about 3ml/l down. A number of animals died at 3.3ml/l and the death rate increased at lower concentrations. Females were slightly more resistant to lower concentrations than males. Stage V copepodites were able to survive considerably lower concentrations.

It is known, however, that in the wild *Calanus* can be abundant in areas in which the oxygen concentration is as low as 2 ml/l.

The following quotation is from Marshall and Orr (1972):

"Immediately after capture *Calanus* has a considerably higher respiration than some hours later. This fall is most marked in the first few hours and is not noticeable after about one day. It is most marked with females, less than males and not noticeable with Stage V *Calanus*".

15. At all stages from nauplius I up, the animal can 'leap' a number of inches away from adverse stimuli, in the laboratory for example from the mouth of a pipette, and in the wild presumably from predators.

It seems likely that this behaviour also occurs when gathering food.

16. One effect of increasing temperature on *C. finmarchicus* is to increase the oxygen consumption. The increase is curvilinear and concave up (second derivative positive), from approximately 0.2 ml/1000/hr to approximately 0.9ml/1000/hr at temperatures of 1°C and 20°C for females. Measurements have also been made for males and some of the larval stages (see Marshall and Orr for details). The general pattern of increase is similar for all classes. 20°C is close to the lethal temperature for *C. finmarchicus*.

Resistance to low oxygen concentration is greater at temperatures below 15°C (see n. 14).

(see also n. 20).

17. Human collectors of plankton, including *Calanus* are classified here as 'malentities', however for a discussion of the difficult question of how to classify humans (i.e., how to interpret H(human)) see General Introduction to this series of Working Papers, 1983 version.

18. The range of temperatures at which *C. finmarchicus* can exist seems to be from just above 0°C to something over 20°C. Upper lethal limits have been found to be between 26.5°C and 29.5°C by one group of workers and 25°C to 27°C by another group.

The lethal temperature is higher in summer than in winter. Stage V is more resistant to high temperatures than adults.

Temperature also affects heart-rate, which increases from 200/min at 5.5°C to 350/min at 16°C.

19. Sudden salinity changes are lethal to the copepod but the animal can adjust to a wide range of salinities if the changes are gradual.

When, in the laboratory, the salinity of their medium is gradually reduced many *Calanus* can tolerate salinities as low as 17‰. As the salinity approaches this low level there is a reduction in oxygen consumption.

Calanus is abundant only when the salinity of the sea is 35.3‰ or less.

Low salinity makes the animal sluggish, and so less able to escape from predators (see n. 15).

20. Feeding, i.e., metabolism, is known to affect oxygen consumptjon.

Experiments on light, salt and temperature effects were done in food-free water to negate this effect.

21. In the laboratory *Calanus* which are subjected to continuous or rapid "shaking" showed poor survival. Presumably this effect could also operate in turbulent waters in the sea.

22. Marshall and Orr (1972) remark that while parasitized specimens of the animal are less healthy and live shorter lives a remarkable amount of body and muscle can be consumed and *C. finmarchicus* will still remain active.

Many parasites prevent normal sexual development probably because they consume the resources needed for sex cell maturation.

The fungus *Ichthyosporidium* has been found in *Calanus* however there is some doubt as to whether the copepod is in fact adversely affected.

The following Dinoflagellata (classification sometimes uncertain) are parasitic on *Calanus*: *Blastodinium*, *Syndinium*, *Paradinium* (The most commonly observed parasite), and *Ellobiopsis chattoni*. The latter is sometimes included among the fungi. In the North Sea infection with *Blastodinium* alone may be 66%.

The Sporozoan *Gregarines* is found in the gut of *Calanus*; it is not known if they adversely affect the copepod.

The Ciliate *Chattonella caloni* is suspected to be commensal rather than parasitic; although, invariably situated at the opening of the maxillary gland it seems likely that the ciliate is competing for the copepod's food, i.e., it acts as a first-order modifier. Another ciliate (unclassified) has been found parasitizing *Calanus* near Tromso (Norway).

The Nematode *Contracaecum* sp. parasitizes the copepod's gonad which then rarely develops, though an occasional female matures sufficiently to lay eggs.

The Trematode *Hemiurus* sp. occurs rarely and singly in *Calanus* and at least one other Trematode has been reported.

Two types of cestode larva have been reported, a cyclophyllid and a tetraphyllid.

It is suspected that a larval stage of epicarid isopods is harmful to *Calanus*, but the evidence is not clear. In some parasitized *Calanus* the ovary seems to be undeveloped.

In a sample of 363 female *C. finmarchicus* over 20% were parasitized as follows:

42 with *Synelinium* or *Paradinium*
27 with tetraphyllids,
3 with cyclophyllids,
6 with nematodes,
1 with *Ellobiopsis*.

23. Diatom increases in the ocean often causes increased oxygen content.

24. Diatom and phytoplankton numbers in general are dependent on temperature, illumination for photosynthesis, and a good supply of nutrient salts.

Because of their dynamic interaction the probability of large zooplankton and phytoplankton populations occurring together is very low. Such populations occur mainly where upwelling is going on, usually where mainstream ocean currents converge, or near icebergs or glacial faces on the ocean, or the edge of the pack ice.

25. In arctic waters is seems likely that some over-winter cannibalism may occur.

26. Some female *Calanus* are badly damaged when laying when large eggs break loose in the body cavity.

27. A large number of planktonic animals prey on *Canalus*:

The arrow worm *Sagitta*.

Ctenophores which develop in number in late spring and early autumn are particularly destructive; where they are abundant *Calanus* is scarce. In some years owing to abnormally high temperatures they appear early and destroy so many *Calanus* that the herring fishing may fail for the year.

Medusae are also very destructive.

Large copepods like *Euchaeta* and *Anomalocera* and some euphausids are also carnivorous and may capture *Calanus*.

28. Many pelagic fish eat *Calanus*. Every stage from egg upwards is eaten. Herrings are important predators; other notable predators among fish are young saithe *(Gadus virens)* in the Clyde sea area and the Sand Lances *(Ammodytes* spp.*)*.

Many studies have been done on the herrings as predators. It has been reported that a young herring will eat any *Calanus* it can successfully mouth (see n. 15 for escape reaction). Herring need good light for feeding; moonlight is sufficient but starlight is not. When a 15-watt bulb was lowered from 7.5m above a tank to 1m above herring predation of *Calanus* increased 5-fold.

29. The Sei Whale *(Balaenoptera borealis)* is particularly adapted to live off *Calanus*, though other whales and plankton feeders e.g., the Basking Shark *(Cetorhinus maximus* (Gunner)) also eat the copepod.

E. REFERENCE

Marshall, S.M. and A.P. Orr (1972). *The Biology of a Marine Copepod.* (Springer-Verlag).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XVII THE WATERFLEA (*Daphnia magna*)

by

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ABSTRACT

The precise environment of the waterflea (*Daphnia magna*) is given, using as a basis for the classification the defining equations of Niven (*Erkenntinis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

CONTENTS

A. INTRODUCTORY NOTE

Harper (1976) reporting on *Daphnia magna* in Scotland writes:

"Water-fleas (Fig. 1A) are very common inhabitants of standing or slow moving waters and swim by means of their branched antennae. The five pairs of limbs, encased in the carapace, have many setae and, beating in unison, filter tiny particles of algae, bacteria or detritus from the water. *D. magna*, the largest British species of *Daphnia* (♀♀ 3-4 but occasionally 6 mm long; ♂♂ about half their size) can be distinguished from other species by the distinct flanges on the head behind the antennae (Fig. 1B *f.*) and by the division of the denticles beneath the claw of the tail into two distinct groups (Fig 1 C *d.*)

D. magna is widely distributed in the northern hemisphere being recorded from all Eurasia east to China and Japan and south to North Africa (Scourfield & Harding 1960). In North America it is recorded from the north and west of the continent but is curiously absent from the south-east (Brooks 1957). Its distribution in Britain also shows an interesting pattern. It is widely found in the south and east of England but absent from the west and Wales. It becomes less common in the Midlands and further north is restricted to the east of the Pennines, with no records from the Lake District. Scotland has only five records of the species. The Institute of Terrestrial Ecology's Wetland Research group has recorded it in the pond in Edinburgh zoo and at three places in Fife: Loch Gelly, Kilconquhar loch and Morton lochs near Tentsmuir National Reserve. These records together with the newest one of Forfar are a natural extension northwards of the species east coast distribution.

D. magna is considered to be a pond dwelling species, thriving in small, shallow bodies of water which are rich in organic substances and are often of a temporary nature. Laboratory studies have shown that it is able to survive at higher temperatures than other species and can filter food more efficiently at these temperatures (Burns 1969). This gives the species a considerable competitive advantage in shallow water where the temperature fluctuations in summer are often considerable. It is much easier to grow in culture than other species, suggesting that it is more versatile in its food and living requirements."

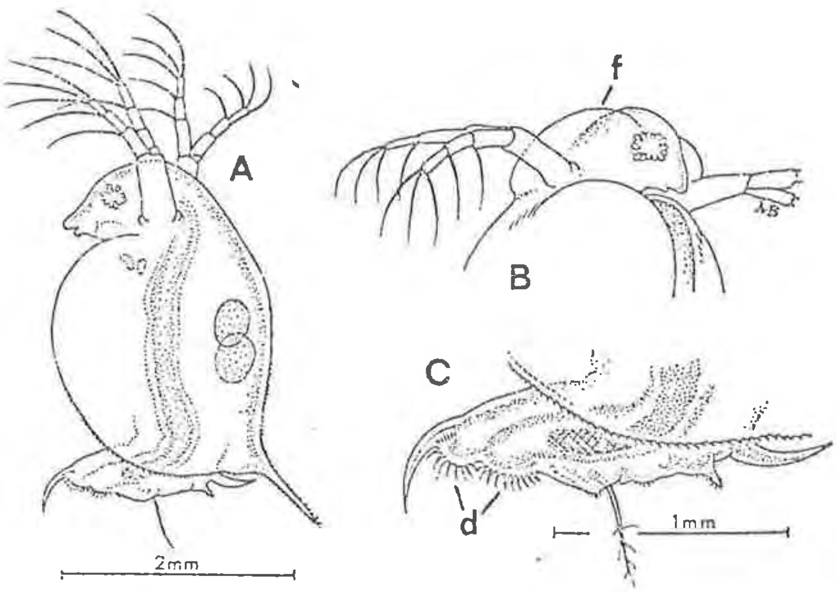
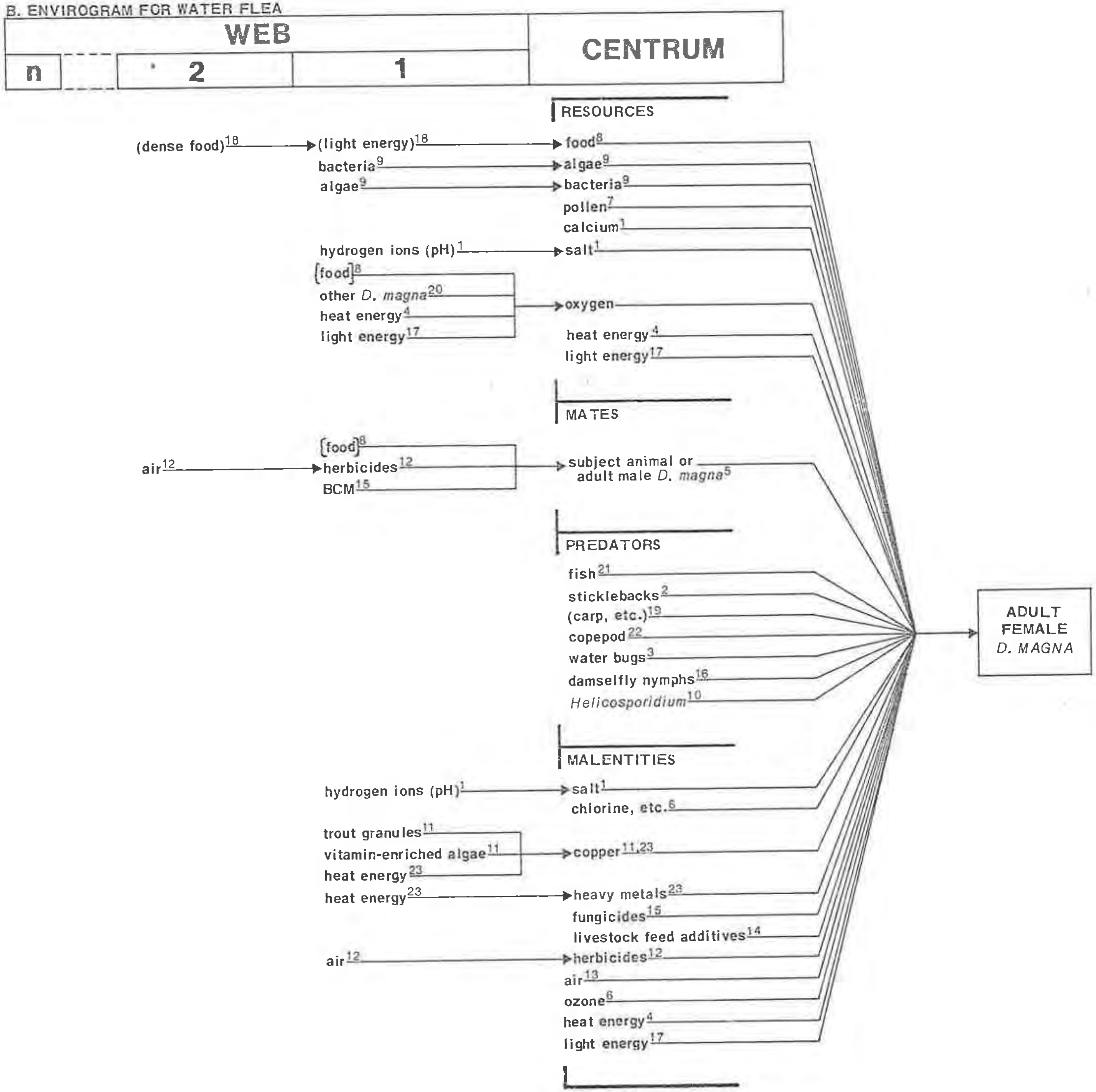


Figure 1. *Daphnia magna* Straus (1820). A. Adult female. B. Enlarged view of head showing flanges (*f*). C. Enlarged view of tail showing denticles (*d*).

Kamiński (1979) reports on its presence in ponds in Poland. Potts and Fryer (1979) write that *D. magna* is usually found in calcium-rich alkaline waters that have a high level of inorganic salts; it may also be found in slightly brackish water (see n.1). They also observed it in northern England in low-lying areas to the east, often on good agricultural ground, in contrast to another freshwater cladoceran *Acantholeberis curvirostris* which occurs on peaty moorlands and in mountainous areas; the two species, as far as is known, do not co-exist. Wulf (1980) found that in a freshwater rock pool on a small island in the Baltic Sea *D. magna* was so abundant as to contribute more than 50% of the total biomass, except in late July (when chironomid larvae were more abundant).

Stobbart et al (1977) report that the animal is highly permeable to water.

B. ENVIROGRAM FOR WATER FLEA



C. NOTES ON THE ENVIROGRAM

1. *D. magna* commonly frequents alkaline waters of moderate to high salt content. The animal obtains most of its sodium by active uptake, the rate of uptake being positively correlated with the concentration. According to Potts and Fryer (1979) differences in the affinity for sodium ions exist in different populations of the waterflea. In some populations the uptake mechanisms are half saturated at concentrations of 0.2 mM Na/l but in one population which they examined this value was only .05. Sodium uptake is depressed in acid waters. The rate of sodium loss increases fourfold between pH7 and pH3; death may occur through sodium loss. They recorded the following values in nature:

pH 6.9 - 10.2 (mean 7.84; SD 0.82; n = 31).

Ca^{++} 5.0 - 164.6 mg/l (mean 96.5; SD 45.89; 0.125 - 4.1 mM Ca/l; n = 31).

Conductivity 300 - 7216 μS/cm at 25°C (mean 1770 ± 1696; n = 24).

Stoddart et al (1977) studied the Na transport mechanism. They report that Na-depleted animals absorb Na from the external medium and regain (asymptotically) their normal Na content (26.3 ± 2.2 (S.E) mM/kg wet weight) after about 15 hours.

2. The three-spined stickleback (*Gasterosteus aculeatus* L.) is a natural predator of *D. magna* and has been used in prey-predator studies by Heller and Milinski (1979). They found that hungry sticklebacks preferentially attacked the densest region of a swarm of waterfleas, but when less hungry preferred less dense swarms. Large waterfleas tended to be eaten more slowly than normal-sized ones. With decreasing hunger sticklebacks increasingly preferred waterfleas with parthenogenetic eggs.

Milinski (1979), also in laboratory experiments, found that the hunting behaviour of three-spined sticklebacks may differ depending on the previous history of the predator-prey relationship with *D. magna*.

Behaviour studies by Ohguchi (1978) show that *D. magna* of unusual colour preferentially are attacked by three-spined sticklebacks. Ohguchi infers from the results that oddity of colour is a greater disadvantage to the waterflea than conspicuousness against a differently-coloured background.

Gibson (1980) found that when offered a choice between a larger and smaller waterflea the sticklebacks take the larger (regardless of absolute size).

The fifteen-spined stickleback (*Spinachia spinachia*) is also a natural predator of *D. magna*.

3. Wulf (1980) reports that the water bug *Deronectes griseostriatus* (de Geer) is a common predator in a fresh-water rock pool on a small island in the Baltic Sea.

The predator-prey interactions of *D. magna* with the water bug Notonecta glauca L. were studies in the laboratory by McArdle and Lawton (1979) (see also McArdle, 1977). All 5 nymphal instars of the water bug as well as the adults attack the waterflea; small predator instars will usually compete with large insatrs for the prey. The authors set up a series of functional response experiments for each instar of the *Notonecta glauca* attacking four size classes of *D. magna*. The resulting attack rate and handling time surfaces are complex, with maximum attack rates for small predators attacking small prey and large predators attacking large prey. Adult *N. glauca* have lower attack rates than instars 4 and 5.

4. Goss (1978) studied the effects on the animal of temperatures ranging from 5°C to 30°C. Developmental times decreased with increasing temperature. Adult egg-bearing females were more sensitive to high temperatures than immature forms. Respiration rates increased with increasing temperatures.

Growth efficiency of *D. magna* is maximal at 10°C, and above 22°C growth efficiency is negative, according to Kersting (1978), which means that the population cannot survive (under circumstances like those of Kersting's experiment) at temperatures above 22°C. Nevertheless Kersting points out that this does not mean that *Daphnia* cannot live at higher temperatures. "It does mean, however, that under certain circumstances these temperatures become lethal to the population and that probably the survival chances of a *Daphnia magna* population decrease under other circumstances also at these temperatures".

Gerritsen (1982) reports that the waterflea tends to swim upwards when the temperature rises and tends to sink when it falls.

Goss and Bunting (1980) measured respiration rates for adult female egg-carrying *D. magna* at 5, 10, 15, 20 and 25°C. They found that the rates increased with increasing temperature (and that rates were less than those for *D. pulex*).

5. The following quotation is from Russell-Hunter (1979):

"Sexual reproduction in cladocerans exhibits certain bizarre features. In general in freshwater populations, relatively few males are found, and parthenogenesis is common. In many cases the annual reproductive cycle appears to involve an alternation of parthenogenesis with ordinary sexual reproduction. The ecological aspect of this is that parthenogenesis can fill the pond with individuals under favorable conditions, while fertilized eggs are desiccation-resistant and can persist through winter or through drought conditions. Such resistant eggs are also of enormous importance as a factor in the passive distribution of these forms. In a few species, all fertilized eggs seem to hatch as females, and it can be shown that selective abortion during sperm maturation is responsible. The chromosome number remains constant, of course, throughout parthenogenesis, but when the unfavorable season approaches, among the parthenogenetically produced young are a few males. How this is achieved is still really unknown, but its adaptive significance is obvious. Simultaneously, eggs which need to be fertilized are produced by a reduction division. It has been suggested that substances are ingested from algal cells (which are already slowing their reproduction rate) and can induce the production of males and of meiotic eggs."

In studies of *D. magna* in the laboratory over a period of two years Young (1978) observed five separate episodes of sexual reproduction, one of which was accompanied by "obvious swarming". Young remarks that swarming occurs only when males are very scarce relative to sexual adult females. On many other occasions sexual reproduction takes place without any change in the gross appearane of the population. The following table is from Young's paper:

TABLE 1. Reproduction in swarming and non-swarming *Daphnia* in the autumn of 1973. Percentages of adult females of each reproductive type are given. Ephip. = ephippial(sexual) females, Imm. = imminently sexual (see text), Parth. = parthenogenetic; remainder of females carried no eggs. Each sample contained 150 - 250 adult females. The number of males is given in the table. 'Size' is the approximate diameter of the swarm (in cm).

Date	Non-swarm				Swarm				
	Ephip.	Imm.	Parth.	♂	Size	Ephip.	Imm.	Parth.	♂/♀
22 Oct	32.6	0	45.4	0	No swarms present				
29 Oct	Swarms present, 5-30 cm diameter, not examined								
5 Nov	21.8	0	21.9	0	30-50	25	52	21	6/200
					15x7	15	53	7	4/150
12 Nov	5	0	18	0	100	11*	8	21	0♂
19 Nov	†2	2	23	0	100	6	5.5	16	3/180
	‡17.5	0.5	16	0					
26 Nov	Pond frozen, population died								

* A third of these had no eggs and no ovarian development

† A sparsely populated site

‡ A dense but uniform region

6. The toxicity of chlorine, bromine chloride and ozone in secondary effluent, also the toxicity of chlorinated effluent that has been dechlorinated with sulfur dioxide has been studied by Ward and DeGraeve (1979). They write:

> "*D. magna* was more sensitive to residual chlorine toxicity than any test organism evaluated (Table 2). Total residual chlorine concentrations of 0.220 mg/l and 0.070 mg/l were lethal to three-day-old *D. magna* in 5.5 and 10.5 hours, respectively. In a 48 hour acute test with *D. magna* less than one day old, an LC50 of 0.017 mg/l total residual chlorine was observed. Thus, extremely low levels of chlorinated

effluent may adversely affect the survival of some invertebrates which are potential food supplies for many species of fish."

and

"*D. magna* was the only species tested which exhibited mortality in 100 percent dechlorinated effluent at normal sulfite residual levels. Since two other acute tests with this same species resulted in 50 and 100 percent mortality in undiluted nondisinfected effluent, the mortality in 100 percent dechlorinated effluent was attributed to the inherent lethal qualitites of the effluent".

In tests with chlorobrominated effluent they observed 90% mortality at 0.072 mg/l (37% effluent). With ozonated effluent there was 30% mortality at 0.03 mg/l residual ozone (100% effluent). They report ozone as exhibiting the least potential for residual toxicity of any of the disinfectants tested and suggest that this is because residual ozone dissipates so rapidly.

7. Stroganov and Kozyar (1979) found that *D. magna* fed on the pollen of a number of plant species can live and reproduce for a comparatively long time. However pollen is not a completely adequate food for *Daphnia*; changes were recorded in the proportions of the parts of the body, the time of maturation and the fecundity. The plants used were: Scots pine (*Pinus silvestris*), common birch (*Betula verrucosa*), European alder (*Alnus glutinosa*), great redmace (*Thypha latifolia*) and Timothy grass (*Phleum pratense*). In the control experiments the waterflea was fed on *Chlorella* and yeast. Details are given in the following tables. The 'variants of experiments' in tables 2 and 3 are:

1. Control: feeding on *Chlorella* alone.
2. Equal proportions *Chlorella* and swollen pine pollen.
3. *Chlorella* and dry pine pollen.
4. Dry pine and reedmace pollen.
5. Swollen pine pollen.
6. Dry pine pollen.

Table 1

Survival and Reproduction of Daphnia Fed on the Pollen of Various Plants

Plant	No. of crustaceans, %	Time of onset sexual maturity, days	Appearance of first litter, days	No. of young produced
Pine	87	8	10	851
Alder	100	10	13	151
Tmothy grass	87	10	11	327
Birch	90	9	10	267
Control (Chlorella + yeast)	100	7	9	2283

Table 2

Fecundity of Daphnia Fed on Different Types of Food

Varient of experiment	*M*	*lim*	Variant of experiment	*M*	*lim*
1	160.7	117-208	4	24.1	19-39
2	96.4	70-119	5	26.2	23-29
3	98.5	83-114	6	14.2	9-20

Survival, Growth and Time of Onset of Sexual Maturity in Daphnia Fed on Different Food

Varient of experiment	No. of live crustaceans on 21st day of exp.%	No. of carapaces (per individual)	Time of appearance of first litter, days	No. of litters by 21st day	Size of Daphnia, mm			As % of length		
					length	width	len. x width	width	spine	helmet
1	100	9.8 (8-11)	7 (7-7)	5.6 (5-6)	9.30	6.55	60.9	70.4	9.6	30.1
2	100	9.2 (8-10)	7 (7-7)	5.0 (4-6)	8.10	5.60	45.4	69.1	13.2	34.5
3	100	10.4 (10-12)	7 (7-7)	5.4 (5-6)	8.30	5.45	45.2	65.8	13.0	34.3
4	90	7.6 (6-8)	8.6 (8-9)	3.6 (3-4)	6.80	4.45	30.3	65.4	9.5	36.7
5	100	6.4 (6-7)	8.2 (7-13)	4.0 (3-5)	6.45	4.50	29.0	69.7	10.9	35.6
6	100	8.2 (8-9)	10 (10-10)	2.4 (2-3)	6.45	4.35	28.0	67.4	8.5	35.6

8. *D. magna* is a filter-feeder. The animal filters food from the water and collects it in its food groove, water being pumped by rhythmic movements of the thoracic appendages (Nauman, 1921: quoted by Kersting, 1978a). Geller and Mueller (1981) classify the waterflea as a 'fine-mesh filter feeder'; the distances between the setulae (which act as filters) are about 0.2 µm. The mesh-size of the filter does not increase significantly with growth (unlike some other filter feeders). The uptake of food is proportional to the food concentration up to a critical level, above which the food intake is constant. (Kersting 1978a). Gophen (1977) concluded from feeding experiments with bacteria and algae that rate of ingestion is influenced by size of particle. Feeding rates have been measured by a number of workers. The following table is from Watts and Young (1980):

Table 2

Author	method	food	Thousands of cells/ *Daphnia*/hour 20°C food conc = 5 x 10^4
Burns (1969)	R Tracer	Yeast	70
McMahon (1965)	R Tracer	*Chlorella*	120
McMahon (1965)	R Tracer	Yeast	120
Ryther (1954)	cell counting	*Chlorella*	160
Rigler (1961)	R Tracer	Yeast	80

Horton et al (1979) have studied the response to low food concentrations. They report that when the suspended food concentration is too low to support reproduction or high rates of ingestion the animal tends to spend some of its time foraging at the bottom of the culture vessel. Nevertheless some proportion of the animal's time is spent swimming (and therefore suspension feeding) at all food concentrations.

Respiration is dependent on food concentration; above a certain critical level there is a negative correlation between respiration rate and food concentration; below the critical level the effect is negligible (Kersting and van der Leeuw-Leegwater, 1976. See also Kersting, 1978b).

Nevertheless growth efficiency is independent of the food concentration (Kersting, 1978a).

Russell-Hunter (1979) remarks that the waterflea can be cultured with only bacteria as food.

See also n.9.

9. In experiments by various authors the waterflea has been fed on the bacterium *Chlorobium*, and on the following algae: *Chlamydomonas*, *Chlorella vulgaris*, *Sphaerocystis schroeteri*, *Euglena gracilis* Klebs, *Oocystis*, *Ankistrodesmus*, *Scenedesmus*, *Closterium*, *Closteriopsis*.

Algal cells can pass through the gut of *D.magna* several times before being completely digested (Kersting, 1978a). Cowgill (1976) found that the animal rejects *Euglena gracilis*. Porter (1976) found that although *Sphaerocystis schroeteri* is ingested many (more than 90%) of the cells are undamaged in their passage through the gut; they emerge intact and viable and, during their passage, take up nutrients such as phosphorus.

Christensen (1973) reports that of the three algae *Chlamydomonas reinhardi*, *Haematococcus pluvialis*, *Pandorina morum*, the latter most often passed through the gut undamaged. The digestion of *Chlamydomonas* was the most efficient. Large animals (2.97 mm) possibly showed a slight preference for the large *Pandorina* colonies, while smaller animals (1.85 mm) differentially removed *Chlamydomonas*. Filtering rate was roughly proportional to the square of the body length. Parthenogenetically-reproducing *Daphnia* filtered out food at a higher rate in the first half of their inter-moult cycle than in the second half.

Gliwicz and Siedlar (1980) showed that the higher the phytoplankton concentration, the narrower is the gape between the edges of the carapace valves. "This response allows *Daphnia* to avoid larger forms, which inhibit efficient food collection and ingestion (decreased frequency of strokes of the thoracic appendages and increased frequency of postabdominal rejectory movements). Narrowing the gape is a response to mechanical, not chemical stimuli. It causes a decrease in the feeding rate due to a lowering of the upper size limit of particles collected. The ability to narrow the carapace gape may be a behavioral strategy to survive summer algal blooms."

Hadas _et al_ (1982) report a higher consumption of bacteria in the presence of algae. In the presence of bacteria algal consumption decreased by 40 to 70%. They used the bacterium *Escherichia coli* and a mixture of the two algae *Chlorella vulgaris* and *Scenedesmus quadricauda*.

See also n.8.

10. Sayre and Clark (1978) report the presence of the protozoan parasite *Helicosporidium* sp. in laboratory cultures of *D. magna* which were being reared as food for fish.

11. Winner _et al_ (1977) exposed *D. magna* to copper concentrations of 0, 20, 40, 60, 80, 100, 120 and 140 μg/l. They found that animals fed on a vitamin-enriched culture of *Chlamydomonas reinhardii* are less sensitive to a chronic copper stress than animals fed a trout-granule diet. This conclusion is based on responses as measured by survival, mean brood size and r, the instantaneous rate of population growth. The two foods differentially affect 'chronic toxicity' (as measured by survival and reproduction) but not 'acute toxicity' (toxic effects, usually death, discernible within 96h). A decrease was found by Winner and Farrell (1976) in the instantaneous rate of population growth at concentrations of copper less than 60 μg/l, also there was a reduction in survival time, but none in brood sizes. The tables below are both from the 1976 article:

Table 2. Vital Statistics for three chronic copper toxicity tests with *D. magna*

Cu concn (µg/*liter*)	$\bar{X}$ Longevity (*days*)			Total young per			$\bar{X}$ Brood size		
	Exp 1	Exp 2	Exp 3	Exp 1	Exp 2	Exp 3	Exp 1	Exp 2	Exp 3
0	79.1	93.2	108.5	2314	3223	3287	10.6	13.1	12.3
20	99.6	99.7	91.7	3180	3863	2850	12.5	14.6	12.9
40	94.2	82.7	106.1	3329	3394	3110	13.3	15.2	13.1
60	45.3	48.8	69.0	1689	2150	2328	13.7	16.5	13.2
80	11.0	22.2	20.6	464	364	696	10.8	14.0	14.2
100	7.5	2.7	3.0	0	26	14	- [a]	13.0	7.0
120	3.1	0.3	0.4	0	0	0	- [a]	- [a]	- [a]

[a] No reproduction occurred.

Table 3. Instantaneous rate of population growth (*r*) as affected by copper for four species of *Daphnia* Horizontal lines indicate that the *r*-values above and below the line are significantly different ($P \leq 0.05$) as determined by Duncan's new multiple range test (Duncan 1955).

Cu (µg/*liter*)	*D. magna*	*D. pulex*	*D. parrula*	*D. ambigua*
0	0.373	0.498	0.423	0.459
20	0.405	0.469	0.424	0.454
40	0.409	0.453	0.390	0.432
60	0.325	0.230	- [a]	0.233
80	0.287	- [a]	- [a]	- [a]
100	- [a]	- [a]	- [a]	- [a]

[a] No reproduction occurred at these concentrations.

(see also n.23)

12. The toxicity of 2, 4-D triethanolamine salt to *D. magna* was evaluated over 24h, 48h and 3 weeks by Claus (1976). Also the herbicide was fed to the waterflea in algal food. The following table from Claus' article shows direct toxic effects:

Table I. Letal concentration values in ppm for 50% of the test organisms, after an exposure time of 24 and 48 hours.

LC_{50} (ppm) 2, 4-D		Daphnia magna	
		adults	larvae
24 h	1	228	210
	2	207	196
48 h	1	153	112
	2	162	98

Claus reports that this herbicide is relatively harmless for the crustacean since the lowest LC_{50} is very high compared to the concentrations used (in the Netherlands) for aquatic weed control. Nevertheless "This conclusion is, however, only valid on a short time basis, since the toxic effect of the herbicide was still increasing after an exposure time of 48 hours. From the long-term experiments it is clear that concentrations of 2, 4-D which do not harm the test organisms only exposed to them for a few days definitely influence the biological processes under chronic exposure." In a comparison of aerated and non-aerated culture systems the effect of the herbicide on reproduction was reduced. The following table shows a reduction in reproduction in systems without aeration and somewhat ambiguous results in systems with aeration (by air-bubbling for 30 secs every half-hour).

Table III: Chronic effects of 2, 4-D on the reproduction of *Daphnia magna*

	Total number of larvae/female	Reproduction Period (days)	Number of larvae/female/day	Mean	% inhibition
Without aeration					
Control	35.86	12	2.99	2.75	0
	25.14	9	2.79		
	23.01	9	2.56		
	31.75	12	2.65		
10 ppm	4.85	12	0.40	0.60	78.2%
	11.00	8	1.38		
	0.86	8	0.11		
	6.03	12	0.50		
1 ppm	15.66	7	2.24	2.04	25.8%
	25.00	9	2.78		
	14.90	9	1.66		
	17.80	12	1.48		
0.1 ppm	31.62	12	2.64	2.16	21.5%
	19.49	12	1.62		
	18.83	12	1.57		
	33.58	12	2.80		
With aeration					
Control	25.00	8	3.13	3.02	0
	29.12	8	3.64		
	18.38	8	2.30		
10 ppm	24.62	8	3.08	3.17	-5%
	27.72	8	3.47		
	26.68	9	2.96		
1 ppm	19.25	9	2.14	2.87	+5%
	27.78	9	3.09		
	30.48	9	3.39		
0.1 ppm	25.12	8	3.14	3.19	-5.6%
	21.57	8	2.70		
	29.83	8	3.73		
Control	36.97	12	3.08	3.13	0%
	39.10	12	3.26		
	36.66	12	3.06		
100 ppm	10.24	11	0.93	0.72	77%
	9.04	12	0.75		
	5.73	12	0.47		
56 ppm	20.57	12	1.71	1.74	44.4%
	18.85	12	1.57		
	23.22	12	1.94		
32 ppm	33.48	12	2.79	3.33	-6.4%
	43.46	12	3.62		
	42.94	12	3.58		

13. The effect on the animal of air-supersaturated water has been investigated by Nebeker (1976). The mean 96-hour LC50 value for *D. magna* was 122.5% total air saturation; the 7-day LC 50 was 120% and the 10-day LC-50 was 117.5%. Bubbles (emboli) were observed in body fluids and tissues and general body distention occurred before death. Lethal threshhold concentrations were about 111%, when about 20% of *D. magna* died. The effect of air-supersaturation on aquatic organisms is that they develop the so-called 'gas-bubble disease (GBD)'. Massive air bubbles may occur in the gut, in the brood pouch and under the carapace.

Nebeker noted that air-supersaturated water occurs in dams on the Columbia River (USA) and can occur in aquaria and hatcheries. Presumably the phenomenon can occur widely (outside N. America) in such places.

14. Canton and van Esch (1976) studied the toxicity to *D. magna* of 13 livestock feed additives (excreted in livestock faeces or urine). The most toxic (LC (EC) 50 < 1 mg/l) were robenidine and stenoral. Moderately toxic (1 < LC(EC) 50 < 10 mg/l) was pyrimethamine. Amprolium, ethopabate, furazolidone and zoalene were slightly toxic (LC(EC) 50 > 10 mg/l). Buquinolate, carbadox, clopidol, decoquinate, grofas and sulfaquinoxaline were found to be not toxic under their experimental conditions.

15. Canton (1976) investigated the toxicity of benomyl, thiophanate-methyl and BCM to *D.magna*. In the two-day studies, thiophanate methyl was the least toxic and BCM the most toxic. Results were:

Substance	LC50 (mg/l)	95% confidence limit
benomyl	0.64	0.63 - 0.65
thiophanate-methyl	16	14 - 18
BCM	0.46	0.38 - 0.56

The influence of BCM on the reproductive capacity of the animal was also studied by Canton. At 50 µg BCM/l water there was no reproduction; at 5 and .05 there was no effect.

16. Nymphs of the damselfly *Ishnura elegans* (van der Lind) were used as predators of the waterflea by Thompson (1975) in the construction of a predator-prey model. Thompson studied five instars of *I. elegans* feeding on five arbitrary size-classes of *D. magna* and calculated parameters of a mathematical model, following this with a discussion of the model.

17. Optimal orientation to light-dark boundaries of the waterflea is called 'contrast orientation' by Ringelberg et al (1975). It had been shown previously by one of the authors that *D. magna* cannot maintain a normal body position in the absence of contrasts in the environment; the animal makes rapid somersaults or lies on the bottom. The lack of orientation disappears when the light intensity from above is increased sufficiently, that is when contrasts are introduced. Ringwood et al distinguish several modes of orientation, propose an 'orientation area' consisting of 3 median pairs of ommatidea and 2 lateral pairs situated dorsally from the eye axis, and present a general model of contrast orientation in *D. magna*.

Light energy also affects respiration of Cladocerans, according to a number of authors quoted by Goss and Bunting (1980). Oxygen consumption tends to be lower for animals tested in the dark; this has not been shown specifically for *D. magna*.

18. Watts and Young (1980) suggest that food intake by the waterflea is based on a visual estimate of the surrounding food concentration using the increase of sideways scattered light with increasing concentration as an index.

19. Pena (1981), writing on cultivation techniques of fish, reports that *D. magna* are used in particular for feeding carp.

20. Zeiss (1963, quoted by Goss and Bunting, 1980) conducted studies on *D. magna* to determine the effect of crowding on oxygen consumption. Densities used were 0.083-, 4-, and 8-organisms per ml. Oxygen consumption at the two higher densitites was 2 to 2.5 times as much as at the low density.

21. The fish *Brachydanio rerio* was used as the predator of *D. magna* in a study of concomitant predation and infection processes by Anderson et al (1978).

22. Herbert and Loaring (1980) found *D. magna* in freshwater ponds in the Churchhill, Manitoba (Canada) area in the case that the predacious copepod *Heterocope septentrionalis* was lacking, but not when the copepod was present. They found in experiments that *D. magna* is much more vulnerable to predation by the copepod than *D. middendorffiana* (morph A) which coexists with the copepod in nature. Laboratory studies showed that at 20°C a single copepod can kill as many as 40 *D. magna* per day.

23. Shcherban (1979) studied the effects of copper, zinc, cadmium, nickel and magnanese on young animals (3 to 5 days old) and on sexually mature females in 'acute' experiments (24, 48 and 72 hours) at 10, 15, 25 and 30°C. The toxicity of Cu^{2+}, Zn^{2+}, Cd^{2+}, Ni^{2+} and Mn^{2+} increases with temperature. In the temperature interval from 25 to 30°C toxicity of cadmium increases by three to four orders of magnitude, that of copper and zinc by two orders. Nickel and manganese are of low toxicity; manganese was the least toxic. The following table gives detailed results:

Effect of Heavy Metals on D. magna at Various Temperatures*

	Agent	t,°C	Exposure, hours		
			24	48	72
D. magna, ♀♀ ov	Zn^{2+}	10	0,0001-1,0 / -	0,25-0,5 / >2,5	0,125 / 2,5
		15	0,0001-1,0 / -	0,25-0,5 / >2,5	0,05 / 2,5
		25	0,0001-1,0 / -	0,01-0,125 / >2.5	0,005-0,01 / 2.5
		30	0,0005-0,025 / 2.5	0,0005-0,005 / 0,125	0,0001 / 0.05
	Cd^{2+}	10	0,5 / 5,0	0,05-0,125 / 1,0	0,05 / 1,0
		15	0,025-0,05 / 2,5	0,0005-0,01 / 1,0-2,5	0,00025-0,0005 / 0,5-1,0
		25	0,001-0,01 / 0,5-1,0	0,001-0,005 / 0,5	0,00025 / 0,125
		30	0,001 / 0,25-0,5	0,0001 / 0,25	0,00025 / 0,025
D. magna, juv.	Cu^{2+}	10	0,025 / 0,25	0,01-0,025 / 0,25	0,005-0,01 / 0,125-0,25
		15	0,01-0,05 / 0,5	0,005-0,025 / 0,25-0,5	0,005-0,01 / 0,125-0,25
		25	0,005-0,01 / 0,25	0,00025-0,001 / 0,125-0,25	0,0025-0,001 / 0,125
		30	0,01 / 0,125	0,001 / 0,125	0,0001 / 0,025
	Zn^{2+}	10	-	0,5 / 2,5	0,05-0,125 / <2,5
		15	1-2,5 / -	0,25-0,5 / >2,5	0,125-0,25 / 2,5
		25	0,5 / 2,5	0,05-0,25 / 2,5	0,05 / 1,0
		30	0,025-0,125 / 2,5	0,001-0,01 / 0,25	0,00025-0,001 / 0,125
	Ni^{2+}	10	100% survival over the whole concentration (LC_0); denominator: lethal concentration (LC_{100}).		
		15	100% survival / -	5,0 / -	5,0 / -
		25	1,0 / -	0,5 / 2,5-5	0,25-0,5 / 2,5-3,0
		30	0,5-1 / -	0,25-0,5 / 2,5-5,0	0,25 / 2,5

*Numerator: vital concentration (LC_0); denominator: lethal concentration (LC_{100}).

(See also n.11.)

E. REFERENCES

Anderson, R.M., Whitfield, P.J., Dobson, A.P. and Keymer, A.E. (1978). Concomitant predation and infection processes: an experimental study. *J. Animal Ecol.* 47, 891-911.

Burns, C.W. (1969). Relation between filtering rate, temperature and body size in four species of *Daphnia*. *Limnol. Oceanogr.* 14, 693-700.

Canton, J.H. (1976). The toxicity of benomyl, thiophanate-methyl. and BCM to four freshwater organisms. *Bull. envir. Contam. Toxicol.* 16(2), 214-218.

Canton, J.H. and G.J. van Esch (1976). The short-term toxicity of some feed additives to different freshwater organisms. *Bull, envir. Contam. Toxicol.* 15(6), 720-725.

Christensen, S.W. (1973). Filtration, ingestion and egestion of different-sized algae by *Daphnia magna* Strauss. *Dissertation Abstr. int.* (B) 34(11). 5334.

Claus, C. (1976). Effect of 2, 4-D on survival and reproduction of *Daphnia magna* Strauss. *Med. Fac. Landb. Rijksuniv. Gent.* 41(2)(ii), 1467-1475.

Cowgill, U.M. (1976). The chemical composition of two species of *Daphnia*, their algal food and their environment. *Science tot. Envir.* 6(1), 79-102.

Geller, W. and Mueller, H.(1981). The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. *Oecologia (Berl.)* 49(3), 316-321.

Gerritsen, J. (1982). Behavioural response of *Daphnia* to rate of temperature change: possible enhancement of vertical migration. *Limnol. Oceanogr.* 27(2), 254-261.

Gibson, R.M. (1980). Optimal prey-size selection by three-spined sticklebacks (*Gasterosteus aculeatus*): a test of the apparent-size hypothesis. *Z. Tierpsychol.* 52(3), 291-307.

Gliwicz, Z.M. and Siedlar, E.(1980). Food size limitation and algae interfering with food collection in *Daphnia*. *Arch. Hydrobiol.* 88(2), 155-177.

Gophen, M. (1977). Feeding of *Daphnia* on *Chlamydomonas* and *Chlorobium*. *Nature, Lond* 265(5591), 271-273.

Goss, L.B. (1978). The effects of temperature on *Daphnia pulex* Leydig and *Daphnia magna* Strauss. *Dissertation Abstr. int.* (B) 39(3), 1111-1112.

Goss, L.B. and Bunting, D.L. (1980). Temperature effects on zooplankton respiration. *Comp. Biochem. Physiol.* 66A, 651-658.

Hadas, O., Cavari, B.Z., Kott, Y. and Bachrach, U. (1982). Preferential feeding behavior of *Daphnia magna*. *Hydrobiologia* 89(1), 49-52.

Harper, D. (1976). *Daphnia magna* in Scotland. *Glasgow Nat.* 19(4), 303-306.

Heller, R. and Milinski, M. (1979). Optimal foraging of sticklebacks on swarming prey. *Animal Behav.* 27(4), 1127-1141.

Herbert, P.D.N. and Loaring, J.M. (1980). Selective predation and the species composition of arctic ponds. *Can. J. Zool.* 58, 422-426.

Horton, P.A., Rowen, M., Webster, K.E. and Peters, R.H. (1979). Browsing and grazing by cladoceran filter feeders. *Can. J. Zool.* 57, 206-212.

Kamiński, K.Z. (1979). On some anomalies in *Cladocera*. *Przegląd Zool.* 23(4), 352-353.

Kersting, K. (1978a). Some features of feeding, respiration and energy conversion of *Daphnia magna*. *Hydrobiologia* 59(2), 113-120.

Kersting, K. (1978b) Growth efficiency of *Daphnia magna*. 1. The effect of food concentration. *Hydrobiological Bull.* 12(1), 3-20.

Kersting, K. and C. van der Leeuw-Leegwater (1976). Effect of food concentration on the respiration of *Daphnia magna*. *Hydrobiologia* 49(2), 137-142.

McArdle, B.H. (1977). An investigation of a *Natonecta glauca* - *Daphnia magna* predator-prey system. *Dissertation Abstr. int.* (C) 37(4), 690.

McArdle, B.H. and Lawton, J.H. (1979). Effects of prey-size and predator-instar on the predation of *Daphnia* by *Notonecta*. *Ecological Ent.* 4(3), 267-275.

Milinski, M. (1979). Can an experienced predator overcome the confusion of swarming prey more easily? *Animal Behav.* 27(4), 1122-1126.

Nebeker, A.V. (1976). Survival of *Daphnia*, crayfish and stoneflies in air-supersaturated water. *J. Fish. Res. Board Can.* 33(5), 1208-1212.

Ohguchi, O. (1978). Experiments on the selection against colour oddity of water fleas by three-spined sticklebacks. *Z. Tierpsychol.* 47(3), 254-267.

Pena, J.B. (1981). Aquaculture in Japan. 3. Cultivation techniques of fishes. *Inf.Tec.Inst.Invest.Pesq.* 0(89), 1-24.

Porter, K.G. (1976). Enhancement of algal growth and productivity by grazing zooplankton. *Science, N.Y.* 4246, 1332-1334.

Potts, W.T.W. and Fryer, G. (1979). The effects of pH and salt content on sodium balance in *Daphnia magna* and *Acantholeberis curvirostris* (Crustacea: Cladocera). *J. comp. Physiol.* 129(4), 289-294.

Ringelberg, J., Flik, B.J.G. and Buis, R.C. (1975). Contrast orientation in *Daphnia magna* and its significance for vertical plane orientation in the pelagic biotope in general. *Netherlands J. Zool.* 25(4), 454 - 475.

Russell-Hunter, W.D. (1979). *A Life of Invertebrates*. (N.Y., Macmillan).

Sayre, R.M. and T.B. Clark (1978). *Daphnia magna* (Cladocera: Chydoroidea). A new host of a *Helicosporidium* sp. (Protozoa: Helicosporida). *J. Invert. Path.* 31(2), 260-261.

Shcherban, E.P. (1979). Toxicity of some heavy metals for *Daphnia magna* Strauss, as a function of temperature. *Hydrobiological J.* 13(4), 75-80.

Stobbard, R.H., Keating, J. and Earl, R. (1977). A study of sodium uptake by the water flea *Daphnia magna*. *Comp. Biochem. Physiol.* 58A, 299-309.

Stroganov, N.S. and Kozyar, L.A. (1979). Growth and fecundity of *Daphnia* feeding on the pollen of anemophilous plants. *Hydrobiological J.* 14(4), 20-24.

Thompson, D.J. (1975). Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *J. Animal Ecol.* 44(3), 907-916.

Ward, R.W. and DeGraeve, G.M. (1978). Acute residual toxicity of several wastewater disinfectants to aquatic life. *Water Resour. Bull.* 14(3), 696-709.

Watts, E. and Young, S. (1980). Components of *Daphnia magna* feeding behavior. *J. Plankton Res.* 2(3), 203-212.

Winner, R.W. and Farrell, M.P. (1976). Acute and chronic toxity of copper to four species of *Daphnia*. *J. Fish. Res. Board Can.* 33(8), 1685-1691.

Winner, R.W., Keeling, T., Yeager, R. and Farrell, M.P. (1977). Effect of food type on the acute and chronic toxicity of copper to *Daphnia magna*. *Freshwater Biology* 7(4), 343-349.

Wulff, F.V. (1980). Animal community structure and energy budget calculations of a *Daphnia magna* population in relation to the rock pool environment. *Ecol. Model* 11(3), 179-225.

Young, J.P.W. (1978). Sexual swarms in *Daphnia magna*, a cyclic parthenogen. *Freshwater Biol.* 8(3), 279-281.

Zeiss, F.R. (1963). Effects of population densities on zooplankton respiration rates. *Limnol. Oceanogr.* 8, 110-115.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XX THE YELLOW-FEVER MOSQUITO *(Aëdes aegypti)*

by

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ABSTRACT

The precise environment of the Yellow-fever mosquito *(Aëdes aegypti)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

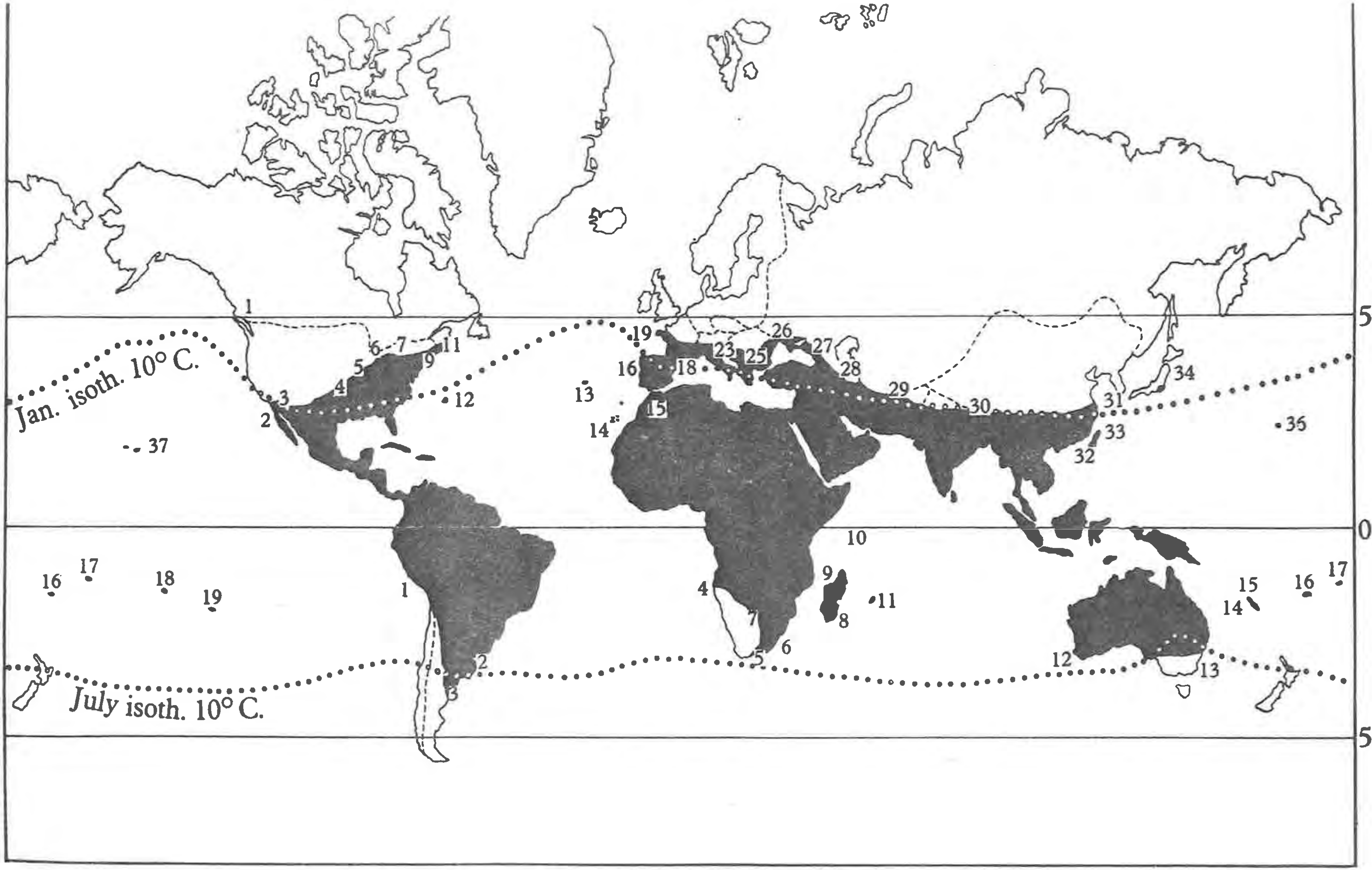


Figure 1. Map showing limits of distribution.

CONTENTS

A. INTRODUCTORY NOTE

Aëdes aegypti probably originated in Africa in or near Ethiopia.

Some varieties of *A. aegypti* have been described but Christophers (1960) considers them all to be the same species. In particular, some behavioural differences have been recorded among animals inhabiting different areas e.g. Malayan *A. aegypti* will not readily bite monkeys whereas African ones do so. Particularly when dealing with temperature effects various authors with discrepant results may in fact be reporting on different varieties.

This mosquito is ubiquitous in equatorial and tropical regions, its distribution being bounded approximately by the 10°C isotherm. In addition to being absent from desert areas (n. 3) and high ground (n. 6) the animal does not occur in areas of extensive forest; we have not been able to classify 'forest' in the environment since the mechanism is not clear to us. The map (see frontispiece) is from Christophers (1960). It shows the northern and southern limits of *A. aegypti*; the region between these limits is coloured black but this does not imply that the mosquito is found everywhere within the limits.

A. aegypti was spread by humans in ships, dhows, junks etc. that almost invariably had warm moist areas and water below decks, enabling the animal to breed while being transported. Christophers (1960) suggests also that eggs may be transported when "cemented" on the sides of pots or other receptacles (notes 9, 13, 23, 32).

A blood meal is obligatory before the female can oviposit (n. 7).

Individuals pass through the following stages: egg; first-; second-; third- and fourth-instar larva; pupa; and finally adult. The adult stage may be either female or male. If we allow 3 days from emergence to the first blood meal, 3 days for egg maturation, 3 days for oviposition and hatching and combine these estimates with the figures in n. 4 we find that roughly speaking the egg-to-egg cycle takes about 16 to 30 days. However, on the Black Sea coast, where the average temperature in May through October is about 21°C the cycle length is about 40 to 45 days.

Only the larval stages of *A. aegypti* grow. Neither the egg nor the pupa take in food and the imago uses the food taken in only for reproduction and to fuel activity. The pupa differs from that of most insects in that it is active - it swims.

The following table (from Christophers, 1960) gives sizes of larvae:

Instar	Length in mm.	Weight in mg.
I	1.97	0.0875
II	3.24	0.313
III	5.17	1.71
IV	6.80, 7.33	3.29, 4.92

The double figures given under instar IV relate to the male and female respectively. At the beginning of the instar both length and weight are approximately identical with the length and weight of the previous instar at the end of its period.

The female is nearly twice the size of the male and much more robust. Males emerge from the pupal state earlier than females and are invariably in the majority, usually forming about 60% of the population. (Estimates of 53% to 77% have been recorded).

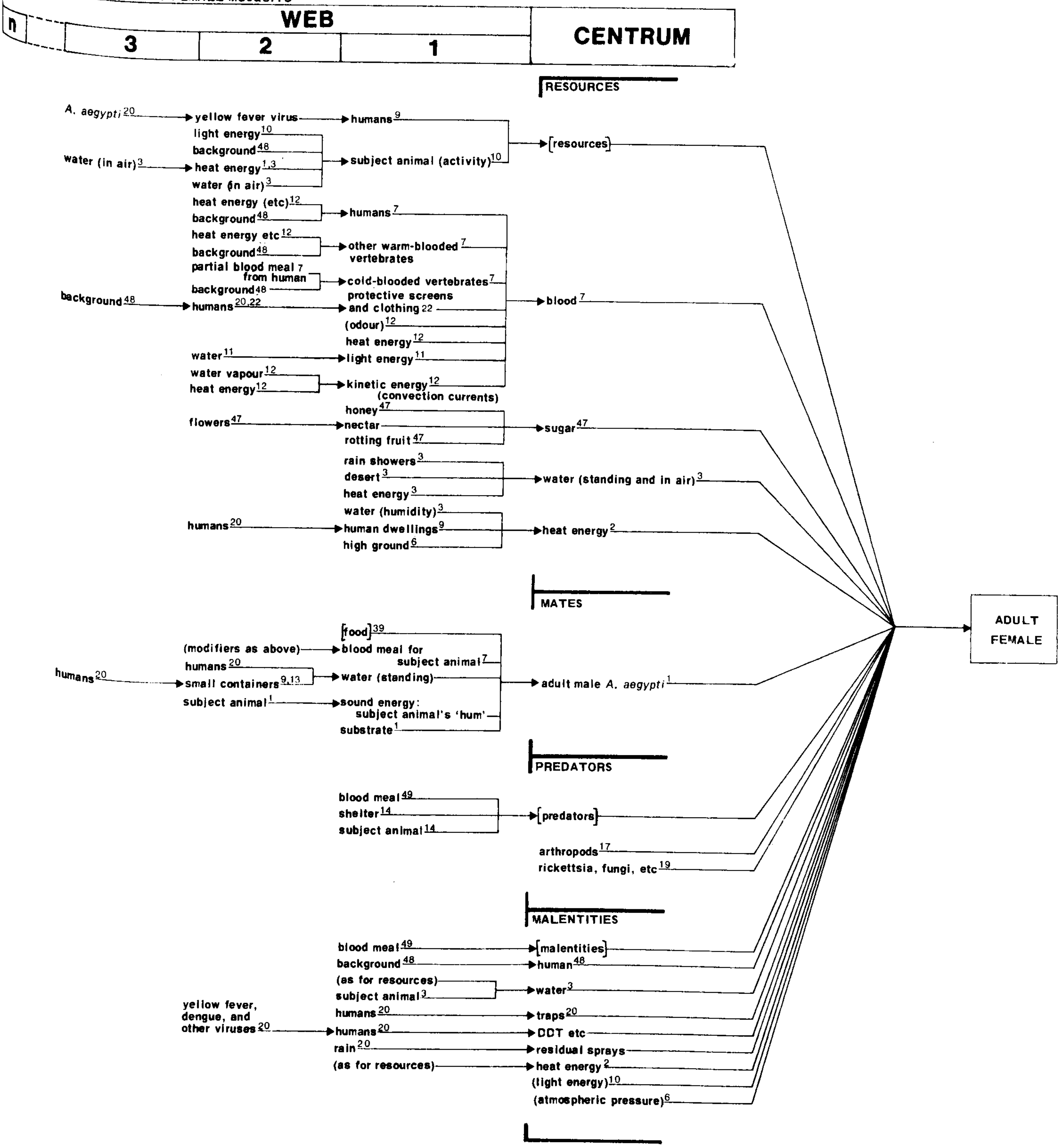
Copulation usually occurs in flight. Males are attracted to females by the 'humming' noise emitted (n. 1, n. 48).

An unfed female has a flying speed of about half to one m/sec; the males are more rapid.

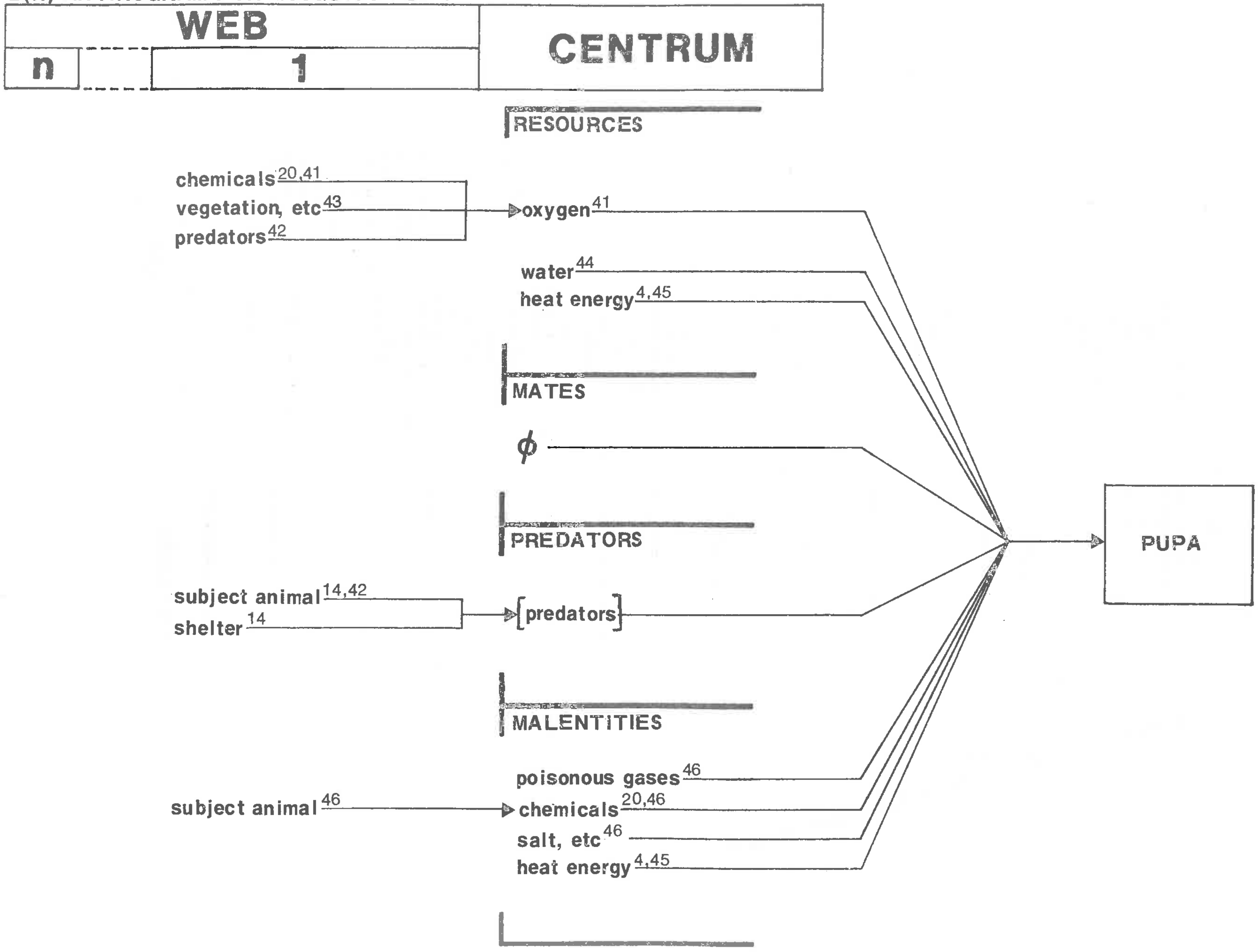
The length of life of the imago in nature is not well-known but probably varies from about 15 days to about 40 days. For some details of laboratory results on longevity see n. 1.

Christophers (1960) gives a detailed account of the "enemies" i.e. predators and malentities, of many different species of mosquito. In this Working Paper we have restricted these two classes to those predators and malentities which are specifically recorded as interacting with *A. aegypti*.

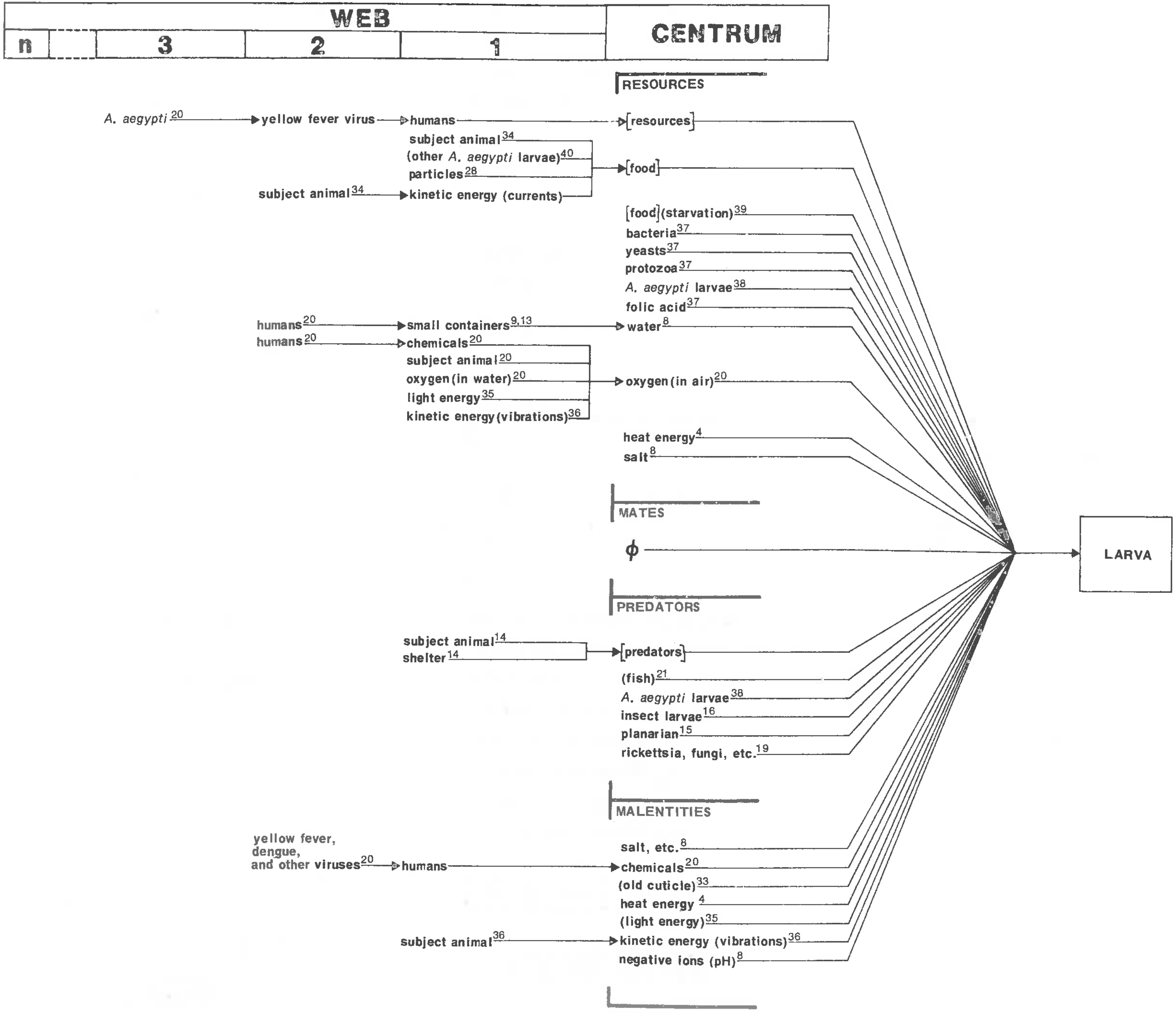
ENVIROGRAM FOR ADULT FEMALE MOSQUITO

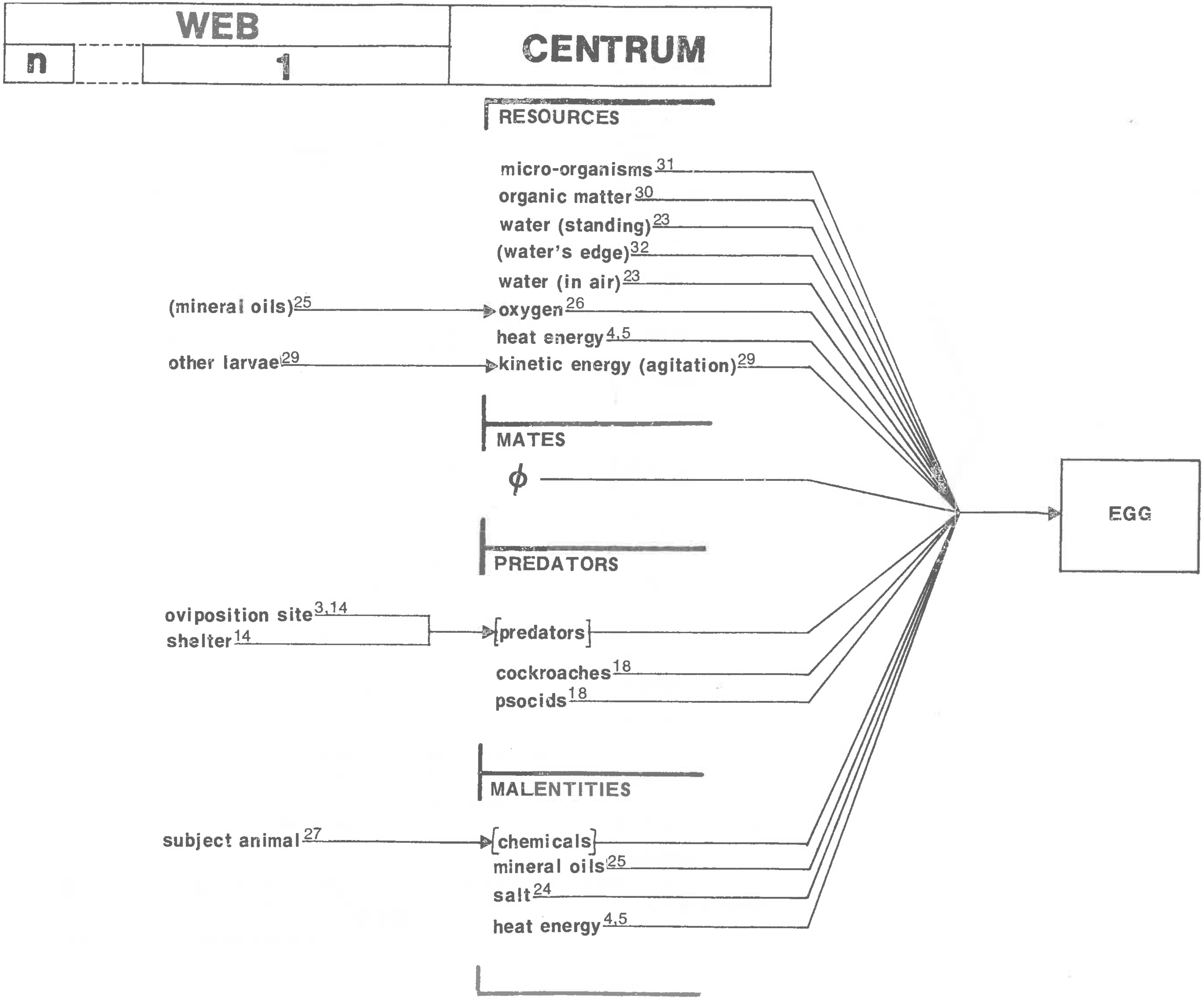


B(ii) ENVIROGRAM FOR MOSQUITO PUPA



B(iii) ENVIROGRAM FOR MOSQUITO LARVA




WEB
n
1
CENTRUM
RESOURCES
micro-organisms 31
organic matter 30
water (standing) 23
(water's edge) 32
water (in air) 23
(mineral oils) 25
oxygen 26
heat energy 4,5
other larvae 29
kinetic energy (agitation) 29
MATES
ϕ
PREDATORS
oviposition site 3,14
shelter 14
[predators]
cockroaches 18
psocids 18
MALENTITIES
subject animal 27
[chemicals]
mineral oils 25
salt 24
heat energy 4,5
EGG

C. NOTES ON THE ENVIROGRAMS

1. In laboratory experiments *A. aegypti* females have been successfully mated (i.e. to give fertile offspring) with *A. albopictus* males, however not all workers have obtained satisfactory results. There is some suggestion that in the case of a successful cross the offspring almost invariably resembled the female parent. Unfertilized females occasionally lay eggs but it is not known whether these eggs are viable.

Forms of *A. aegypti* having mixed sex characteristics (i.e. gynandromorphs) are reported as being not uncommon. We are not clear whether these gynandromorphic forms are fertile and have normal offspring or are sterile.

Males are attracted by the 'humming' noise emitted by the females. *A. aegypti* has the ability to determine the direction from which sound is emanating. The appropriate organ is particularly well-developed in the male.

Copulation usually begins very soon after emergence. Males chase the females, sieze them belly to belly and copulate for about a minute, usually while flying, though occasionally the female will settle on a substrate pinning the male under her. Males have never been seen to alight on resting females (i.e. those on a substrate).

Once mated, the female is capable of laying fertile eggs for many days. A particular female/male pair has been observed to copulate several times soon after emergence, however it is not known whether a female will mate with more than one male either before or after ovipositing. There is heavy mortality after oviposition; one observer reported 70% of females died following the oviposition of the first batch.

Most oviposition occurs in the afternoon; it is not clear whether this is induced by the higher temperatures or by some other factor(s).

A female has been observed to lay at the rate of 3 eggs/minute, resting after every sixth or eighth egg before continuing. Up to 15 eggs are laid at a time. There appears to be no relation between the size of the female and the number of eggs laid. The following quotation and tables are from Christophers (1960):

> "Since more than one batch of eggs is normally laid in the lifetime of the female, provided there are further blood meals, the total number of eggs laid by one female may be considerable. Macfie (1915) records instances of fifteen and ten ovipositions, the first at intervals of 3 days by a female that lived 50 days, the second at longer intervals by a female that lived 60 days. Fielding records a female which laid 752 eggs in 72 days. In the first 31 days it fed eight times and laid 437 eggs (55 eggs per feed), in the next 31 days it fed six times and laid 260 eggs (43 eggs per feed) and in the next 10 days it fed twice and laid 55 eggs. Owing, however, to heavy mortality at oviposition the number of females with such numerous ovipositions is small and even after the first oviposition there is a considerable reduction in numbers. Howard, Dyar and Knab note that the French Commission (Marchoux *et al.*) found that out of 100 females only thirty laid eggs a second time and twenty-one from three to seven times. The largest number of ovipositions observed in a single female was seven. H.A. Johnson (1937) records females producing viable eggs to an age of 6 weeks."

Number of eggs Laid

Very varied estimates of the number of eggs laid at an oviposition by *A. aegypti* are given in the literature. Among earlier records are the following.

Marchoux *et al.* (1903)	First batch up to 100. Later batches below 30.
Otto and Neumann (1905)	20-40 or more
Howard, Dyar and Knab (1912)	
J.R. Taylor (Havana)	35-114
American Commission	40-150
French Commission	First batch 70-95; max. 144; later batches max. 30
Goeldi	50-100
Boyce (1911)	27-97
Howlett (1913)	About 50
Macfie (1915)	100 to as few as 7
Buxton and Hopkins (1927)	20 on each occasion in nature
Connor (1924)	35-150
F.H. Taylor	Up to 80
Roy (1936)	Average max. 76

TABLE 38: Frequency distribution of number of eggs laid

Number of eggs per batch	80-9	90-9	100-9	110-19	120-9	130-9
Number of mosquitoes laying	2	2	4	14	8	0

2. The following table gives approximate temperatures for the limits of distribution of *A. aegypti*:

	°C January	°C July		°C January	°C July
N. America	1.8	23.9	S. America	15.6	26.7
Europe	4.4	23.9	Africa	15.6	26.7
China	10.0	26.7	Australia	10.0	21.1
Mean	5.4	24.8	Mean	13.7	24.8

Laboratory measurements indicate that temperatures of 10°C are lethal to many adults (and larvae, see n. 4). One author suggests that the mosquitoes' distribution will fall into three temperature zones: first, one in which continuous breeding occurs, secondly a borderline zone in which the species overwinters as an egg and thirdly a temporary summer zone in which the mosquito breeds and spreads during the summer weather but becomes locally extinct during the colder weather.

The animal has been observed around Lake Chad where the temperature regularly exceeds 40°C and it still survives in India in areas where in the hot dry season the temperature may exceed 46°C for many hours in a day. (see n. 9 for humans as modifiers of heat energy).

The lower limiting temperature for adult activity is about 15°C. At 15°C humans are freely attacked and mating occurs. When the mean daily temperature is 11 to 12°C the species disappears.

The effect of temperature on adult size is as follows:

Temperature	Adult size
Under 19.5°C	Undersized
23°C	Largest specimens
23.8°C-25.9°C	Equally fine specimens
Above 30.8°C	Undersized

Generally, within the temperature range, lower temperatures produce larger adults (as for *Calanus finmarchicus*; see No. XVIII of this series of Working Papers).

The following table shows the effect of temperature on adult behaviour:

Temperature (°C)	Effect on *A. aegypti*
0	Dies quickly.
4	Survives 1 hour then dies.
7-9	Almost immobile. Crawls sluggishly on horizontal surfaces. About half the females survived 30 days in experiment. Some lived up to 82 days.
10	Approximately the threshold for crawling.
14-17	Slowly becoming more active. Biting starts. Can fly sluggishly at 15°C. Females will

Temperature (°C)	Effect on *A. aegypti*
	oviposit at 16°C., and take blood meals at 17°C.
18-19	Seems to be the lower limit for a population to maintain itself.
20	Fertilization seldom occurs below this temperature.
19-25	Females slow to bite.
26-35	Females very active and quick to bite.
28	Ideal temperature.
35	About 17%, or less, actively biting.
35-38	Insects 'uncomfortable'.
39-40	Insects remain motionless in apparent death but will recover.
40	No feeding.
41-43	Actual or apparent death. May survive short exposure.
44	Almost instant death with few recoveries.

(For interaction of heat with humidity see n. 3).

3. Distance from the sea and desert conditions are factors limiting the distribution of the mosquito (but see also n. 6), presumably because of the shortage of water for breeding and drinking. The animal is more likely to be found in warm places with high humidity, along coasts and in towns, particularly sea-ports. Showers of rain will often provide small temporary ponds for breeding purposes. For adult *A. aegypti* "the degree of activity and duration of life is largely dependent on a suitable humidity" --- "and, to judge from experience in the laboratory, upon access to water to drink, for the species soon dies in captivity, even in a relatively moist atmosphere, if it is unable to drink." (Christophers, 1960). A cage containing about 600 mosquitoes was accidentally left at 25°C and 70% R.H. but without drinking water. All these mosquitoes died in 4 days - whereas there was negligible mortality in two similar cages with water. Although high humidities are favourable to the life of the species in general, it is known to feed at fairly low humidities. However, high temperatures

(34°C and higher) and very high humidities (95% and above) have a deterrent effect on activity.

In the laboratory a female at full maturation of the ovaries will deposit eggs freely on any water or wet surface that may be available. In the absence of a wet surface she will hold her eggs, which will perish after a short period. In nature it seems likely that the female will choose to deposit a line of eggs on the wet surface just above the water's edge rather than on the surface of the water. The eggs are retained in position by their sticky chorionic pads until, when dry, they are firmly cemented into place by the same substance.

A body of water as such can damage the adult mosquito. During emergence the pupal skin opens out into a rigid floating base, like a small boat, on which the insect continues its emergence; here the subject animal acts as a first-order modifier in its own environment.

The interaction between water and heat is shown in the following table:

Table 45: Number of *Aëdes aegypti* females feeding at different temperatures and humidities (Lewis, 1933)*

Temperature	Relative humidity (percentages)			
(°C)	0	60-70	77-88	91-95
15	-	-	0 (27)	-
20	-	-	-	5 (37)
25	6 (34)	12 (33)	-	33 (43)
30	11 (36)	17 (35)	-	38 (39)
35	-	-	11 (36)	17 (36)
40	-	-	0 (24)	-

* The figures in brackets are the numbers of mosquitoes used, those not in brackets the numbers that fed.

4. Laboratory measurements indicate that temperatures of 10°C are lethal to the larva (as well as the adult - see n. 2). However at least one author has described *A. aegypti* as overwintering during the larval stage, the implication being that larvae are more resistant to low temperatures than adults. The evidence for this result is weak.

The following tables give approximate temperature effects on the duration of the early stages, from hatching to adulthood (i.e. larval + pupal stages):

Location	(Temperature)	Time
Tropics	High	About a week
Cuba	28-31 C (day)	9-10 days (mode=10 days)
French Sudan	rainy season	12-15 days
French Sudan	cold season	18-20 days

The larval stage lasts about 9 days at 23°C, about 7 days at 27°C and about 6 days at 28°C. The following table gives some detailed results at 28°C.

TABLE 11

Duration of instar periods

Hours	I	II	III	IV	P	Timing of stage
20	100	-	-	-	-	All first instar up to 20 hours
22	100	+	-	-	-	-
23	89	11	-	-	-	-
24	67	33	-	-	-	-
25	56	44	-	-	-	50 percent ecdysis I-II 25-26 hours
26	44	56	-	-	-	
27	31	69	-	-	-	-
28	3	97	-	-	-	-
30	-	100	-	-	-	-
						All second instar 30-42 hours
42	-	100	-	-	-	-
45	-	74	26	-	-	-
46	-	37	63	-	-	50 percent edysis II-III 46 hours
47	-	17	83	-	-	-

Hours	I	II	III	IV	P	Timing of stage
48	-	27	73	-	-	50 per cent ecdysis II-III 46 hours
49	-	+	100	-	-	-
50	-	15	85	-	-	-
52	-	+	100	-	-	-
54	-	2	98	-	-	-
						All third instar 54 - 68 hours
68	-	-	100	-	-	-
69	-	-	73	27	-	-
70	-	-	60	40	-	-
71	-	-	58	42	-	50 per cent ecdysis III-IV 71-72 hours
72	-	-	32	68	-	
73	-	-	24	76	-	-
76	-	-	17	83	-	-
78	-	-	-	100	-	-
92	-	-	9	91	-	-
94	-	-	-	100	-	-
96	-	-	6	94	-	-
98	-	-	-	100	-	-
102	-	-	-	100	+	First male pupa 102 hours
117	-	-	9	91	-	-
122	-	-	-	50	50	Bulk of males pupated 122 hours
139	-	-	-	+	100	-
141	-	-	-	12	88	-
144	-	-	-	+	100	Bulk of females pupated 144 hours

A plus sign indicates that a few of this stage were present in the sample taken but too few to show as a percentage.
The cultures were from eggs hatched within 15 minutes.

Young instars prefer temperatures from 23^{o} to 32^{o}C.,older instars from 28^{o} to 32^{o}C.

The larvae will survive short exposures of 0^{o}C. and have been known to recover after being encrusted in ice, however in an experiment those frozen for more than 11 hours did not recover. Two to three hours exposure to 4.4^{o}C. caused larvae to become dormant at the bottom of the vessel; they resumed activity at 27^{o}C. Low temperatures progressively cause sluggish movement, inactivity and death.

Detailed experiments have been carried out showing that first instar larvae are more resistant to low temperatures than later instars. At 10°C (indefinitely) growth takes place but pupation does not occur.

One hour exposure at 39°C is lethal to larvae, nevertheless larvae exposed for a few minutes to temperatures up to 47°C. may recover. The following table shows the temperature limits of effective development.

TABLE 13

Lethal effect of high temperature on larvae of *Aëdes aegypti*

	Periods of Exposure							
	3 minutes		15 minutes		30 minutes		60 minutes	
Temperature (°C.)	a	b	a	b	a	b	a	b
47	100	100	100	100	100	100	-	-
46	90	100	100	100	-	-	-	-
45	70	30	100	100	-	-	-	-
44	11	44	100	88	-	-	-	-
43	27	27	100	67	100	100	-	-
42	8	7	73	53	100	-	-	-
41	-	-	60	50	25	45	-	-
40	-	-	0	0	25	42	34	38
39	-	-	-	-	-	-	8	42

a Number apparently dead at end of experiment
b Number dead overnight

There is general agreement that the effective development range is 16° to 34°C. However adults hatched in constant temperatures above 30.8°C have been found to be small and feeble. It may be assumed that within the effective range development will occur more quickly at higher temperatures.

The tables in this note are all from Christopers (1960).

5. Eggs of *A.aegypti* have been shown to be much more resistant to low temperatures than either larvae or adults. Some authors have described the species in various areas as overwintering during the egg stage. Several authors have commented that a drop of 6° to 10°F. can cause some eggs to hatch.

The following table gives the effect on the viability of eggs exposed for 24 hours to various temperatures :

Bacot (1916) notes the following effects on viability of eggs exposed for 24 hours to different temperatures.

29°F.	(-1.7°C.)	81 per cent hatched
75°F.	(24.0°C.)	80 per cent hatched
95°F.	(35.0°C.)	28 per cent hatched
102°F.	(39.0°C.)	12 per cent hatched
107.6°F.	(42.0°C.)	0 per cent hatched

The eggs can withstand 5 mins exposure to temperatures up to 48°C., at which some still survive. Over 49°C is considered lethal and for longer exposures temperatures as low as 40°C may be lethal.

For low temperatures also the effects depend on the exposure time. A prolonged exposure to 10°C is unlikely to be lethal. Once the larva is formed the egg can withstand sub-zero temperatures. However if the egg is exposed to very low temperatures before embryonic development then the situation differs in that it is thought that temperatures below 16°C. will arrest development. Eggs exposed to 18°C. shortly after oviposition did not hatch after 21 days, but hatched almost at once when exposed to 28°C.

The average times for incubation at various temperatures are :

Temperature (°C.)	Time (hours)	Round figures (days)
28	74	3
25	96	4
23	114	5
18	-	12
7	Development inhibited	
1	Development inhibited	

Once hatching has started the process is very quick - usually only seconds or minutes.

The maturation of eggs is also temperature-dependent, as shown by the following table :

Temperature	Time from blood meal to oviposition
29-30°C.	48 hours, almost always by third day, sometimes fourth
25-27°C.	Fourth to fifth day
20-25°C.	Fourth day, sometimes seventh to ninth
Under 20°C.	May be retarded 26-7 days

Notice, however, that eggs in one batch may take a few days to lay (at a rate of about 20 at a time).

The tables in this note are from Christophers (1960).

6. Altitude is a factor in the distribution of the mosquito, perhaps because of the temperature effect (but possibly because of changed atmospheric pressure). The greatest altitude recorded for A.*aegypti* is 7,800 ft., at the top of Mt. Bizen in Eritrea. The mosquito has been seen at 6,000 ft. in Kenya and south of the Himalayas; these latter mountains seem to have blocked its spread to suitable regions further north.

7. Without a blood meal the female is unable to form eggs. *Homo sapiens*, other primates such as forest monkeys, and some other vertebrates e.g. bats, birds and cattle supply the blood. Because of the habits of A. *aegypti* (see n. 9) this particular species of mosquito is most likely to obtain blood from humans. In the laboratory the animal will feed adequately on guinea pigs only if they are shaved. For oviposition to occur often severalmeals are required from a rabbit, whereas only one is necessary from a human. The situation with cold-blooded verterbrates is confused.

Various authors have successfully used frogs and turtles but have failed with lizards and geckos. Meals from such animals are usually small. If disturbed from a human-blood feed a mosquito is much more likely to feed from a cold-blooded animal than if undisturbed. There is no clear evidence that any one particular class of human (young, hairy, etc.) is favoured by *A.aegypti*.

The males do not feed on blood.

The following table shows that to obtain, on average, about 85 eggs (rather more than is the norm) a full meal of 3 to 3.5 mg of blood is required and that for any eggs at all at least 0.6 mg blood is necessary. For the continuous production of eggs the female must have a continuous supply of blood.

TABLE 36

Number of eggs laid following upon different amounts of blood feed (from data given by Roy).

Range Blood (mg)	Number of females	Mean weight blood (mg.)	Total number of eggs laid	Mean number of eggs laid	Number of times no eggs laid	Number of eggs per mg.
0.0-0.5	21	0.38	0	0	21	-
0.6-1.0	28	0.77	197	7.04	21	9.14
1.1-1.5	35	1.22	1197	34.2	2	28.06
1.6-2.0	34	1.79	1699	47.03	1	27.77
2.1-2.5	11	2.17	544	49.45	1	22.71
2.6-3.0	6	2.72	404	67.33	0	24.77
3.1-3.5	2	3.2	171	85.5	0	26.72

From emergence a minimum of 18 hours must elapse before an imago is ready for its first blood meal. The usual time is about 48 to 72 hours. Once fully gorged on human blood a female will not take another blood meal until after depositing the current batch of eggs. However, she will feed immediately after oviposition. The cycle from blood meal to oviposition takes about 3 days; another cycle can begin immediately (within the life-time of the animal and given that conditions are suitable). Delays may occur here similar to those described by Kitching(1977) for the sheep blowfly (see Working Paper XIII in this series). Altogether up to 15 cycles may occur.

Females will feed on blood both before and after mating; there seems to be no relation between time of mating and time of feeding.

For a comparison of blood as a food with sugar substances see n. 47.

8. Water is necessary for larval life. "For the larva there must exist breeding places where the larva can obtain food under conditions for which it is adapted, that is, neither very foul water, in which the species is rarely found, nor open natural water, for which some mosquitos are adapted, but not *A.aegypti*" (Christophers,1960). The larva, however, can survive for considerable periods in "almost clean" water, by drawing on its own food reserves.

Larvae are found in brackish water, but usually sea-water in any concentration over 50% (i.e. 1.6% salt) is lethal. The following data, quoted by Christophers (1960), have been collected about the effect of salt on the larvae:

Macfie (1914)	0.5 per cent salt.	Little effect
	2.0 per cent salt.	Many dead at 6 hours; all dead at 12 hours.
	2.3 per cent salt.	Larvae rapidly killed.
Macfie (1922)	Pure sea water.	Larvae killed in 2-4 hours
	50 per cent sea water (1.6) salt).	Larvae killed in 24 hours
Wigglesworth (1933c)	0.9 per cent salt or less.	Larvae not effected
	1.0 per cent salt.	Larvae die in about a week
	1.3 per cent salt.	Larvae die in about 72 hours
	1.4 per cent salt.	Larvae die in about 48 hours
Pantazis (1935)	0.5-1.0 sale per mille.	Optimum salinity
	5.0 salt per mille.	No development over this concentration.

In slowly increasing salinity larvae will adapt and can survive at 1.75% salt. At the other end of the scale a larva has the ability to obtain its necessary salt from extremely dilute solutions.

It is generally agreed that pH has little effect; in the wild larvae occupy media with pH from 5.8 to 8.5. When the pH is reduced to about 3.6 to 4.2 emergence is reduced and the development period is increased. Development at pH 9.2 to 9.5 is slightly extended.

9. *A. aegypti* is very often associated with human dwelling-places, particularly within towns. Christophers (1960) lists the domestic water pot, the cistern, the anti-formica, the flower vase and shaded rooms with cupboards and hanging equipment all as used by the mosquito. Humans also supply the obligatory blood meal (n.7) for the adult female. In particular "the dock side and water front of teeming harbours in moist and rainy tropical climates, with miscellaneous collections of water in machinery, country boats and even in the old days in ships, whereby it is spread to other ports and harbours, the species obtains conditions optimal for its proliferation. It does not find conditions so suitable where communities are well housed with permanent water supply and good drainage system and tidier house habits."

Human dwelling-places are likely to be particularly important in the very hot areas where the mosquito is found (n.2). In cold areas also buildings may supply protection.

10. *A. aegypti* is known to be most active by day although it is recorded as biting at night. The extent of its night activities is unknown (and controversial).

An unfed female flies at about 50 to 100 cm/sec. (Males fly faster, with probable maximum velocity about 150 cm/sec.) The insect can make headway against winds blowing at 40 cm/sec. or less; at this speed and in stronger winds the mosquito makes its way to a suitable position and lands; in winds of 150 cm/sec. it cannot take off again.

The flight direction is largely controlled by visual response to background (n.48).

Single flights are usually limited to within 28m of the breeding place. Dispersal can be 400 to 1000m and one author noted that the species can fly over 1 Km of water.

A. aegypti is reported as avoiding bright light and open spaces.

11. The location of a victim for a blood meal is largely through the visual stimulus of a dark, moving object (but see also n.12).

In the laboratory depriving the mosquitos of water combined with exposing them to light increased the biting response.

12. The warmth of a potential victim (for a blood meal) assists the animal to find that victim (but see also n.11). However, feeding on a human corpse has been observed several times (and is important in spreading yellow fever).

Smell may play a minor role in the location of a victim.

A series of experiments and observations have shown that convection currents set up by warm animals 8 to 16°C. above the ambient temperature are very important in attracting mosquitoes to feed. The presence of water vapour assists greatly to set up convection currents; dry air soon achieves temperature equilibrium.

Exhaled breath from warm animals is also highly attractive to A.*aegypti*.

The following quotation is from Christophers (1960):

"THE FORM IN WHICH WARMTH ACTS AS AN ATTRACTANT

In the last section it has been noted that for temperature to be effective as a stimulus to feed there must be a difference in the temperature of the attractive object and that of the general environment. Further than this Petersen and Brown (1951), studying the effectiveness of warm bodies to A. *aegypti*, found that such attractiveness was eliminated by the interposition of an air-tight window that allowed almost all the radiant heat to pass through but prevented heat convection. These authors thus concluded that radiant heat in itself was not the attractive factor and that heat was effective through the formation of warm convection currents, curiously enough what Howlett had shown in his simple experiment with a warm test tube. There can indeed be no doubt that the effective factor (disregarding for the moment certain visual reactions at a distance discussed later) causing A. *aegypti* to attack to feed are warm convection currents set up by the host.

Experience with the species over a number of years indeed has shown that this sensitiveness to convection currents is very highly developed in the species and amounts almost to a special sense. What sensilla are responsible is not at present known, but the abundance of such sensory organs about the coxae and associated structures (see ch. XIX(g) suggests that these might be concerned.

It is easy to give demonstrations of the sensitiveness to such currents. Thus, if a hand be held against the glass side of a cage of hungry A. *aegypti*, females will soon begin to collect in flight, not opposite the hand, but a little way above this where the warm glass has evidently set up ascending convection currents of warm air. If in a cage the arm be exposed enclosed in a box with gauze top and sides, it will be noted that the females congregate above rather than at the sides, even if the arm be placed much nearer the sides than the top. Again the females settle rapidly on a white cloth stretched a little distance over the arm since this gets warmed or allows warm air to pass through. The mosquitoes, however, take very little interest in such a cloth without the arm, even if it has been well rubbed over the arm, so that it can scarcely be smell that has affected them. The possibility of CO_2 being the attractive factor is not ruled out, but from what is said later this is unlikely to be the main reason for the behaviour described."

13. The mosquito breeds near man; its breeding places are almost totally confined to small artificial collections of fresh water - in vases, cups, and jugs, also water-pots and similar outdoor receptacles and wells - also bilge water in ships, pockets in cranes etc. It also uses small puddles of water in appropriate leaf axils e.g. *Colocasia*, banana and pineapple leaves or in tree stumps or tree holes. It is rarely found in puddles of water on the ground, or drains, where the edges are earth or mud, but has been seen in rock pools; the difference here may be due to predators.

14. A.*aegypti*, in all its life stages, tends to be protected from predators (relative to other species of mosquito) because of its secluded 'artificial' breeding places and its indoor habits.

18. In the laboratory the chief predator of stored eggs of A. *aegypti* are psocids and cockroaches.

19. Rickettsial forms have been found in A.*aegypti* adults infected with the virus of dengue.

Yeasts have been recorded as present in the coelemic cavity of the adult mosquito.

Larvae have been found in the laboratory covered with fungal hyphae (*Nocardia* and an unidentified fungus), also infected in nature with a brown fungal mass (*Fusarium*) in the thorax.

A mould has been found in the digestive tube and coelom of the larvae.

A large spirochaete has been found in the gut of the larva and the Malpighian tubules of the adult.

The flagellates *Leptomonas algeriensis* has been found in the larva in Algeria - but not in the adult. *Herpetomonas* (another flagellate) has been found in the adult in Madras and Martinique.

A parasitic cilate, probable a form of *Glaucoma pyriformis* has been found in the body cavity of the larva in Zambia, however, A. *aegypti* is not a suitable host for the ciliate, which is found in other mosquito larvae.

Immature nematode parasites, *Agamomermis*, have been found in the body cavity of the larva. They occur in the body cavity in pairs, a large and a small form, and escape through the perianal membrane when the larva is about to pupate. These parasites have been successfully cultured in the laboratory and then used to infect A. *aegypti*. The larval stages of the nematodes *Foleyella ranae* and F. *dolichoptera* infesting certain frogs in North America have been found in the head, abdomen and thoracic muscles of adults fed on infected frogs.

Black spores formed by deposition of chitin on dead structures in the body of the adult mosquito occur when the animal is infected with *Plasmodium gallinaceum*.

15. A planarian was recorded by Lischetti (1919) as destroying larvae of *A. aegypti* in a glass tank. (Christophers, 1960).

16. Shannon (1929, quoted by Christophers, 1960) observed the larvae of the tipulid, *Sigmatomera*, preying on *A. aegypti* larvae in tree-holes in Brazil.

Carter (1919, also quoted by Christophers, 1960) records larvae of the mosquito being preyed on in West Africa by a species of *Forcipomyia* (Ceratopogoninae).

Cannibal larvae of other species of mosquito are judged by Christophers to be "the most effective and important of all insect enemies". Attacks are made, for example, when *A. aegypti* is breeding in bamboo stumps (a common breeding-place) or breeding-places of a similar type which are also used by various species of *Megarhinus* the larvae of which are extremely voracious. A single megarhine larva has been observed to devour 21 *A. aegypti* larvae in a night. In another instance 2 larvae of *M. inornatus* in 5 days destroyed 127 III- and IV- instar larvae of other *Aëdes* spp. (but only 7 pupae). The larvae of *Toxorhynchites immisericors* (*Megarhinus splendens*) commonly prey on the larvae of *A. aegypti* in earthenware water storage pots in Calcutta. Attempts have been made, not always with success, to use *Megarhinus* spp. to control *Aëdes* spp.

One larva of the African species *Lutzia tigripes* was reported as eating 88 larvae of *A. aegypti*, preferring this to other species. In India *Lutzia* larvae are also found with the larvae of *A. aegypti* in some types of breeding-places. *L. bigotti* larvae have been observed destroying larvae of *A. aegypti* in 'artificial' containers in Rio de Janeiro.

17. The spider *Uloborus feniculatus*, the arachnids *Monomorium pharaonis* L. and *Solenopsis geminata* F., also a scorpion, *Isometrus maculatus* have beer seen attacking *A. aegypti*.

In Cuba, a wasp *Monedula* has been observed capturing adult *A. aegypti*, one specimen capturing on the wing 20 in 5 minutes.

Ants have been seen in Somaliland attacking newly-emerged adults.

20. A. *aegypti* is the chief vector of the yellow fever virus. Other mosquitoes are also vectors. Some species of forest monkey may also be infected with yellow fever (see also n. 7). A. *aegypti* acts as a vector for other viral diseases of both humans and their domestic animals (e.g. dengue fever).

The fact that A. *aegypti* is such an important vector of a major disease has resulted in humans taking strong control measures. Spraying with D.D.T. has been found particularly effective against the mosquito in some areas. However, by 1954 resistance of A. *aegypti* to D.D.T. was being noticed in the West Indies. Other sprays and aerosols are used in households. Traps are sometimes used. Residual spraying of surfaces is also used, but the effect is reduced by rain.

Humans also act as modifiers in the environment of the adult and larva when they replace open water-tanks by piped water and carry our other Public Health measures such as the removal of water-holding receptacles (vases etc. see n.13).

The larva needs to spend considerable time near the surface siphoning oxygen. The animal's siphon that sits on the surface is so designed as to keep the animal at the surface by surface tension alone, allowing complete freedom of movement horizontally and rotationally.

Measurements are very variable, however it appears that larvae can survive several hours of submersion if necessary; younger larvae for longer periods than older. Submersion is possible for longer periods in aerated water.

On a household scale Creasol and Kerosene as used to cover potential breeding water, also various oils, benzene hexachloride and cement tablets, chlorine, carbon bisulphide, toluene, and carbon tetrachloride. Soap in suitable concentration can be lethal. All these substance affect the surface tension of the water so that access to oxygen is denied to the larvae.

Since these measures prevent the mosquito from breeding we have entered 'humans' on the envirograms as second-order modifiers of mates.

21. Larvivorous fish of various species have been used in attempts to control mosquitoes in general. We are not clear as to how successful these attempts have been in controlling A. *aegypti*, however the animal's habit of breeding extensively in small containers in and around dwelling-places (n. 9) suggests that fish are not an important predator of this species of mosquito.

22. Screening of houses and the wearing of protective clothing prevent the female A. *aegypti* from acquiring the obligatory blood meal for breeding (n. 7).

23. The higher the relative humidity the higher, in general, is the viability of the eggs. However eggs are strongly resistant to desiccation. Providing moist conditions prevailed when they were first laid eggs stored on filter paper for 15 months in temperatures ranging from 6.6 to 17.8°C. remained viable. The longer eggs are stored the greater is the mortality, as seen in the table below.

Dry Period	Percentage of hatchings	Means
1 month	60,60,23,14,100,52,40	46.5
2 months	4,12,13,10,36,66,18,44,26,28,60, 3,60	34.0
3 months	65,0,0,8,12	17.0
4 months	4,8,6,0,0,0,0,0,0,0,0	1.6
5 and 6 months	0,0,0,0	0.0

The following table gives the results of drying eggs at different times after oviposition.

Maximum time left on water (hours)	15	20	25	37	43	48	60	65	70
Percentage collapsed after drying 12 hours	100	100	100	62	28	2	0	0	0

Eggs must be submerged in order to hatch, however submergence before the eggs are ready for hatching may be fatal. It has been found that for eggs kept moist and exposed to air (i.e. 'conditioned') at 24°C for 60 to 81 hours the first larvae hatched in 8 mins when submerged; those conditioned for 40 to 60 hours took 18 hours to hatch and those 'conditioned' for 87 to 111 hours all hatched in 10 minutes.

The following table gives some detail of the time to hatching:

TABLE 7

Number of larvae hatching at intervals of 20 minutes from eggs kept various times in the dry state and then submerged

Minutes from submersion	Number of days eggs kept in the dry state						
	7	8	20	66	69	75	77
15	Very many	1178	c.200	-	-	-	-
20	-	-	-	4	0	-	0
30	Less	1604	Larger number	-	-	-	-
40	-	-	-	5	-	-	7
60	Still fewer	841	Still larger	-	c.100	Many	72
80	-	-	-	-	-	-	70
100	-	-	-	-	-	-	39
120	-	1780	-	23	Fair Number	Many	25
140	-	-	-	-	-	-	22
160	-	-	-	-	-	-	15
180	-	-	-	-	-	-	7
220	-	-	-	-	-	Much Fewer	1
Over 240	-	3	-	38	Many	-	3
Over 480	-	-	-	-	-	-	-

Bacot (1916) after storing eggs 50 hours under moist conditions, found hatching took place in the majority of cases within 30 minutes and that eggs dried 1-7 days hatched out to the extent of 58-84 per cent in from 1 to 4 days. Shannon and Putnam state that well-conditioned eggs on submergence hatch in from 10 seconds to 10 minutes. Conditioned eggs dried 1-4 weeks began to hatch in 30 minutes, but in water in which food had lain for 12 hours they hatched in 7 minutes. With floating eggs eclosion was irregular, requiring 1-5 days or more. Eggs laid round the water's edge were more favourably situated.

All 3 tables above are from Christphers (1960).

If the egg is protected from desiccation the embryo develops to the larval stage (while still inside the egg membrane). At this early stage the larva is able to lie dormant until the egg is submerged or until it is destoryed by a slow desiccation or until the food reserves for the larva are exhausted. Thus diapause for this animal occurs somewhat later than for most insects.

24. A. *aegypti* eggs do not survive in a water solution containing one-third sea water (about 1% salt) but do survive at lower concentrations. (see n.8 for the effect of salt on hatched larvae).

25. Various mineral oils are lethal to eggs. Mortality depends on viscosity; it is slight with viscosity under 40, rises to a peak at 108 and falls at higher viscosities. No oil is absorbed and oxygen deprivation is believed to be the reason.

26. Eggs usually die within 24 hours if deprived of gaseous oxygen. However, the time to death is dependent on other components of the atmosphere; it is short when nitrogen and carbohydrate are present in quantities but longer when hydrogen is present.

Anaerobic conditions do not completely militate against hatching (but the larvae will die unless they are given some oxygen).

27. After the end of the embryonic development when the impervious endochorion is formed the eggs are resistant for short exposures to many chemicals.

28. Particles suspended in the medium may clog the larva's hairy epipharynx and the base of the mandibular hairs and make later feeding difficult.

29. Undisturbed eggs, even if submerged, may remain unhatched for 5 months and, in general, it seems that some agitation of the medium is an important stimulus to hatching, as indicated by the following quotations (from Christophers, 1960):

"The following count made of the hatching of floating eggs when subjected to agitation will serve to illustrate such an effect. The hatching in the shaken eggs occurred within less than half an hour from the shaking.

1.	Still floating in original vessel	20 per cent
2.	Submerged by sinking with a needle	44 per cent
3.	Transferred to test tube and shaken	93 per cent "

The 'nibbling' of the eggs by larvae and their presence in active movement may act as a source of agitation in nature. "This may be the explanation of the observation made by Thomas (1943) that when hatching eggs under sterile conditions, the degree of hatching was increased as the number of eggs was greater. Thus with one egg per tube 6 per cent hatched, with two eggs per tube 21 per cent and with fifty-three to sixty eggs per tube 80-84 per cent hatched."

30. In the laboratory eggs hatch less readily in clean tapwater or distilled water than in media rich in organic matter such as infusions or fluids containing food material. The most effective additive is a "grass infusion".

Neverthless a large proportion of eggs will hatch in distilled water.

See also n.31.

31. Micro-organisms (together with organic matter, n.30) provide a powerful stimulus to hatching. Sterilized eggs hatch quickly when exposed to pure cultures of yeast or bacteria.

Nevertheless the absence of micro-organisms will not prevent hatching.

Their effect is difficult to distinguish from that of organic matter.

32. Floating eggs are reported to hatch irregularly, requiring 1 to 5 days or more. Eggs laid round the water's edge are more favourably situated. We have entered 'water's edge' tentatively as a resource on the envirogram, since the mechanism here is not clear.

33. The cuticle of the larva is soft except for the head capsule, respiratory siphon and hair plaques. When moulting occurs there is sometimes difficulty with the thin cuticle tearing near the head. We have tentatively classified 'old cuticle' as a malentity here (c.f. the Working Paper on the Marine Copepod, *Calanus finmarchicus*, No. XVIII in this series, n. 8:).

34. The following quotation with reference to the larva, is from Christophers (1960):

> "Feeding may be carried out in three entirely different ways, namely (1) by pharyngeal filtration of minute particles from currents produced by the brushes in the body of the medium, (2) by the gnawing and swallowing of solid particles of food using the mandibles and (3) by browsing.
>
> The first method which is characteristic of all mosquito larvae, except those of purely carnivorous habits, is naturally much in evidence with larvae of A. *aegypti*. Nevertheless, it is very largely supplemented in this case by the other methods, the relatively small head of the A. *aegypti* larva probably being an indication that the species is not one that specialises on feeding on very fine matter in suspension as are some open-water feeders such as *Culex vishnui*, where the head is very large, presumably to accommodate a correspondingly large pharynx (see p.289). It is true that the larvae of A.*aegypti* are commonly found in clean drinking water, for example in native water pots, cisterns, etc. But in such situation there is usually a copious deposit of fragments of food and other organic debris. Further, it is doubtful how far the species could thrive in such a medium as clean water in the absence of fairly heavy organic contamination, as will be apparent when dealing with starvation effects."

(See also notes 28,39)

35. Negative phototropism is especially a characteristic of *A. aegypti* larvae, which will swim as far away from light as quickly as possible. Any sudden change in light intensity, increase or decrease, causes the larva to dive, thus modifying oxygen resources.

36. The larva is reported as "extremely sensitive to vibrations" The reaction is to dive; in one experiment larvae were induced to descend 8ft by repeated tappings on the containing vessel. 'Kinetic energy (vibrations)' thus modify oxygen resources.

37. Bacteria and yeasts are both almost essential food for larvae nevertheless some workers have reared larvae on pure yeast cultures. Both must be living. The yeast contains the heat and alkali-stable Vitamin B_2 which is essential for larval growth. Unlike other mosquito larvae, the *A. aegypti* larva does not require the heat-labile Vitamin B_1 for its growth.

Guineapig faeces have been found particularly suitable for rearing the larvae; it is not clear to us whether this is only because of the bacteria present, or whether other particles are consumed.

A sterile broth of the protozoan, *Eglenia*, is also a satisfactory food.

Folic acid has been found to be a necessary constituent of food for strong individuals which are able to rise from the water when newly emerged.

Optimum feeding conditions include food material in fine suspension and coarser particles as sediments with yeasts and bacteria growing freely.

38. Cannibalism among *A.aegypti* larvae has been recorded, but is rare.

39. Generally, with starvation the period of development increases and the size of the individual decreases. The adults tend to be less effective in reproductive activities and less fecund. Normally fed larvae reach a length of about 7 mm in 8 days, however, 'starved' larvae (it is not clear to us if the animals are kept totally without food) are reported as reaching a maximum length of only 4mm in 10 days.

40. When the number of A, *aegypti* larvae approaches 1000/ℓ. an 'overcrowding' effect, which may be at least partly due to competition for food, appears, in that the size of the larvae (and hence pupae and adults) is reduced.

41. The pupa requires oxygen not only for breathing but also to maintain its correct orientation; this is achieved by an enclosed air sac, outside the pupa but inside the puparium. The entire pupa-puparium is lighter than water, and thus tends to float. Chemicals have a lethal effect on the pupa, just as on the larva, by lowering the surface tension of the water. (See also n. 42).

42. When disturbed a pupa will swim downward (and due to its buoyancy will have to make active movements to do so). Thus the subject pupa acts as a modifier of predators in its environment. However the pupa, unlike the larva (n. 20) is unable to submerge and use dissolved oxygen. A submerged pupa will use up the oxygen in its enclosed sac and its tissues, thereby losing its buoyancy, and is likely to die after only about 2 hours (See also n. 41).

43. On occasions pupae may become trapped under water by vegetation or surface irregularities, be unable to rise and thus drown.

44. Although it is a necessary resource for the pupa the animal will survive for several hours if removed from the water. Pupae have been known to live and eventually emerge when kept on moist blotting paper. Also individuals dried for 24 hours following pupation may still hatch normally when returned to water.

45. The following table shows the effect of temperature on pupae:

Temperature (^{o}C.)	Effect
7	Pupae move feebly, if at all. No emergence
17	Pupae active. Emergence prolonged or does not occur
18	Pupal period 116 to 120 hours. Emergence usual
36	Prolonged exposure may greatly shorten life
41	For short exposures no obvious deleterious effects
43	Not completely lethal for exposures of 1 hour
44	All pupae dead in 30 minutes or less
45	All pupae dead in 15 minutes or less
48	All pupae dead in 3 minutes or less

The following table (from Christophers, 1960) gives the duration of the pupal period :

TABLE 24

Time from pupation to emergence at different temperatures

			Number emerging at different hours											
Temperature (^{o}C.)	Sex	Number observed	43	44	45	46	47	48	49	50	51	52-69	116-120	Mean in hours
29	F	43	40	3	-	-	-	-	-	-	-	-	-	43
28	F	55	-	-	-	14	30	11	-	-	-	-	-	47
26	F	31	-	-	-	-	1	5	12	10	3	-	-	49
23	F	12	-	-	-	-	-	-	-	-	-	12	-	60
18	F	6	-	-	-	-	-	-	-	-	-	-	6	118
7	F						failed to emerge							
29	M	38	37	1	-	-	-	-	-	-	-	-	-	43
28	M	32	-	-	-	13	15	4	-	-	-	-	-	47
26	M	9	-	-	-	1	8	-	-	-	-	-	-	47
23	M	31	-	-	-	-	-	-	-	-	-	31	-	60
18	M	7	-	-	-	-	-	-	-	-	-	-	7	118
7	M						failed to emerge							

(See also n. 4)

46. The pupa is enclosed in an almost impervious cuticle and is remarkably resistant to chemicals other than gases (which it breathes in). Pupae may remain alive for many hours in alcohol and other liquids used in laboratories. In water containing 2% salt (i.e. two-thirds sea water) pupae continue to hatch normally after which they will die. Development seems to be speeded up or enhanced when the salt concentration is low.

Nevertheless, as for the larvae, wetting agents act as first-order modifiers of oxygen (n. 20).

47. Both females and males readily take fluids which contain sugar. Females have been kept from 31 to 102 days on honey alone. Other fluids taken are nectar from flowers and fluids from raisins and bananas. However, the passage of such food through the female differs markedly from the passage of blood (see n. 7 about the obligatory blood meal).

The following table from Christophers (1960) compares the effectiveness of various foods:

Not fed	Lived up to 7 days
Fed on sugar	Lived up to 20 days
Fed on milk and sugar	Lived up to 19 days
Fed on bananas	Lived up to 68 days
Fed on blood	Lived up to 93 days

Christophers also gives an account of the comparison with blood meals, as follows:

"Most accounts of very prolonged life relate to females that have been allowed to feed on some form of sugary substance or fruit, with or without occasional blood feeds. Such records probably almost always relate to some few individual mosquitoes that have survived and become conditioned to the environment. Marchoux, Salimbeni and Simond give for females up to 106 days, males 50 days; survival of one mosquito for 154 days is recorded by Guiteras, as quoted by Howard (1923); MacGregor (1915) gives females up to 4-6 weeks, males 10-21 days; Macfie (1915) found no female living beyond the sixty-second day, maximum for males 28 days; Bacot gives a maximum of 74 days if water is not available for oviposition. Beeuwkes, Kerr Wetherbee and Taylor (1933) give the maximum for females at 131-225 days with average of 70-116 days, and for males maximum of 82-135 days with average of 40-61 days. The most detailed data of a statistical kind are given by Putnam and Shannon (1934). These authors give two series, namely (*A*) one of 118 females offered frequent and regular blood meals, and (*B*) one of 190 females given only honey and water. The longest lived female, was amongst those not fed on blood. The weekly mortality was as follows :

Weeks	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
A	0	3	6	1	10	10	9	12	8	8	12	10	13	7	5	3	1	-
B	0	1	0	0	1	0	3	0	1	37	41	20	32	12	31	10	0	1

From these figures it would appear that there was very little mortality among the honey-fed mosquitos until the ninth week when heavy mortality began. In the blood-fed series mortality was more uniformly distributed. Since there were more than half as many again mosquitoes in the second series, the final result in longevity was not very different."

48. The shady background from which *A.aegypti* makes its attack modifies a human's ability to swat it. The difficult question of the classification of *Homo sapiens* in the environment of the mosquito will be dealt with in the General Introduction to this series of Working Papers (No. XXVII, 1983). In the present Working Paper we have classified 'humans' as malentities in the environment of the mosquito, since, from the mosquito's point of view, being swatted by a human might well seem to be accidental - also the human does not eat the mosquito and thus cannot be classified as a predator in the normal sense. The following graphic description of the mosquito's attack is from Christoper's (1960):

" Few biting insects are more apparently intelligent, cunning and cautious than *Aëdes aegypti* in its behaviour when attacking. It rarely attacks blindly as some mosquitoes do or makes a frontal attack. Usually it approaches from the shady side and from behind, and it is difficult to get the attacking insect plainly visible against a suitable background. Commonly after failure to achieve its object at a first trial is makes a renewed attack from a quarter different to that which is engaging the victim's attention. Its approach is silent."

According to Howard, Dyar and Knab (1912) a good description of the stealthy attack has been given by Parker, Beyer and Pothier (1903). The male, though it does not bite, behaves very much as the female, hovering and darting about the seemingly intended victim apparently without any object, since it rarely settles. Only under one condition does the female mosquito appear to disregard all caution, namely when it has been interrupted in the act of feeding. It may then literally precipitate itself upon the victim regardless of consequences.

The male mosquito will settle on a host, without however taking a blood meal. The 'dance' of the male before settling is far longer than that of the female (15 minutes as against 2 minutes) and the pitch of his 'humming' noise differs from the female. The female does not usually 'hum' when approaching a host. The female's 'hum' attracts the male (see n. 1).

49. Having completed a blood meal the female mosquito becomes lethargic, after remaining on the host's body for up to 15 minutes if not disturbed, and will then find a nearby retreat to rest. Because of her swollen abdomen her flight is sluggish. During this period she is thus more vulnerable to both predators and malentities, thus 'blood meal' acts as a modifier for both these classes.

E. REFERENCE

Christopers, S. Rickard (1960) *Aëdes aegypti (L), the yellow fever mosquito, its life history, bionomes and structure* (Cambridge University Press).

Kitching, R.L. (1977) Time, resources and population dynamics in insects. *Aust. J. Ecol.* 2, 31-42.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XXV THE COMMON HONEYBEE (*Apis mellifera*)

by

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ABSTRACT

The precise environment of the Common Honeybee (*Apis mellifera*) is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A INTRODUCTORY NOTE

The genus *Apis*, the honeybees, contains four species. Three of these occur abundantly in south-eastern Asia. The fourth, *Apis mellifera*, the subject animal of this Working Paper, occurs naturally in Europe and northern Africa. It has been distributed very widely throughout the world by humans.

The following quotation is from Butler (1974):

> "It is in colonies of *A. mellifera* and *A. indica* that we find the highest degree of social development amongst the bees. The composition of these colonies and the caste differentiation involved will be discussed later on (Chapter 4, p.34), but we may say here that a very distinct worker caste is present consisting of sterile females and that each colony normally only possesses a single queen who is the mother of all the bees forming her colony. Queens of all four of the species of honeybess (*Apis sp.*) have no trace of pollen-collecting apparatus; wax-secreting and special scent-producing glands and their hypopharyngeal glands are also vestigial. These queens have become immensely fertile and capable of producing many thousands of eggs in the course of their lives, which may last for several years.
>
> The colonies of all true honeybees are perennial and the development of new colonies takes place by swarming. At the height of its strength in the summer a good colony of the Western honeybee may consist of a single queen, a few hundred drone or male bees, and as many as 50,000 or more worker bees, together with their combs containing brood and food."

In general, the maximum size of a hive seems to be from 20,000 to 60,000 workers, several hundred drones and one fertilized queen, together with a number of combs containing brood in all stages of development and stores of honey and pollen. According to Morse (1978) there must be a minimum of about 200 worker bees and a fertilized queen for a normal colony to exist; such a small number cannot survive except under the most favourable conditions. The incubation of all egg-types is about 3 to 4 days. 'Female' larvae (resulting in workers or queens) remain in this stage for about 5 days, 'male' larvae (drones) about 6 days. A queen becomes an adult about 15 days after the egg was laid and often emerge from the hive on the 16th day. Workers emergy about day 21 and drones about 24.

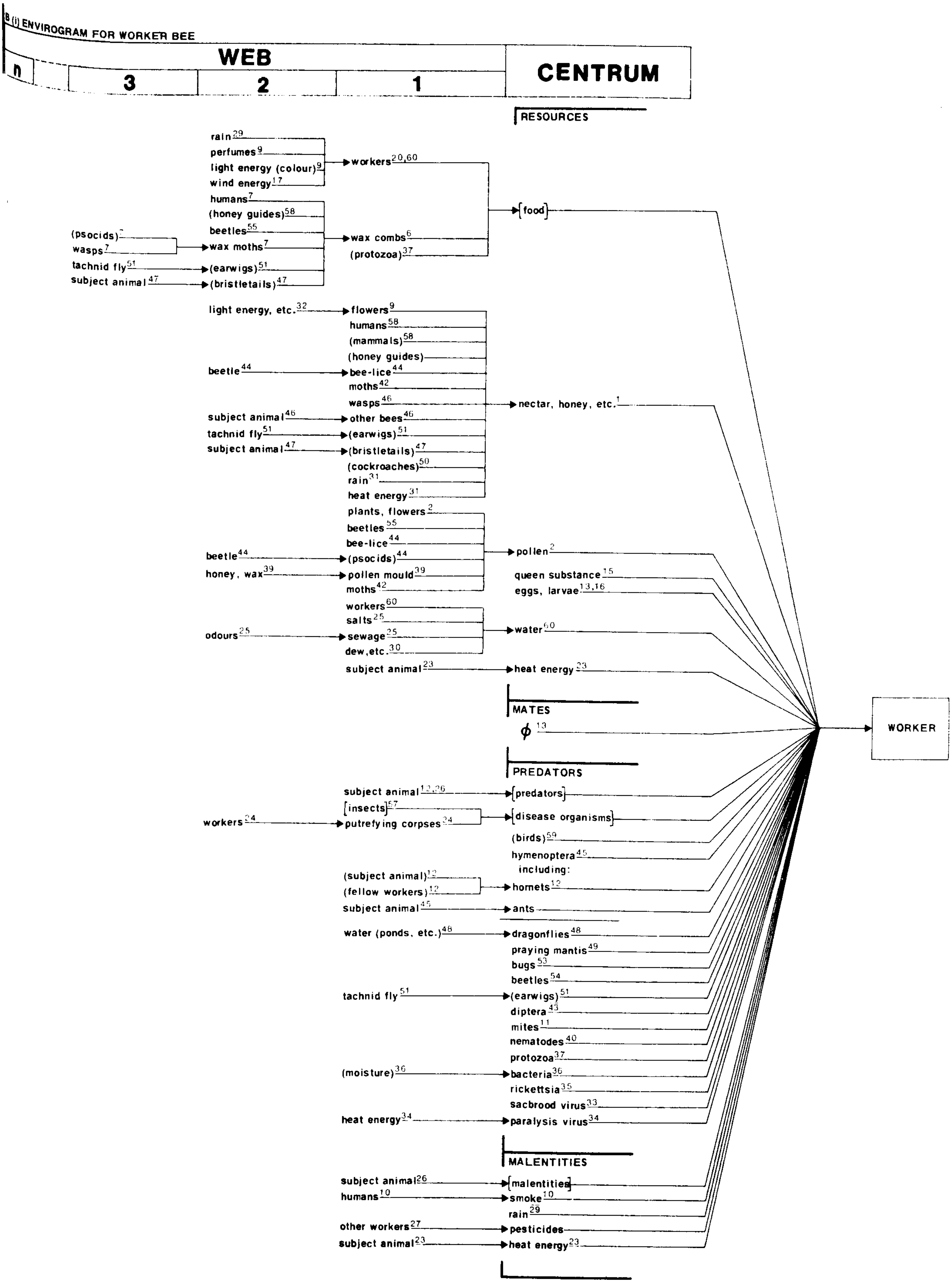
The various duties carried out by workers of various ages (see n.5, n.24...) are flexible; if conditions demand then a worker of any age can do any job. In general a young 'household' bee patrols the combs in her hive seeking work. If she is unable to find work to be done she will give up household tasks and join the foraging force.

It is believed by some workers that a foraging honeybee measures 'time spent in flying' between the hive and a source of food and can convey this information to fellow workers by means of a 'dance'. Most bees do not forage until they have learned via dance language the location of food. However, occasionally some bees will go scouting for new sources. Workers can fly at about 12 to 15 mph (about 18 to 23 km/h) and queens a little faster.

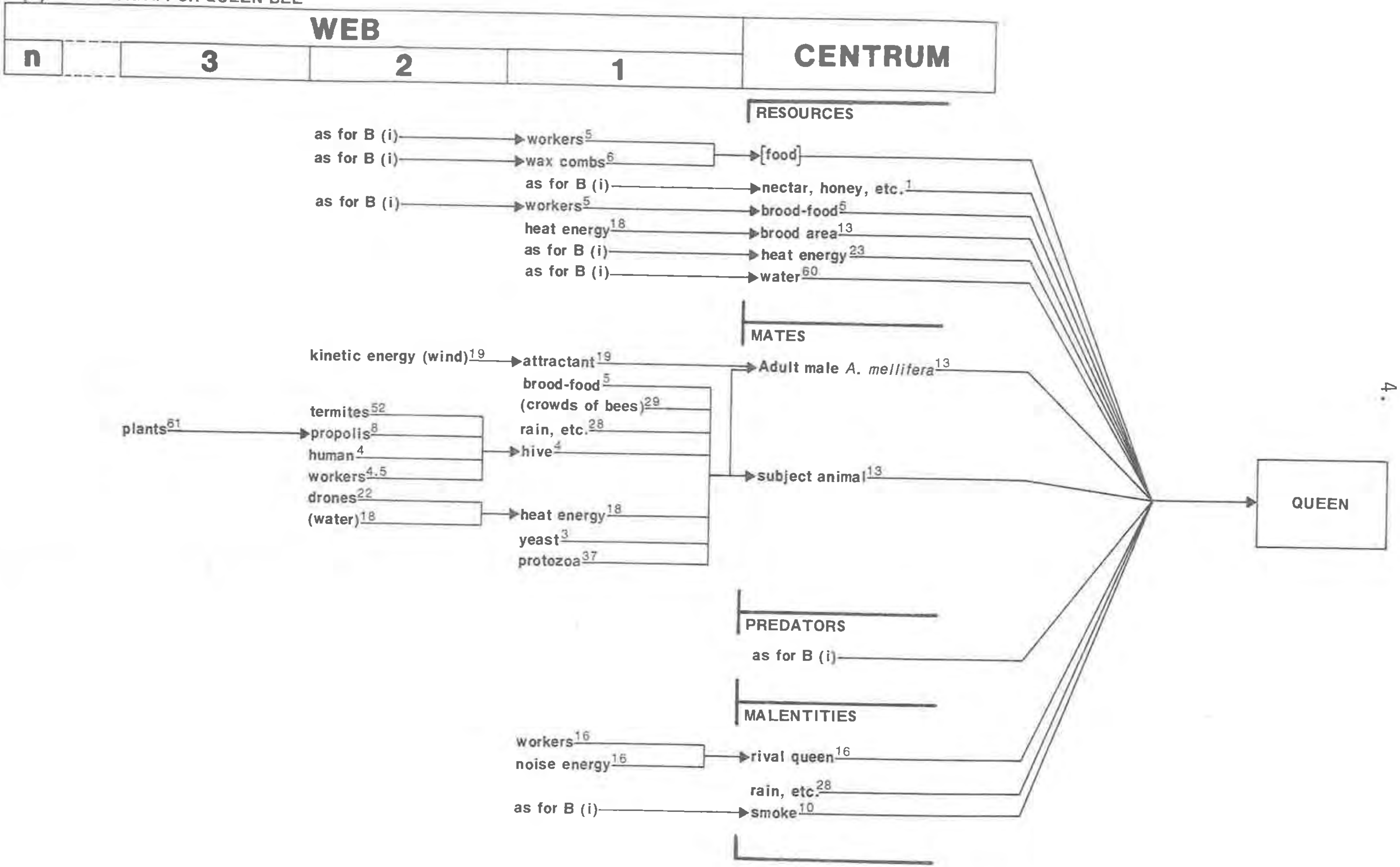
Different colonies have different odours. Bees returning from foraging expose scent glands on their abdomens and fan with their wings to distribute it as a guide to other workers. Hive differences are small and bee scent seems to attract other bees, sometimes to a food source, irrespective of the hive of origin.

In this Working Paper certain fungi have been tentatively classified as 'predators' of larvae (n.38). Strictly speaking, a predator must be an animal (see General Introduction) and the sub-classes of the Centrum have not yet been extended to such organisms as fungi. As for other Working Papers bacteria etc have been included in this sub-class.

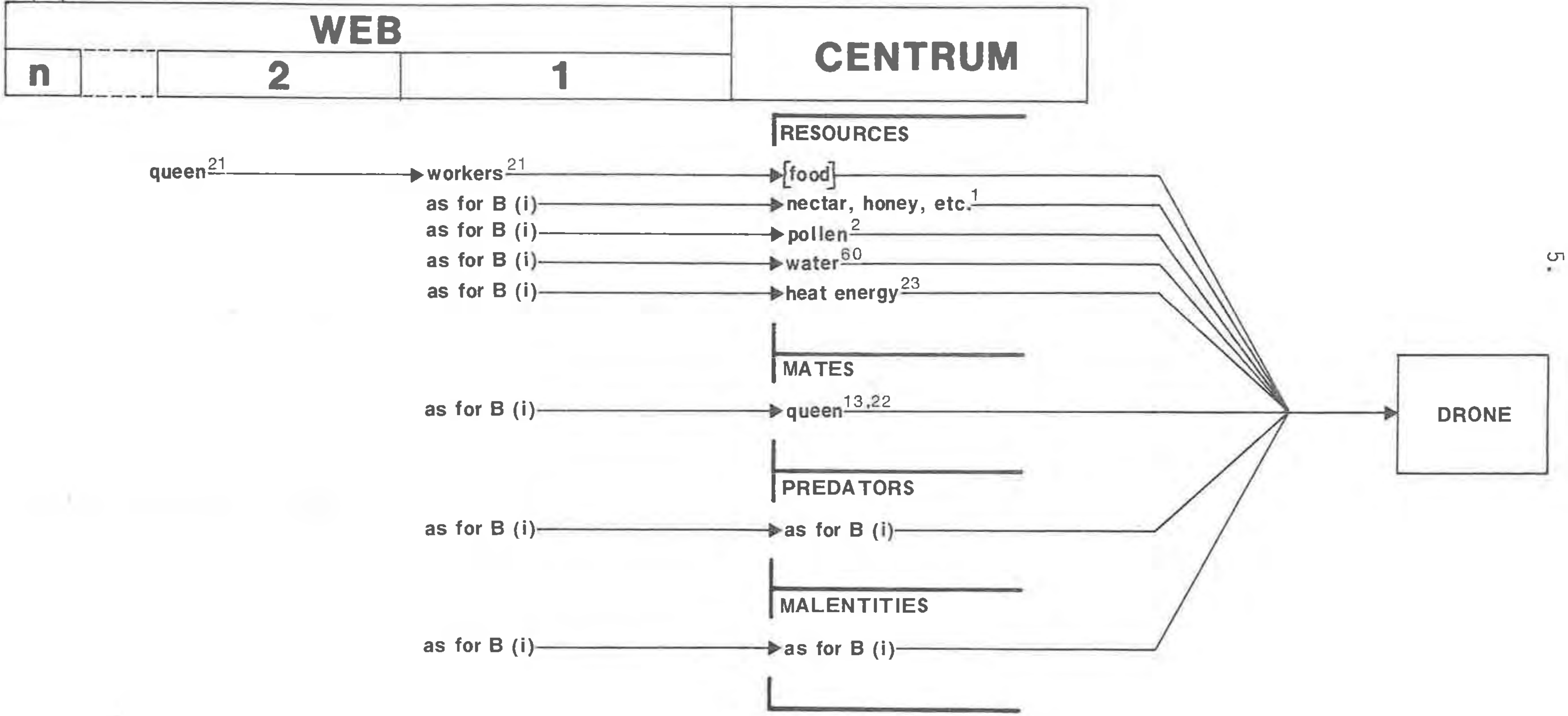
B (i) ENVIROGRAM FOR WORKER BEE



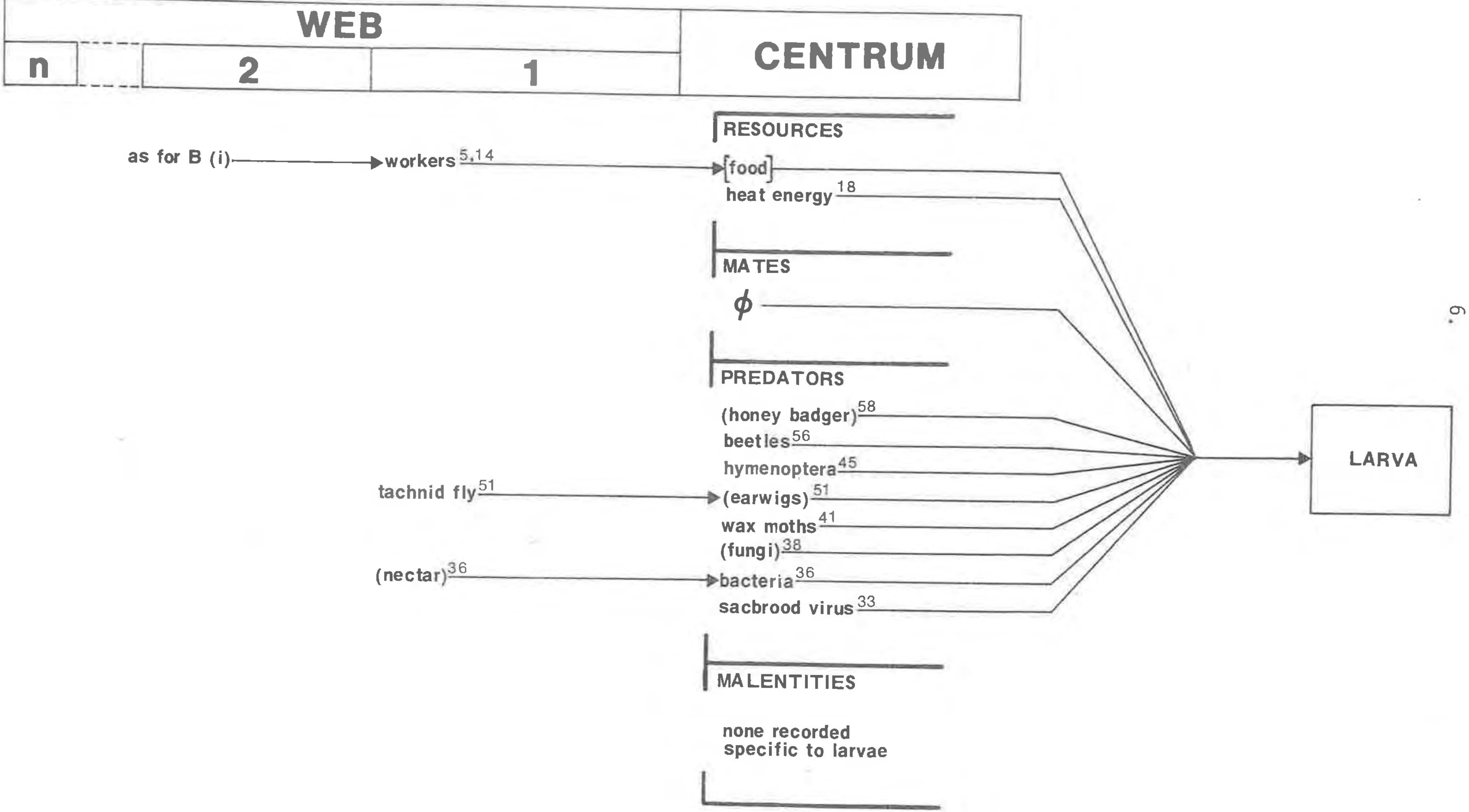
B (ii) ENVIROGRAM FOR QUEEN BEE



B (iii) ENVIROGRAM FOR DRONE



B (iv) ENVIROGRAM FOR BEE LARVA



C NOTES ON THE ENVIROGRAMS

1. All bees have a vegetarian diet, with carbohydrates (from nectar, honey, honeydew) a major component.

When about fifteen days old a worker bee will start the duty of relieving incoming foraging workers of the greater part of their loads of nectar, which they then convert to honey and store.

Nectar is a solution in water of sugars, together with traces of proteins, salts, acids, enzymes and aromatic substances. In most nectars three sugars preponderate: glucose, fructose and sucrose; often as much as 40 to 50% of the total sugar is sucrose. When coverting nectar into honey much of the sucrose is broken down into glucose and fructose and the water content is reduced from about 60% to about 20%.

Bees seldom collect nectar with a sugar concentration of less than 20%.

It has been shown in laboratory experiments that the honeybee has a preference for solutions containing equal proportions of sucrose, glucose and fructose.

The queen helps herself to honey from the stores.

2. Bees acquire a taste for pollen when dusting off their bodies during the search for nectar. The pollen is inadvertently collected when the nectar is being collected. It is sometimes discarded in the field.

Nearly all the protein content of the bee's diet is contained in pollen. Newly-emerged workers that do not have access to pollen store are not able to provide brood-food (see n.5) since the hypopharyngeal gland does not develop normally. Such workers tend to die young. The protein content of pollen varies from about 7 to about 30%.

In addition to protein, pollen contains 20% water, about 5% fats, oils and waxes and small quantities of potassium, phosphorus, calcium, magnesium, iron and some vitamins.

Pollen grains which are caught on the hairs of the body are gathered and mixed into a thick paste with nectar or regurgitated honey and packed into the 'pollen baskets' for transportation. Collected pollen is packed into cells within the hive, covered with a layer of honey and sealed with wax until required. Workers aged about fifteen days or more are responsible for pollen storage.

The average colony probably requires from 50 to 100 lbs of pollen annually, i.e. from 2 to 4 million bee loads annually.

Although bees collect pollen from many kinds of plant (over 100 types in one study), leguminous plants, chiefly red and white clover, predominate. Roughly 54% of pollen is from leguminous plants, 15% from rosaceous trees and shrubs and 11% from trees such as birch, elm, beech and oak. The highly concentrated nectar of the common lime tree, *Tilia vulgaris*, is a favourite source.

When their colonies are very short of pollen workers will sometimes collect almost any dry, fine powder, irrespective of nutritional value, such as flour, cement, coal dust etc.

A queen bee probably does not eat pollen.

3. Queens may be rendered sterile by a yeast infection called 'melanosis'.

4. Both *A.mellifera* and *A.indica* have been domesticated by humans to the extent that they can be induced to build their nests in conveniently placed accessible places, modern beehives for example. A great many *A.mellifera* are now kept in such hives. The practice has been observed for at least several hundred years.

The worker bees are responsible for comb-repairing and building which they do when their wax-producing glands have developed about a week after emergence from the pupal stage. (See also notes 5,6 and 60)

On occasions a colony of honeybees may not be able to find a suitable nest site (such as a hollow tree) and begin constructing a nest in the open e.g. low down in grass. Exposed nests of this kind are rare and seldom survive for long.

5. Workers belonging to the hive provide food for the queen-larva and the adult queen. A mature queen occasionally solicits food (successfully) from the workers. A mated queen gets more attention; she is fed 'brood-food' a proteinaceous and highly nutritious substance secreted by a worker's hypopharyngeal gland. Brood-food stimulates the queen's ovarian growth and production so that within 4 days of mating she starts laying eggs. It is usually the young worker bees, up to 3 weeks old, that remain in the hive to attend the queen; older workers go out to forage. Workers start producing brood-food about day 5 after emergence from the pupal stage.

6. Food, both honey and pollen, is stored in wax 'combs' (honeycomb) which are constructed by the workers.

7. Humans pilfer and destroy the wax combs in order to steal honey.

Wax moths may also destroy a nest by attacking the wax of the honeycombs. The larvae of the Greater Wax Moth (*Galleria mellonella*) may quickly reduce the combs to a mass of debris. The moth is usually found when the colony has been weakened by lack of food, disease (e.g. Americal foulbrood, see n.36), failing queens, queenlessness or marked reduction of worker population as a result of pesticide poisoning. The female moth lays eggs in tiny cracks which afford protection against removal by worker bees and predation by other insects. Upon hatching the larvae feed on honey, nectar or pollen and burrow to the middle of a comb. Wax moth depredations are one of the most common causes of the colony absconding to a new site.

The moth *Vitula edmondsae* and the Lesser Wax Moth (*Achroia grisella*) act similarly to the Greater Wax Moth but are not as successful in their attacks.

The bumble-bee wax moth (*Aphomia sociella*) will occasionally attack honeybee combs.

The wasp *Apanteles galleriae* attacks both the Greater and Lesser Wax Moths and psocids (book-lice) may predate the wax moth eggs.

8. The older, foraging, workers occasionally bring back to the hive a resinous exudate of certain plants known as 'propolis' which is used to fill cracks and crannies in the hive.

9. Colour and perfume seem to be the two attributes of flowers which are most important in attracting bees.

According to Butler (1974) particular colours and odours are instrumental in attracting particular bees to the flowers. Strong floral scents e.g. from masses of hawthorne or white clover will attract bees from a distance. In the laboratory it has been shown tha olfactory stimuli are more powerful than sight. If a bee is offered the choice of a perfume to which it has been trained, in close assocaition with an unknown colour, and a colour to which it has been trained, in close association with an unknown perfume then the bee will always select the former.

The worker has the ability to learn to seek food in a certain place and to associate particular floral colours, patterns and perfumes with food. The honeybee can probably recognise four distinct colours: yellow, blue-green, blue and ultra-violet. A bee does not seem to be able to distinquish red.

Flowers in the reasonably near vicinity provide the essential nectar in the diet. A temporary lack of nectar-producing flowers may occasionally render a locality so unfavourable that the colony deserts its site for a new one, however this is rare. The honeybees' habit of storing food enables them to withstand protracted periods of a such adverse conditions. As food abundance declines the number of 'scouting' worker bees increases. Bees will not 'dance' (i.e. recruit other foragers) if the food source is more than 3 miles from the hive. When foraging most bees will usually visit only one species of flower. Occasionally a bee will work two flower crops in close proximity.

Bees can recognise and use landscape features for direction finding and the sun and the plane of polarization of light reflected from the sky. The angle from the sun is indicated in a returned forager's dance.

10. Bees are readily subdued by smoke. This not only occurs naturally but is also widely used by humans in search of honey.

11. The parasitic mite *Acarapis woodi* reduced the British population of honeybees by 90% according to Butler (1974) during the years 1909 to 1918. (However starvation may also have been a factor).

12. Butler (1974) reports, somewhat tentaively, that *A.mellifera* in Cyprus and possibly northern Africa and the Middle East have a defensive strategy like that of other species of honeybee called the 'shimmering behaviour' which produces a hissing sound. When a hornet, ant, wax-moth or other intruder approaches the hive the worker bees shake their bodies violently from side to side in concert; this usually results in the hasty retreat of the intruder.

Some workers act as 'guard bees', particularly from late summer on, to protect foreign robber bees and wasps from plundering stores (see also n.26). The guard bees examine all incoming bees; the mechanism for spotting intruders is unkown, but possibly to do with odour (although the flight pattern of a robber bee is characteristically erratic and may alert the guard bee).

13. The queen honeybee alone is responsible for the production of eggs from which all the members of the colony arise - workers, drones and, infrequently, other queens. Worker honeybees, although female, do not as a rule lay eggs although they may do in exceptional circumstances. In a thriving colony, in early summer, a queen may produce as many as 1500 eggs/day, i.e. more than her own bodyweight every 24 hours. In a year, a queen in a prosperous colony may produce up to 200,000 eggs.

As soon as a new queen is established (after eliminating rivals, see n.16) she begins making short flights. Mating is always away from the hive and on the wing. A queen may be pursued by up to 100 drones but will usually mate with about 5, often in quick succession on the same day. The nuptial flight can last as long as half-an-hour. The queen may be anything from 4 to 16 days old. It is believed by some workers that an older queen may mate again.

After mating the queen returns to the hive and, unless she is disturbed, will probably spend almost her whole life in the brood area. She lays two kinds of eggs:

(i) Unfertilized eggs which develop into drones.
(ii) Fertilized eggs which develop into females which can become either queens or workers.

(Nevertheless very rarely workers and queens have been produced parthenogenetically i.e. from unfertilized eggs). An old queen tends to lay only unfertilized (drone) eggs.

During the summer months eggs and larvae are found in two kinds of cells, the 'worker brood-cells' and the 'drone brood-cells'. The drone cells are slightly larger. At certain times a third kind of cell, a 'queen cell', is built, totally different in appearance from the others. In each cell only one larva is reared at a time; worker and drone cells are used repeatedly but each queen cell is used only once and then destroyed by the workers. The queen normally lays unfertilized eggsin drone cells and fertilized eggs in worker and queen cells. Up to 3 days after hatching a larva in a worker cell can be successfully transferred and raised as a queen and *vice versa*.

It is believed that the food given by workers to larvae destined to become queens differs markedly from that given to worker larvae, resulting in the different adult forms. However, the exact mechanism is not yet clear; a queen has not yet been reared in the laboratory although workers have.

If the queen is lost then the workers normally rear a new queen immediately. Nevertheless Anderson (quoted by Butler 1974) has reported that the so-called 'Cape Bee' of South Africa (*A.mellifera capensis*) has been known to maintain queenless colonies for months.

The brood area contracts during cooler weather and expands in warmer weather. It may be restricted following a heavy honey-flow because all available area is needed for storage; in this case the queen simply drops her eggs in the hive until her production rate declines to the level provided for and workers greedily sieze her eggs and devour them.

14. All food for the larva is provided by the worker bees. Apparently different food is offered to larvae in 'worker-cells' and 'queen-cells', resulting in the two kinds of mature individuals. The mechanism is not clear.
See also n.5.

15. The queen secretes a 'queen-substance' which is apparently responsible for providing the cohesive force which keeps the hive functioning as a social unit. When a queen begins to fail to produce enough queen-substance the workers set about raising a new queen, who will often co-exist for a while with her mother.

16. Usually several queen-cells are made but normally one queen will emerge before the others. If two emerge simultaneously a bitter fight takes place until one is killed through having her body pierced by the other's sting. They may find each other by making a series of shrill piping sounds. Worker bees throw the loser's carcass from the hive. If only one queen emerges she will seek out and kill any potential rivals, often with the aid of workers. The whole process of ensuring that there is only one queen is completed within a day or two.

Queen cells are nearly always present in a hive but if the colony is not preparing to replace the queen then any eggs that hatch will be killed and eaten.

17. The animal seldom continues foraging if the wind speed is more than about 14 to 15 miles per hour (21 to 23 km/h).

18. Temperature is regulated in the brood area of the hive where the queen lays her eggs; the temperature is maintained around 90°F (32°C). In winter this area is small and generally only workers are produced. The temperature-regulating mechanism involves clustering (which maintains the temperature of the brood-area during cold weather) and dispersal and active ventilation - in extreme cases even involving the evaporation of water within the hive - (which reduces the temperature in this area during hot weather). The mechanism functions so well that brood-area temperatures are kept remarkably constant in hives in all parts of the world, resulting in almost constant development times. Clustering usually starts in earnest when the ambient temperature falls to about 56°F (13.3°C).

Most flights of the queen are made between noon and 4 pm when the drones are most active, presumably because of the higher temperature (although possibly because there is more light).

See also n.22.

19. The queen in flight secretes 9-Oxodecenoic acid from here mandibular glands which attracts drones who are flying to leeward of her and not more than 50 yards away.

20. Workers feed each other as well as the queen. This food is almost certainly mainly nectar and honey from the 'honey stomach' and not 'brood-food' (see n.5).

21. Drones never visit flowers. They obtain all their food from workers or from honey stored in the hive. Provided they have a laying queen a colony of bees will not tolerate drones in the hive at those times of the year when they cannot collect much nectar in the field. At such times drones are refused food and soon die.

22. During summer a drone lives about 4 to 5 weeks and becomes sexually mature after 10 to 14 days. They always congregate together in the warmest part of the hive, i.e. the brood area (n.18) and thus probably fortuitously aid in maintaining warmth. In summer a colony will contain a few hundred drones but most will never mate. The drone is damaged in the mating and dies immediately afterwards.

If a bee's body temperature falls below 46°F (7.8°C) it becomes almost incapable of movement. Vigorous muscular activity causes her temperature to rise, so on sunny days in winter, when the air temperature is only slightly above freezing point, bees leaving the hive are all right only if they continue to fly. (They leave the hive in order to excrete).

See also n.18.

24. Workers aged 15 days or more are responsible among other duties, for removing dead bodies and other debris from the hive.

25. It has been shown experimentally that bees prefer water containing some dissolved salts e.g. sodium chloride and ammonium chloride. However, they are far more attracted to sewage effluent, cow-pot water etc.; odour is the main attractant.

See also n.30

26. The venom contained in a bee sting can be used to drive off many other animals which might be predators or malentities (but see notes 43, 55). The sting of a bee is quickly fatal to other bees. If the sting is broken off during use (usually the case when a human is stung) then the bee will die within a day or two.

27. Because of the worker's ability to distribute food widely (see n.60) food contaminated with pesticides spreads through a hive very quickly and has been known to cause substantial mortality.

28. If a virgin queen after having killed her rivals (the old queen having died or departed) is prevented by bad weather from mating for three or four weeks then she may not mate at all. In this case she will produce drones only and the colony is doomed.

29. It is believed by some that swarming with a new virgin queen in order to set up a new colony happens when there is overcrowding of an occupied hive. Overcrowding may possibly be due to a rapid increase of stored food as a result of good foraging conditions, or to the confinement of bees to the hive by bad weather. Rain markedly reduces the activity of the workers.

30. Water is collected by workers from many different sources: dew, raindrops on grass and other herbage, ponds, ditches, puddles on cowpats and so on.
See also n.25.

31. Hot dry weather tends to concentrate nectar, thus making it more acceptable. Conversely rain can dilute nectar in open or unprotected flowers , making it less aceptable.

32. The rate of photosynthesis, by means of which a plant builds up the necessary carbohydrates to produce nectar, depends on such factors as light intensity, temperature, quantities of water and carbon dioxide. The quantity of nectar will rise (to a limit) with the availability of carbon dioxide.

Soil type also influences nectar production; Butler (1974) reports that little work has been done on this point.

Different plants have different optimum temperatures for nectar secretion; for clovers it is about 80 to 85°F (26.7 to 29.4°C).

33. Larvae affected by sacbrood disease die due to a disruption of the moulting process. Infected adults seem to age more rapidly. Workers stop foraging at an early age. (There is no information about the specific effects on queen or drone). The virus may be passed on through the hive via mutual feeding and the feeding of larvae. (Gochnauer, 1978).

34. Paralysis disease affects adult bees only. Paralysis of one or more legs is common. Temperature affects different strains of the disease: 'chronic' bee paralysis is associated with highest mortality at 35°C; 'acute' bee paralysis is more likely at 30°C. Bees tend to lose their hair (this is called 'the black bee syndrome'). Severely infected bees die before they become hairless and the attacking behaviour of healthy bees towards sick bees is reduced at lower temperatures (Gochnauer, 1978).

35. Gochnauer (1978) reports that *Rickettsia* spp. which infect fat body tissue have been recorded in bees (and other insects).

36. The following bacteria are reported as affecting honeybees by Shimanuki (1978):

(i) American foulbrood disease. This disease is highly contagious. It can wipe out an entire colony. It may occur all the year round but is especially prevalent in the active brooding season. Spores of the bacillus can remain active at least up to 35 years. The disease is spread to other colonies by robbing or drifting bees. The causative agent is *Bacillus larvae*, also known as *B.brandenburgiensis* or *B.burri*. The susceptibility of bee larvae to the disease decreases with increasing age. (Shimanuki found that a larva could not be infected 53 hours after hatching).

(ii) European foulbrood bacterium. The disease is not as serious as the American foulbrood disease. The causal agent is *Streptococcus pluton*, also known as *Bacillus pluton*. Transmission is by nurse bees inadvertently affected. The bacteria may overwinter on the sides of a cell or in faeces and wax debris on the bottom of the hive. "The onset of the disease usually coincides with the first nectar flow". A good steady nectar flow will sometimes result in the elimination of the disease.

(iii) Bacteria causing septicemia. The causal agent is *Bacillus apisepticus*, recently reclassified as *Pseudomonas apiseptica*. The spread of the disease is probably aided by the presence of moisture. Infection, once established, kills the bees quickly.

(iv) Bacteria causing powdery scale disease. The causative agent is *Bacillus pulvifaciens*. This disease affects only larvae. It is rare and the aetiology is unknown.

37. According to Fergula and Mussen (1978) protozoan infections differ from those of bacteria and viruses in that protozoans grow more slowly and infected bees live longer. "A slow debilitation of the bee occurs, vitality is sapped, fecundity reduced, life span shortened, movement decreased and response to stimuli gradually

impaired". They list three important protozoan infections:

(i) Nosema disease, caused by *Nosema apis*. This is a disease of adults. All adults in a colony may be affected. Infection is spread when the spores are ingested. The infection causes physiological damage, reducing the production of royal jelly and possibly causing workers to age more quickly. An infected queen will be superceded.

(ii) Amoeba disease, caused by *Malpighiamoeba mellificae*. There is no evidence that drones or queens become infected in nature. Infection is probably by ingestion of cysts.

(iii)Rarely (usually only in the tropics or subtropics) honeybees may be infected by Gregarinida; it is not clear as to whether they are pathogenic. Thus these protozoa may act only as first-order modifiers by utilizing some of the food resources of the honeybee, rather than directly as predators.

38. Gilliam (1978) names two diseases of honeybees caused by fungi (see A and revised version of General Introduction for fungi as predators):

(i) Chalkbrood. This is a fungal disease caused by *Ascosphaera apis* which affects only brood. Diseased larvae become mummified.

(ii) Stonebrood. Both larvae and adults are attacked and killed by several species of the genus *Aspergillus*, including *A. flavus*, *A. fumigatus*, *A. niger* and *A. oryzae*. The disease is rare and usually the colony will not be seriously affected.

39. Pollen mould is caused by the fungus*Bettsia alvei*. It renders pollen useless for the bee's purposes but does not attack either larval or adult honeybees. Cells which are filled with pollen, finished with honey and sealed with wax will not be attacked but unsealed cells without honey may be.

40. The nematodes *Mermis nigrescens* and *M. acbicans* have been found in honeybees. However this infection is very rare. (Lehnert, 1978).

41. In addition to attacking the structure of the nest (n.7) wax moths can cause a condition called 'bald brood'. The moth larvae perforate the wax cap over a late-stage honeybee larva's cell causing abnormalities to the honeybee.

42. According to Williams (1978) the following moths will occasionally attack bee pollen stores:

(i) Indian meal moth (*Plodia interpuctella*)

(ii) Mediterranean flourmoth (*Anagasta kuehniella*)

(iii) Death's Head moth (*Acherontia* spp., including *A. atropos*).

Death's Head moths will occasionally also take nectar and honey.

43. Knutson (1978) gives the following information on diptera as predators of the honeybee:

Many species of the Robber Flies (Asilidae) capture and feed on honeybees. The sting of the honeybee does not provide immunity from attack by asilids. (The mimicry of asilids to honeybees afford the asilids some protection from their own predators.)

The following flies cause apimyiasis: *Zodion notatum*, *Thecophora apivora*, *T. longirostris*.

The Flesh Fly *Senotainia tricuspis* attacks bees as they leave the hive and deposits one or two larvae per bee. The bees die within two to four days.

44. Knutson (1978) reports that the bee-lice *Braula coeca coeca*, *B.c.angulata*, *B.schmitzi*, and *B.orientalis* apparently eat nectar and pollen at the bee's mouth(and feed also off the bee's bodily secretions). Eggs are laid on the caps of the honey store cells.

Caron (1978) believes that psocids (book lice) may feed on pollen, thus competing with bees. Caron also reports that unidentified scarabid beetles are known carriers of the bee louse *Braula coeca*.

45. De Jong (1978) reports on the following hymenoptera as predators:

(i) Ants. Predation can be serious, particularly from the families Dorylinae and Ecitonina. Army ants can devour a hive in a few hours; bees have no defence against them. The red-wood ant *Formica rufa* can be a serious predator. Species of the genus *Camponotus* are occasionally a danger. Bee defence against ants includes fanning to blow ants away from the hive entrance, also kicking backwards.

(ii) Hornets. These large wasps predate bees easily both while foraging and at the entrance to the hive. They may also enter the hive and destroy larvae and pupae, preferring pupae. In particular the species *Vespa cabro*, *V.mandarina* and *V.orientalis* are important predators. They may transport bee pupae and larvae and even adult bees to their own nest to feed their larvae.

(iii) Yellow-Jacket wasps (*Vespula* spp.). These are minor predators (but see n.46).

(iv) Beewolves. Solitary digger wasps of the genus *Philanthus* use honeybees to feed their larvae.

(v) Velvet ants (*Mutilla* spp.). Several species of these wingless wasps enter hives and eat brood. They may lay their own eggs there.

46. The Yellow-Jacket Wasps *Vespula germanica* and *V.vulgaris* are important robbers of honey, particularly during autumn and early winter when bee colonies contract their cluster.

Bumble bees (*Bombus* spp.) occasionally try to enter hives to steal honey. Apparently the honey bees are usually able to kill them.

Honey bees (*Apis* spp.) themselves are reasonably successful at stealing honey from other honeybees (But see n.12, n.26).

47. The bristletails, i.e. insects of the order Thysanura (including silverfish) probably eat honey and may eat wax although they do not destroy combs. They live in the hive and their droppings may contaminate stored food. Bees in a thriving colony usually keep bristletails under control. (Caron, 1978).

48. According to Caron (1978) large dragonflies e.g. *Aeschna grandis* feed on bees after capturing them on the wing. They are, however, rarely found far from ponds, rivers and lakes.

49. Caron (1978) reports that several species of praying mantis attack and eat honeybees, in particular *Mantis religiosa*.

50. Cockroaches, in particular *Periplaneta americana*, may eat some honey and some of the comb. They are not an important pest of honeybees and are easily controlled by thriving colonies (Caron, 1978).

51. Earwigs, e.g. *Forficula auricularia* may eat honey and the injured, dead and dying honeybees. They may also eat wax and (in doing so) bee larvae. Earwigs also eat flowers, thus acting as competitors of the honeybee.

A parasite of the earwig is the tachnid fly *Digonochaeta spinipennis*, which does not harm the honeybees.

Earwigs are carriers of the European Foulbrood bacterium (n.36).

52. Termites have been known to attack the wooden hives supplied by humans. They do not seem to be a pest of honeybees in nature.

53. The assassin bug *Pyrrchoris apterus* may frequent hives and predate bees, however strong colonies have little trouble from the Hemiptera. A few species recorded as feeding on honeybees usually feed on or around flowers where foraging bees inadvertently become their meal.

54. Caron (1978) reports the following beetles as being predators of the adult honeybee:

Carabus, *Calosoma*, *Trichodes*(occasionally, see n.56), *Meloe variegatus*, *M.proscarobaeus*, *M.cavensis*, *M.hungarus*, *M.violaceus*, *M.faveolatus*, *M.tuccius*. The *Meloe* spp. larva perforates the integument of the honeybee to seek nourishment from the bee's blood. *Meloe* sp. larvae have even been reported attacking a queen. The first stage larva of *Meloe*is very agile and climbs upon flowers where it awaits foraging bees; as many as 230 have been counted on one foraging bee.

55. According to Caron (1978) the following beetles may invade the hive and feed off stored pollen:

(i) *Cetonia cuprica, C.cardui.*

(ii) The larder beetle *Dermestes lardarus* infests the honeycomb but only in weak colonies. Adults and larvae of this species feed on pollen, brood remains and debris (see also n.57).

(iii) *Tragoderma glabrum* destroys combs and eats the remains of combs and some honey.

(iv) Some *Meloe* spp. eat pollen and nectar and do not feed on the bees (see n.54).

(v) The spider beetles *Ptinus fur* and *P.raptor* will attack comb in weak colonies and also eat stored pollen.

(vi) Several species of the scarabs *Protaetia* and *Anomala* feed extensively on stored pollen.

(vii) A dung beetle *Corpis lunaris* is reported as stealing honey; its hard exoskeleton prevents the bees from stinging it.

56. According to Caron (1978) beetles of the genus *Trichodes* usually feed on dead or dying adult bees; it may eat occasional adults or larvae in a weak colony. *Meloe cicatricosus* feeds on bee larvae (and eggs).

57. It seems likely that many disease organisms are carried to the bees by invading foreign insects e.g. the larder beetle *Dermestes lardarus* (n.55) has been reported as carrying *Nosema apis* (n.37) and earwigs (n.51) carry European foulbrood bacterium (n.36).

58. Certain birds in Asia and Africa known as 'honey-guides', family Indicatoridae, are reputed to 'guide' humans, ratels (honey-badgers) and perhaps baboons and other mammals to a hive. Once the mammal has opened the nest for the honey the bird picks up the scattered remains. Members of the genera *Indicator* and *Melichneutes* eat the wax of the honey combs. (Friedmann, 1955; Grzimek, 1974).

The birds may possibly also play this role with introduced *A.mellifera* in Asia and Africa. There does not seem to be a bird with similar behaviour in Europe.

The ratel or honey-badger (*Mellivora capensis* Schreber, 1776) will climb trees in its native Africa to open wild bee nests. It eats the larvae as well as the honey. It allows itself to be led to hives by the wax-eating honey-guide *Indicator indicator* (Haltenorth and Diller, 1977).

59. Gill (1950) reports that in Africa the Drongos (*Dicrurus adsimilis* and *D.ludwigii*) are 'very fond of bees'; presumably these are the native bees. No information is to hand as to whether Drongos eat the imported *A.mellifera*.

The bee-eater (family Meropidae) have a preference for wasps, bees, bumble bees and hornets, which they capture on the wing. The genus *Merops*, including the Common or European Bee-eater (*M.apiaster*) has the most species (9) and is to be found from southern Europe to Australia (Grzimek, 1974).

60. Older worker bees, usually more than three weeks old, bring back from their foraging expeditions water, nectar and pollen. It has been demonstrated with the aid of radiocative tracers that a tiny quantitiy of food - one tablespoon of sugar syrup - collected by only 6 workers, had within a few hours become widely distributed among the adult members of the colony and amongst the older larvae.
See also notes 1, 2, 5, 14, 10 and 21.

E REFERENCES

BUTLER, C.G. (1974). *The World of the Honeybee* (London: Collins).

CARON, D.M. (1978). Chptr. 10 in Morse (Ed.). Other insects.

DE JONG, D. (1978). Chptr.9 in Morse (Ed.). Insects: Hymenoptera.

FRIEDMANN, H. (1955). *The Honey-guides.* (Washington D.C.: Smithsonian Institution).

FURGALA, B. and MUSSEN, E.C. (1978). Chptr. 4 in Morse (Ed.). Protozoa.

GILL, E.L. (1950). *A first guide to South African birds.* (Cape Town: Maskew Miller).

GILLIAM, M. (1978). Chptr. 5 in Morse (Ed.). Fungi.

GOCHNAUER, T.A. (1978). Chptr. 2 in Morse (Ed.). Viruses and Rickettsiae.

GRZIMEK, B. (Ed-in-Chief) (1974). *Grzimek's Animal Life Encyclopedia* (Van Nostrand Reinhold).

HALTENORTH, T. and DILLER, H. (1977). *A field guide to the mammals of Africa.* (London: Collins).

KNUTSON, L. (1978). Chptr.8 in Morse (Ed.). Insects: Diptera.

LEHNERT, T. (1978). Chptr.6 in Morse (Ed.). Nematodes.

MORSE, R.A. (Ed.)(1978). *Honeybee pests, predators and diseases.* (Ithaca, N.Y.: Cornell University Press).

SHIMANUKI, H. (1978). Chptr.3 in Morse (Ed.). Bacteria.

WILLIAMS, J.L. (1978). Chptr.7 in Morse (Ed.). Insects: Lepidoptera.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS
XIII THE SHEEP BLOWFLY *(Lucilia cuprina)*

by

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ABSTRACT

The precise environment of the sheep blowfly *(Lucilia cuprina)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis,* 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (1) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9; a revised version will be available in 1983.

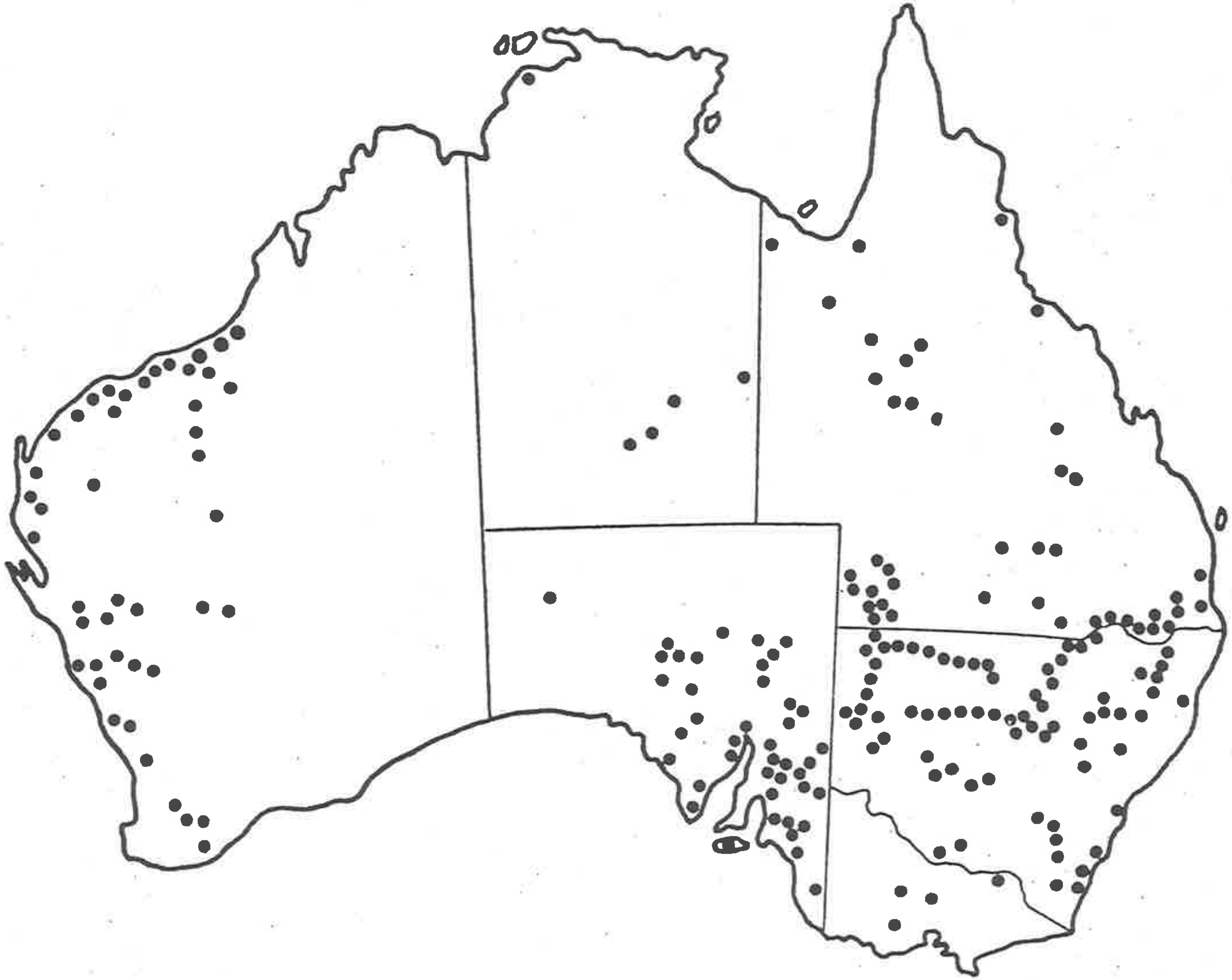


Fig. 1—Map showing the known distribution of *Lucilia cuprina* prepared by Waterhouse and Paramonov (1950).

CONTENTS

A. INTRODUCTORY NOTE

In Australia *Lucilia cuprina* (Wiedemann) is commonly known as the sheep blowfly, the primary green blowfly and the oriental greenbottle. Most recent opinion is that the species was accidentally introduced into this country with stock from Africa (possibly via India) in the late nineteenth century. It seems to have been recognized as a pest in the Riverina district of New South Wales by 1897 and had become widespread throughout Australia by the early years of this century.

Since delineation from *L. sericata* (Meigen), the taxonomy of the species has been fairly settled though some Hungarian and South African authors still treat *L. cuprina* as a form of *L. secicata*. The two species are difficult to distinguish, at least on external characters, however, in Australia *L. sericata* is predominantly a coastal species while for the most part *L. cuprina*'s distribution is inland. It is generally recognized that *L. cuprina* exists in two distinct forms, distinguished on the nature of their overall body colouration: the 'dull' form - *L. c. cuprina* (= *L. pallescens* (Shannon)); and the 'bright' form - *L. c. dorsalis* (Robineau - Desvoidy). Though agreement on sub-specific status is not unanimous, the two forms are allopatric over world range. It is safe to assume that the entire Australian population is *L. c. dorsalis* - only two specimens of *L. c. cuprina* have been found in Australia, high on Cape York early this century and frequent searches since have failed to unearth any further specimens (Kitching, pers. comm.).

Of the two forms only *L. c. dorsalis* (hereafter *L. cuprina*) is a serious pest because of its increasing utilization of live, often farm, animals for larval development while *L. c. cuprina* is almost exclusively saprophagous. In Australia, the principal live host is the sheep and while not solely responsible *L. cuprina* most often initiates myiasis or 'strike' in sheep. The suppurating wounds attract other blowfly species and the developing condition can cause debilitation and death in sheep.

Because of the resultant cost to the grazing industry, fairly intensive study of *L. cuprina* has been done in Australia, particularly within the CSIRO. Most of the work has been done in New South Wales, particularly around Canberra and the envirograms that we present should be considered as being for individuals in that area.

The Australian distribution of *L. cuprina* is more or less co-extensive with the sheep grazing areas though it extends into North Queensland and the northern coastal regions (but not into the tropical belt running from the Kimberleys in the west to the Gulf country in Queensland). The map (see frontispiece)is taken from Shanahan (1965) (after Waterhouse and Paramonov (1950)).

Gilmour *et al* (1946) estimated the following population densities around Canberra:

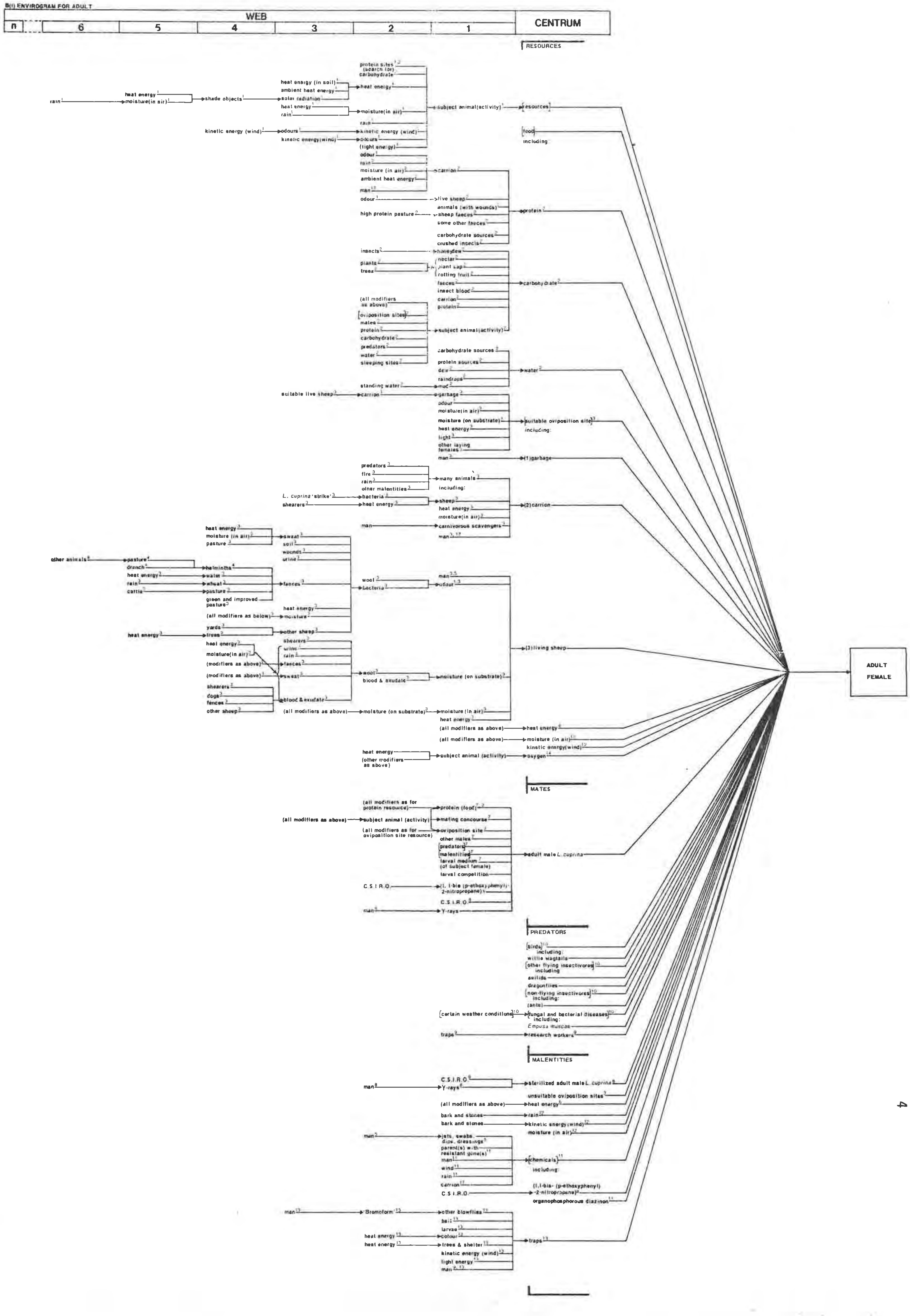
TIME	FLIES/ACRE
late spring	3-4 (≃ 9/ha)
December	5-7 (≃ 15/ha)
January	less than 1-2 (< 5/ha)
March	1-2 (≃ 4/ha)
June-August	absent

We divide the *L. cuprina* life cycle into four stages - adult, egg, larva and pupa - and an envirogram is given for each stage. In fact if the adult envirogram were placed last the four could be taken as being for one individual at successive stages of its life. It is important to note that the formal definitions which generate an envirogram are written in terms of an instant of time 't' so that the envirograms we present are something like the integration of many envirograms for an individual during the duration of a particular stage of its life.

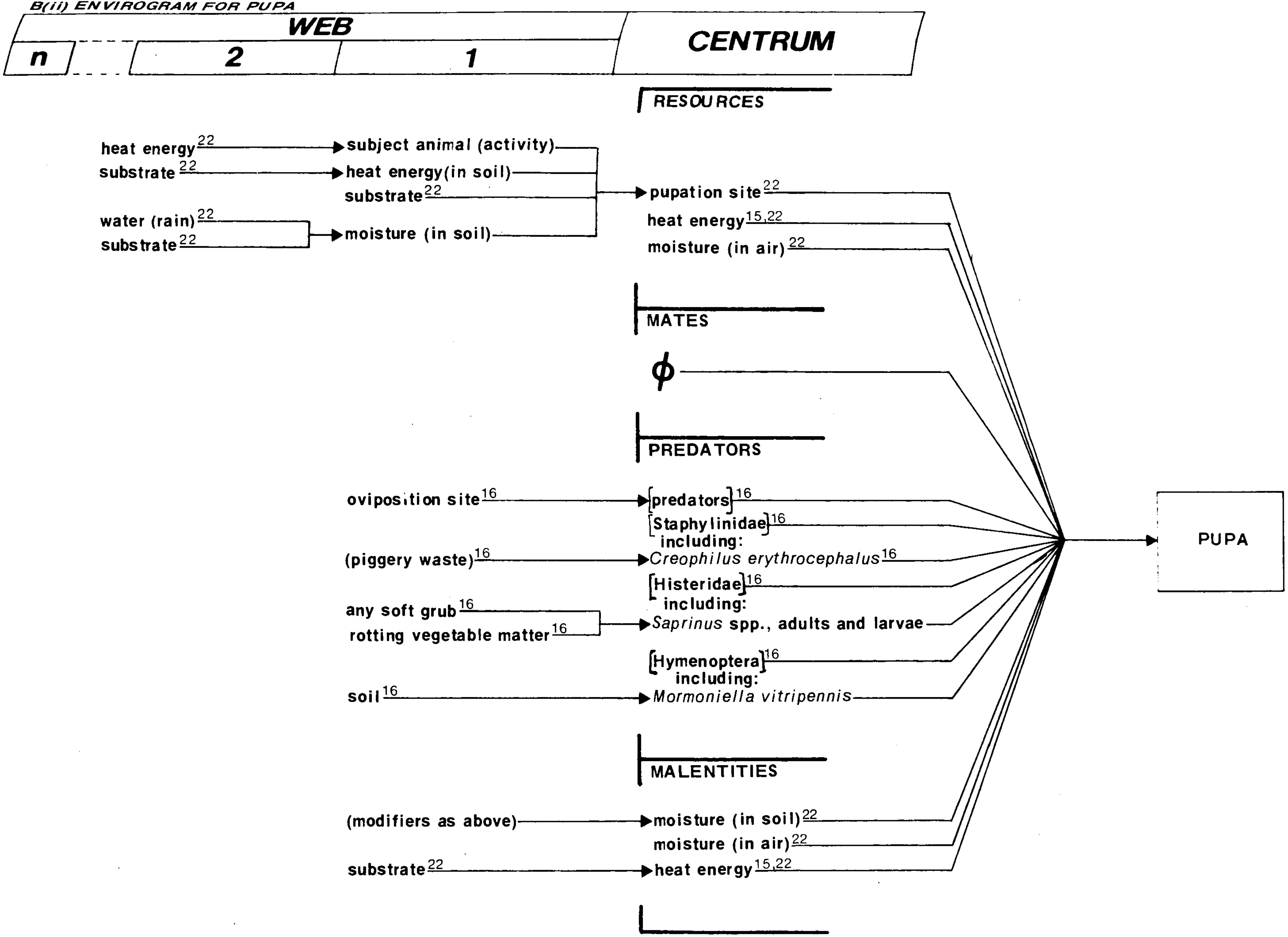
The envirogram for the *L. cuprina* adult is among the most complex we have drawn in the course of this study, and it is useful to make a number of general points. For a number of years it has been thought desirable to apply the techniques of exact science, where possible, to the life sciences in general and in the present context, ecology. Although this process has begun and is continuing there has remained the pervasive assumption that animals and the interaction between animals and other animals and their environments, are too complex to be more than superficially represented by mathematical models. Now the adult envirogram is not yet a mathematical model but it does show that staggering complexity can be captured by the application of a simple set of definitions - and even on this envirogram we have only scratched the surface. On just one front, the reminded that each time an animal appears somewhere on an envirogram the whole envirogram of that animal is generated and extends into the web of the subject animal. The central insight is that one can go into a locality where an animal lives, focus attention on some object or individual or measurable quantity of energy and either that object will satisfy one (or more) definition(s) (or any definition a multitude of times) and that definition will indicate where the object fits functionally in the animal's environment or no definition will be satisfied, in which case the object is ecologically irrelevant for the animal concerned. But that is not the finish - any object that can be placed on an envirogram can be quantified by a field or experimental ecologist and it is up to the ecologist concerned to generate just the level of complexity required.

We are indebted to Dr R L Kitching of this School at Griffith University, for lending us his collection of reprints on the sheep blowfly and for many helpful comments.

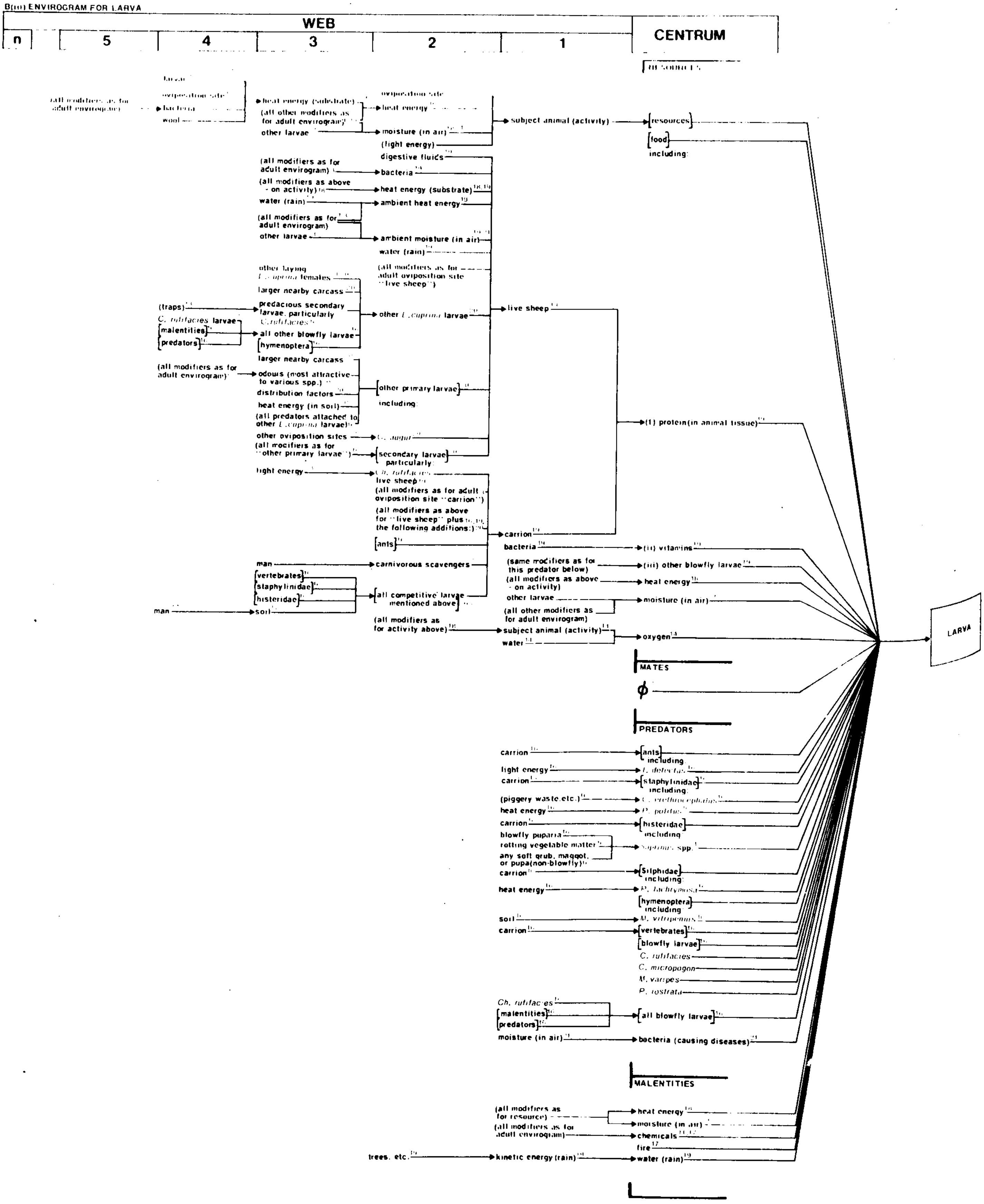
B(i) ENVIROGRAM FOR ADULT

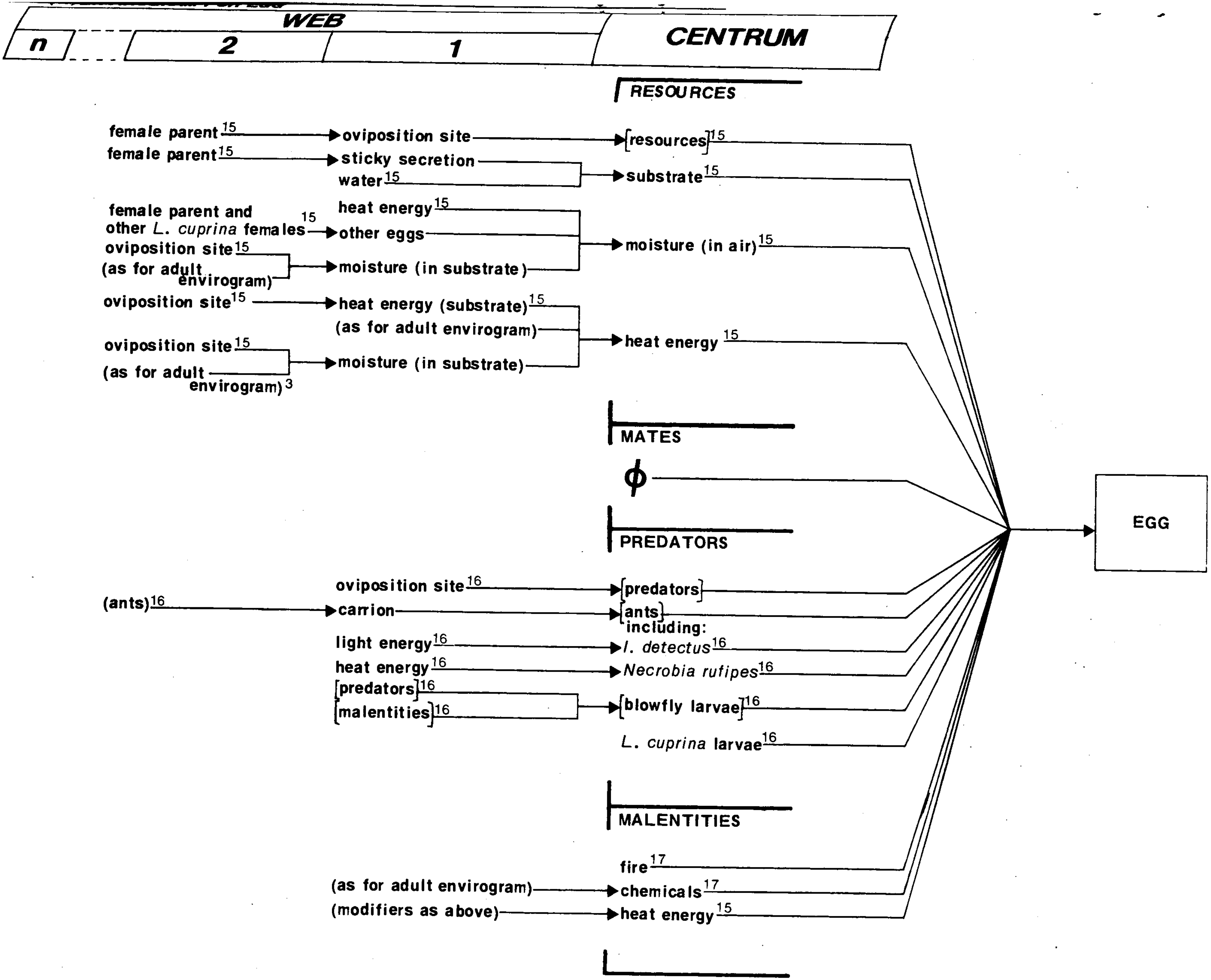


B(ii) ENVIROGRAM FOR PUPA



B(iii) ENVIROGRAM FOR LARVA




WEB
n
2
1
CENTRUM
RESOURCES
female parent 15
oviposition site
[resources] 15
female parent 15
sticky secretion
water 15
substrate 15
female parent and other L. cuprina females 15
heat energy 15
other eggs
moisture (in air) 15
oviposition site 15
(as for adult envirogram)
moisture (in substrate)
oviposition site 15
heat energy (substrate) 15
(as for adult envirogram)
heat energy 15
oviposition site 15
(as for adult envirogram) 3
moisture (in substrate)
MATES
φ
PREDATORS
oviposition site 16
[predators]
(ants) 16
carrion
[ants] including:
light energy 16
I. detectus 16
heat energy 16
Necrobia rufipes 16
[predators] 16
[malentities] 16
[blowfly larvae] 16
L. cuprina larvae 16
MALENTITIES
fire 17
(as for adult envirogram)
chemicals 17
(modifiers as above)
heat energy 15
EGG

C. NOTES ON THE ENVIROGRAMS

1. Three of the four classes of objects that constitute the centrum of an animal's environment - i.e. the resources, predators and malentities - are defined in terms of the animal being in the appropriate physical circumstances with respect ot the object and the effect that the object will have on the animal's life expectancy and ability to produce viable offspring (mates, the other class of the centrum, is a special case - for all four cases, see the General Introduction to this series). The point we wish to make for the moment is that if an animal is capable of independent movement or activity - i.e. if the animal is capable of changing the physical circumstances in which it finds itself and it the animal's environment is not a homogenous and ubiquitous mix of resources, mates, predators and malentities then the animal's ability to move from place to place and all the factors which effect that ability will determine the animal's length of life and reproductive success - i.e. given its place of birth and the physical attributes of the locality that fall inside the limit of the animal's potential lifetime movement. In less general terms and for our present subject animal this means the activity required by *L. cuprina* to find resources or a mate or to avoid predators or malentities.

The primary determinants of levels of activity for adult *L. cuprina* are adult age (state of development) and radiation augmented ambient temperatures (Kitching 1977). As an example of the former Kitching and Roberts (1975) report that in the laboratory at 26°C there was a continuing increase in activity over a three day period beginning at the time of emergence from the pupal stage - they equate this approximately 31.4 day degree period with the teneral period of the adult fly. Vogt *et al* (1974) and Woodburn *et al* (1978) give considerable information on age and states of development (see note 6) but we have been unable to find further information on age related activity differences.

We resolve temperature into the specific "heat energy" experienced by the animal; it has a direct effect on flight ability and is therefore a second order modifier of "subject animal (activity)". This heat energy is turn will be modified (3rd order) by the "ambient heat energy" and the intensity of "solar radiation" experienced. Woodburn *et al* (1978) showed in laboratory studies that the body temperatures of insects exposed to radiation exceed the ambient temperature by an amount that is directly proportional to the intensity of the radiation and the size of the insect - this result was also shown to be independent of the colour of the insect's cuticle. Kitching (1977) investigated the effects of this appropriately summated heat energy on the activity levels of adult *L. cuprina*. He found that the lower threshold of activity was 15.5°C. Above this temperature levels of activity rose steadily to a maximum at 26.7°C. This maximum was maintained until approximately 38°C and at higher temperatures activity declines until the flies suffered ill-effects (see also note 6, on heat energy).

The radiation mentioned above will in turn be modified by any objects giving shade ("shade objects". 4th-order modifier). Tillyard and Seddon (1933) report that in the warmer months of the year adult *L. cuprina* tend to congregate in the dappled shade of trees in the sparse Australian sheep country while in winter they seek all possible sunshine. They add that both temperature ("heat energy", 5th order) and humidity ("moisture (in air)", 5th order) play an important part in these preferences: the former, fairly clearly, because of the difference between shaded and unshaded temperatures and the need, in winter for the radiation supplement; of the latter we can find no specific information though the same authors comment that given sufficient warmth more blowflies will be active on a humid day than on a dry one - thus "moisture (in air)" as a second-order modifier also, and "heat energy" again as third order. Also clearly "rain" will be both a third-and sixth-order modifier of moisture (in air). However, several authors remark that blowflies are not active during rain, but will be very active after it - in both cases "rain" will be a second-order modifier (see also note 12).

Several authors report that wind ("kinetic energy (wind)", 2nd order modifier), particularly when strong, will tend to depress blowfly activity. In the absence of more specific information on *L. cuprina*, Norris (1965) offers the following: it has been shown that activity in the American screw-worm, *Cochliomyia hominivorax*, is depressed in winds exceeding 5 m.p.h. (≃ 8 k.p.h.) and is totally inhibited in winds over 15 m.p.h. (≃ 24 k.p.h.) - he adds that it is likely that other flies are similarly affected (see also note 12). For wind strengths below those which terminate activity, Tillyard and Seddon (1933) comment that experiments by Gurney and Woodhill (1926) show that blowflies normally travel either with the wind or slightly across it - the utility to the fly would seem to be that it can forage over greater areas in this way. However, the same authors note that in response to powerful odours a blowfly will travel directly into the wind if necessary. Thus "odours" are a modifier (3rd-order) of wind and being wind-carried (on occasions) "kinetic energy (wind)" is also a fourth-order modifier. However, these last statements have taken us away from the physical determinants onto the motivational determinants of activity - before pursuing that transition we can briefly summarize the weather conditions which most favour blowfly activity: moderately high temperatures (27-38°C) with intermittent rain and cloud cover to keep humidity high and sufficient wind to optimize foraging area. (We will see below that such conditions help foster 'strike' susceptibility in sheep - *L. cuprina*'s principal oviposition site).

It seems clear that *L. cuprina* is capable of detecting many of its resources and life requirements from some distance using its well developed sense of smell. This applies particularly to the odours of decomposition which characterize its 'protein-nutritional' sources (see note 2), its 'mating concourses' (see note 7) and its oviposition sites (see note 3). In fact these three objects form one class - all will be, typically, decomposing or purulent animal proten from one source or another; we spearate them functionally and for the utility of the envirogram. All clearly modify activity and to save space we represent them as the second-order modifier - "protein sites (search for)". As the motivating factor "odours" will also appear as a first order modifier whenever *L. cuprina* must locate one of the above and will modify activity (as a 2nd-order modifier). After smell has guided the fly to within a certain distance, sight probably plays a major part, while the final selection of food or position etc. will be governed by touch and taste (Tillyard and Seddon 1933). The possible 'sight' component above raises the question as to whether light is either a physical or motivational constraint on activity. We could find little information though comments by Norris (1959) and Kitching and Roberts (1975) seem to imply that *L. cuprina* is not normally active at night - thus we provisionally included "light energy" as a modifier of activity (2nd order). Kitching (pers. comm.) subsequently confirmed this. Tillyard and Seddon (1933) make some comments about the attractiveness of light sources and dark and light colours; however, while the comments apply to traps their generality is doubtful and a better explanation would seem to relate the behaviour to the heat-governed attractiveness of shade (see note 13).

In the general statements at the beginning of this note we referred to the limits of an animals potential lifetime movement. (Of course, measures could be taken over any useful time period). The work we have seen is summarized on the following table:

DISTANCE	TIME PERIOD	DIRECTIONALITY	SOURCE
0.6 - 3.5 km	60 hrs	No	Gilmour *et al* (1946)
1.2 km (mean)	2 days	Yes, upwind	Norris (1957)
1.6 km (mean)	9 days	Yes, upwind	Norris (1957)
0.6 - 4.2 km	60 hrs	No	Foster *et al* (1975)

Kitching (1981), in summary, comments that the above figures show that *L. cuprina* is a relatively sedentary species and that there is no evidence for long range movements. As further circumstantial evidence he adds that there are distinctly different levels of resistance to organophosphorous insecticides (see note 11) along a north/south transect line in eastern Australia and that this would not be maintained unless *L. cuprina* were sedentary. However, Foster *et al* (1975) comment that unpublished data from 'poor' blowfly areas indicates that migration involving much greater distances than those above may be important in finding 'good' areas.

With the exception of the last paragraph we have been discussing *L. cuprina*'s activity over short time-scales (i.e. appropriate to the envirogram) but it is known *L. cuprina* has a yearly cycle in that it is not found on the wing during winter - over-wintering as either hibernating prepupae or as puparia. Fuller (1934) reports that the appearance and disappearance of the adults was correlated directly with soil temperature. She gave the following information for several species of blowfly:

TEMP. °C (6" in soil)	SPECIES BEGINS EMERGING
12	*Calliphora stygia*
15	*C. augur* and *Lucilia* spp.
21	*Chrysomyia* spp.

She adds that as the cold weather approaches the flies cease to emerge in the same order at about the same temperatures. If we relax rigour and count an individual just on the point of emerging as an adult and if we regard this "heat energy (in soil)" as acting on that adult then we can represent *L. cuprina*'s yearly cycle on the envirogram by making this heat energy (in soil) a modifier (3rd-order) of the heat energy actually experienced by the animal - if the former was not present then the latter would not be applicable.

On the adult envirogram we have made "subject animal (activity)" and the attendant modifiers a modifier of resources in general - the only particular case where this may be difficult to follow is "heat energy" (note 6) but we have seen that *L. cuprina* at times shows preferences for shade or sunlight, activity mediating the choice. In fact as was argued generally in the first paragraph of this note activity will modify the whole centrum but to save space on an already crowded envirogram we will not show the modifiers attached to the other three classes. The only differences would probably be some specific predator-avoiding behaviours or strategies but we have found no details in the literature.

Finally, we will see in note 2 a special relation between activity and carbohydrate; the appearance there of "subject animal (activity)" as a first-order modifier is for reasons additional to those discussed in this note. The connection in note 14 between activity and oxygen is similar.

Also see note 12 for some activity related malentities.

2. Tillyard and Seddon (1933) state that the belief that adult blowflies grow after emergence is false; nutrition being used to fuel activity and for (cyclical) sexual maturation (see note 7). The first of these uses is catered to by carbohydrate and the second by protein. Water uptake is the only other necessity.

(i) WATER. Roberts and Kitching (1974) showed, in experiments, that flies subsisting only on larval reserves and water can survive for 4-5 days. Water uptake increased each day, the highest means being 0.87 µl/fly/hour for males and 2.23 µl/fly/hour for females. Even when denied water (and all other food) from the time of eclosion *L. cuprina* may live three days in a reasonably active state. These two results indicate that *L. cuprina* is often able to escape from adverse conditions to more nutritionally favourable environments. Although Roberts and Kitching showed that *L. cuprina* was capable of ingesting dry foodstuffs, such would be rare in the wild and most of the fly's water requirement would be taken up in the characteristically liquid sources of "carbohydrate" and "protein". Apart from these latter *L. cuprina* can utilize the water in "dew", "raindrops" and the "mud" around standing water, when (occasionally) needed. All will be first-order modifiers of water and "standing water" will be a second-order modifier.

(ii) CARBOHYDRATE. Blowflies can and do utilize virtually any sugar-rich source to obtain carbohydrate: the honeydew from aphids, coccids and psyllids (e.g. the cabbage aphid *Brevicoryne brassicae*) and other sweet secretions from insects; insect blood; nectar from the blossoms of many plants - particularly from the tea-trees (*Leptospermum* spp. and *Melaleuca* spp.), *Angophora* spp. and *Eucalyptus* spp.; plant sap; and, rotting fruit. Even dung and carrion, usually utilized for protein content will provide some sugar. All of these will be first-order modifiers of "carbohydrate". Highly concentrated sources of carbohydrate are more attractive to the fly though experiments by Roberts and Kitching using sucrose solutions of different concentrations (and dry sucrose) showed no significant differences in the actual amount taken up. Not suprisingly *L. cuprina*'s carbohydrate uptake is proportional to its level of activity (axiomatically, more activity implies more food). Consequently, any activity by the fly will be a first-order modifier of this resource and given the assumption, implicit in the literature, that all *L. cuprina*'s activity is teleological we can list a number of objects as second-order modifiers, theoretically, all the following: oviposition sites, mates, protein (see below), carbohydrate, water, predators (evasion of) and perhaps sleeping sites. In practice carbohydrate and water (particularly) are seldom in short supply, sleeping sites are probably ubiquitous and the expense of evading predators is likely to be inconsequential; so only oviposition sites, mates and protein are likely, at times, to be imporatnt (see note 7, on delays).

(iii) PROTEIN. Protein is available to *L. cuprina* principally from the juices of meat and decaying animal tissue in carrion, established strikes and other open animal wounds. Also, the faeces of humans and carnivores and some from the faeces of some herbivores - Norris (1959) names cattle, horses, poultry, rabbits and sheep. Several workers comment that sheep dung contains insufficient nitrogen for *L. cuprina*'s purposes but Norris notes that this is not so if the sheep have been grazing on high protein pasture (Perhaps this applies to herbivores in general). In experiments, Norris used crushed insects (spiders and flies) as protein sources and Kitching (1981) comments that some protein in available from the amino acids contained in many of the carbohydrate sources mentioned above. Again Roberts and Kitching have shown that *L. cuprina* can ingest dry protein - nevertheless several workers suggest that dry conditions tend to desiccate available protein and render it inaccessible to the blowfly. On the other hand, prolonged dry conditions (drought - c.f. "rain" as a second-order modifier of "carrion", note 3) tend to increase the supply of carrion (and thus protein). This must be balanced against its shortened usable life. In summary, Kitching (1981) concludes that in the Savannah country, usually associated with sheep grazing, the availability of protein will rarely be abundant - consequently the absence of "protein" will modify "activity" (searching) and consume "carbohydrate" fuel.

During the teneral period (see note 1) the female fly requires only carbohydrate and water for nutrition. The teneral period is followed by the first of a series of cycles of ovarian development each of which terminates in oviposition (see note 7). During each of these cycles the female must obtain protein to initiate vitellogenesis and allow the eggs to mature. One feed may be sufficient though many can occur. Experiments by Roberts and Kitching (1974) show that in any ovarian cycle protein ingestion will reach a single peak relatively early in the cycle and will then decline to a fairly low level. As a corollory to the earlier observation, the finding of "protein" again modifies "activity" and "carbohydrate" consumption - this time the search is directed towards finding a mate and then an oviposition site. (Note 7 covers the effect or mating success of the absence or shortage of protein).

The sexual development of males is not cyclical but somewhat similarly to the females they show a lower more extended peak in protein consumption which gradually dwindles with age. However, unlike the females there is apparently no physiological reason for protein utpake and it is suggested that the protein motivation of males is to utilize protein sources as mating concourses or contact sites (again see note 7). This is consistent with males being primarily carbohydrate motivated throughout their lives - i.e. to fuel their movements from mating site to mating site, and repeated matings.

Finally, despite the general tendency in the literature to partition blowfly nutrition into the sections treated above, several authors make it clear that a balance between protein and carbohydrate consumption is important to both males and females: both live longer and females produce more eggs more quickly if the appropriate balance is achieved.

3. It is a formal characteristic of the equations we use to define and classify animal environments that objects which positively modify mating success will also appear on the envirogram as resources (for fuller discussion see the General Introduction to this series of papers). In the present case "suitable oviposition site" is a positive first order modifier of any mate for our subject female because unless such a site is found neither will have any viable offspring as a result of their mating.

Kitching (1981) comments that blowfly eggs are laid in one of three potential larval habitats:

(i) garbage
(ii) carrion
(iii) living sheep.

Because of the significant differences between the above three cases, in treating oviposition sites as a resources we have resolved it into the three classes mentioned; all the various modifiers would appear as second-order (and higher) modifiers of mates in the particular cases. Modifiers attached to "suitable oviposition site" apply in all cases.

(i) garbage - this class of objects and media are invariably associated with man (a first-order modifier). In addition to household and slaughterhouse refuse the class includes old sheepskins, saddle-blankets, hemp sacks, faeces and anything else that a gravid female finds sufficiently attractive (see below). This class of sites is infrequenlty utilized by *L. cuprina* though not so rarely as to be insignificant. *L. cuprina* is well adapted to breeding in rubbish tips - such tips being the primary habitat of the species beyond the range of the sheep (Kitching (1974)).

(ii) carrion - is available to blowflies throughout the year from an obviously wide range of sources - any animal that dies in fact (all first-order modifiers). However, Fuller (1934) and Waterhouse (1947) showed that not all carrion was equally attractive to all species of blowfly. Some unknown factor(s) is probably involved though it is likely that the progress of succession and competition in larval media between various species is also operative. To take just one example, *Calliphora augur* is notably successful on small carcasses; probably because its 'larviposited' young get a twelve hour start over egg-laying species, on a medium which will decompose or desiccate extremely quickly. Many factors will effect the abundance of carrion: "fire" and drought as causes of animal death, both tend to provide carrion in abundance and variety. The latter appears (as a second-order modifier) on the envirogram as "rain" because drought is not an object; "rain", when present reduces the amount of carrion (from this source) and its absence from the envirogram is equivalent to drought. Of course, drought, this time realized as hot ("heat energy"), dry (low humidity - i.e. "moisture (in air)") conditions will also tend to reduce carrion supply because the available carcasses tend to desiccate and become unusable for *L. cuprina* more quickly. In this case, the modifiers are first-order. Predators of animals provided that they do not consume the whole carcass will also be second-order modifiers; as will any malentities resulting in death (i.e. other than the two specifically named above). Macroscopic "carnivorous scavengers" will compete with blowflies for carrion and are thus first-order modifiers: Fuller (1934), in her experiments near Canberra found that carcasses were consumed by dogs, cats, birds and lizards; wild pigs consume and dismember carcasses; and Smit (1931), in South Africa, reported that the hunting by graziers of carnivorous birds and mammals because of the danger to their flocks also removed the scavenging activity which had greatly reduced the carrion available to the blowflies. Consequently this tactic of flock husbandry had the adverse effect of increasing the blowfly problem. He mentions that this has occurred, to at least some extent, in Australia thus "man" is a second-order modifier. The same two modifiers "carnivorous scavengers" (2nd-order) and "man" (3rd-order) will also appear as modifiers of "carrion" as a protein source (food) for *L. cuprina* larvae - they provide another type of competition (see note 20). In an attempt to control the blowfly problem "man" also disposes of (or treats in some way) carcasses directly (see note 17). Unseasonal and sudden cold snaps, particularly following shearing will kill sheep - thus "heat energy" is a second-order modifier and "shearers" are third-order modifiers. *L. cuprina* and other blowflies also supply sheep carrion: in all 'strikes' there is bacterial activity which produces products toxic to the sheep and in bad cases this may lead to death. Usually, the sheep will recover either naturally or by good management in which case it becomes eligible for re-strike - some sheep have been struck up to 20 times in a year. The 'myiasis carcass' ensuring from death following strike has unique properties - i.e. different from other carrion - see note 18.

In South Africa the utilization of carrion by *L. cuprina* remains important (on a par with living sheep) (Smit 1931) but Waterhouse (1947) and Fuller (1934) provide experimental results which suggest that in Australia *L. cuprina* is less successful in carrion than on live sheep (see the larval envirogram and notes 16, 18 and 20). In summary, Kitching 1981 comments that in Australia *L. cuprina* appears to have evolved farther down the road towards obligate parasitism.

(iii) live sheep - all sheep are potential oviposition sites for gravid female *L. cuprina*. Whether or not a particular sheep is actually 'struck' depends on a combination of the qualities and conformation of the individual sheep and outside or environmental factors. Many of the former, as characteristics of the object "living sheep" cannot appear independantly on the envirogram but the latter will all be modifiers). To make clear the significance of many of the 'sheep conformation' factors we will first have to outline some more general consideration.

First we consider the factors of "odour" (first-order modifier of oviposition site), sight, touch and taste used by *L. cuprina* to find and position itself around a resource - see note 1. Shanahan (1965) reports that recent tarsal contact with moisture is essential to promote oviposition, which is still low unless the oviposition (with its highly developed tactile sense) is in a nearly saturated atmosphere at the time of egg-laying. Both "moisture (on substrate)" and "moisture (in air)" are thus first-order modifiers of "oviposition sites".

Together with the acceptable temperature range - i.e. "heat energy", - the three first-order modifiers of the previous paragraph give us the critical requirements for oviposition.

Thus, to return to the class of oviposition sites "living sheep": Appropriate "odour" can be induced in sheep by a great complexity of factors. Norris (1959) argues that "wool" (2nd-order mod.) has a slight attractiveness to blowflies, in any case, in that it is dead - though not yet decomposing. Tillyard and Seddon (1933) also comment that ammonia-producing "bacteria" (2nd-order mod.) have been isolated from urine-free wool. The suggestion is that ammoniacal odour serves to attract *L. cuprina*.

The conditions where this, and other, bacteria will flourish, will quickly transform any slight attraction into definite susceptibility to 'strike'. Moisture retained in the wool from whatever source is essential and provides a good medium for bacterial growth. "Moisture" is a third-order modifier in this context and higher order modifiers of it will be the same as those that modify "moisture (on substrate) as a first-order modifier of oviposition sites (mentioned above, see below).

"Soil", "organic matter" and faecal matter ("faeces" and "urine") retained in the wool provide nutrients for bacterial growth - all are third-order modifiers. "Green and improved pasture", because of high water content favour faecal staining and are fourth-order modifiers. Morley *et al* (1976) comment that drought feeding with "wheat" or moving a flock to a pasture which had been grazed by cattle may induce digestive disturbances leading to diarrhoea - thus we have "wheat" and "pasture" as fourth-order modifiers and "rain" and "cattle" as fifth-order modifers. Increased "water" intake (4th-order) in hot conditions ("heat energy", 5th-order) can have similar effects, and infection with "helminths" (4th-order, see note 4) also favours faecal staining. "Sweat also aids bacterial growth; hot conditions ('heat energy", 4th-order) tend to cause sweating and high humidity ("moisture (in air)" 4th-order) will tend to prevent it evaporating. In addition, Holdaway (1932) suggests that progressive changes in Australian pastures have affected the skin secretions of sheep rendering them a more suitable medium for bacterial growth - thus "pasture" in a fourth-order modifier. Bacteria are transferred from sheep to sheep ("other sheep" 3rd-order) particularly when they are yarded together ("yards" 4th-order); transferance is also aided when sheep congregate in the shade ("trees" 4th-order) on hot days ("heat energy" 5th-order). Cold weather ("heat decomposition of yolk (wool grease), faecal material, sweat, wool and skin detritus tends to cause an inflamatoray reaction in the skin and skin exhudations as the conditions favouring strike develop.

The "moisture (on substrate)" required by *L. cuprina* for oviposition is also induced by a great complexity of factors. The first necessary requirement is an adequate amount of "wool" (2nd-order) to trap the moisture. Sheep with markedly wrinkled and folded skins consequently have denser wool in those areas resulting in greater water retention both in the corrugations and in the wool. Wool yolk is hydroscopic so fleece with a high yolk content will hold more water, as will wool of fine fibre.

For all the above reasons Merino sheep are particularly susceptible. "Shearers", who remove the wool, are third-order modifiers. The sources of moisture - all third order modifiers - include: "rain", "urine", "faeces", "sweat" and "blood and exudate" from wounds. (Wool is not required to trap the moisture from the latter so that "blood and exudate" can also appear as a second-order modifier with the same higher order modifiers attached.) Hot weather ("heat energy", 4th order will tend to dry up all moisture sources while high humidity ("moisture (in air)", 4th-order) will tend to prevent such evaporation. Wounds may be caused in several ways - all will be fourth-order modifiers: by careless "shearers", "dogs", accidents with "fences" and fights between male sheep ("other sheep").

The principal modifier of "moisture (in air)" (1st-order) - i.e. high humidity in the oviposition microclimate will be "moisture (on substrate)" (2nd-order) with the same higher order modifiers as above. In summary, the weather conditions most favouring strike will be just those mentioned in note 1 as being most conducive to blowfly activity.

Another significant factor of sheep conformation favouring strike is being 'narrow' behind - i.e. having the hocks approaching each other. This favours faecal staining. It is clear that most strikes occur in the breach-crutch-tail region, particularly among ewes, hoggets (young ewes) and weaning lambs but given the right conditions strike can occur virtually anywhere on a sheep's body. Body strike, most commonly on the withers, back, loin and side can effect all sheep, though most frequently ewes and wethers. Head strike effects only rams either because of a predisposition of horn configuration or because of head wounds from fights. Pizzle strike effects wethers and young rams, usually because urine evacuation has been impaired by careless shearing. Young sheep generally are more susceptible to strike because they have more open fleeces which enable the gravid *L. cuprina* to find the dark cavities they favour for oviposition - this "light" factor applies to all oviposition sites and is a first-order modifier.

Man, as a supplier of sheep, is a modifier (1st-order) of this resource. However, he also takes many steps to control any predisposition that his sheep have for strike - see note 5.

Norris (1959) reports that one laying female *L. cuprina* serves as an attractant to others so that many females may mass eggs in one situation. Thus, "other laying females" is a first-order modifier of all oviposition sites; this behaviour will also have effects on the egg and larval envirograms - see notes.

On the envirogram we can indiciate *L. cuprina's* preference in oviposition sites by showing "carrion" as a first-order modifier of "garbage" because the latter is less likely to be selected by a gravid female in the presence of the former. Similarly, we show "suitable living sheep" as a modifier of "carrion".

Finally, we have been discussing suitable oviposition sites for *L. cuprina* but many cases are recorded in which a female has laid eggs where they cannot survive - this may be in healthy wool or in rotting vegetable matter or in some of the more curious sites given under garbage (above). For the same reason that a positive modifier of mates is a resource, a negative modifier of mates will be a malentity - thus "unsuitable oviposition site".

4. Morley *et al* (1976) conducted several experiments to gauge the effect of helminth parasites on sheep and the relationship between infestation and strike.

The most important and numerous nematode parasites present were *Haemonchus contortus, Trichostrangylus sp., Ostertagia sp.* and *Nematodirus sp.*. The presence of these parasites tended to favour breach soiling with soft, wet faeces. There was a significant difference between sheep drenched at weaning with an anti-helminth drench - 20% had soiled breaches - and those not drenched - 55%. Of the sheep weaned onto 'clean' pasture only 30% were infected with helminths, while 44% of those weaned onto pasture occupied previously by other affected sheep became infected.

"Helminths" appear on the envirogram as a fourth-order modifier of the oviposition site "living sheep"; "drench" and pasture" will appear as fifth-order modifiers and "other animals" previously infected and responsible for infecting the pasture will appear as sixth-order modifiers.

By the suppression of helminths the incidence of strike in the radically mulesed weaner sheep was reduced from 50% to 5%.

5. Man is a first-order modifier of *L cuprina's* oviposition site, "living sheep" by employing a number of protective measures for his flocks. The experience and judgement of a grazier is important in timing the use of, and implementing, these measures. Many of these measures will also appear as malentities or modifiers of malentities on the envirogram.

It has been shown that the factors of conformation which predispose sheep to fly-strike tend to be passed on to their offspring. Consequently, breeding programs against these factors have been undertaken by the C.S.I.R.O. and many private breeders.

In addition, several tactics can be employed in husbandry. Shearing incidentally falls into this category, but particularly the Mule's operation (with some modern refinements), tail-docking, crutching, pizzle-ringing, and horn-chipping. All were developed to counter specific problem areas.

"Jets", "swabs" and "dips" (1st-order mods) are used to apply various chemicals (malentites - see note 11) both to prevent and treat strikes. "Dressings" are also used (again with chemicals) to treat strikes and if they act as a protective covering of the wound they will tend to prevent re-strike. In their preventive capacity all these application methods will be modifiers of chemicals (malentities) on the adult envirogram while as treatments they will function similarly on the larval (and probably the egg) envirogram(s).

Both the chemicals and the appliances should appear as modifiers of the oviposition site "living sheep" but to save space we have used "man" (1st-order) as their proxy and represent them in full as malentities (where "man" will be a second-order modifier.)

Similarly on the larval envirogram we show "man" as a second-order modifier of protein (food) as obtained from living sheep - again the full chains appear under malentities.

6. Both rates of development (loosely - 'ageing') and ecological activity for *L. cuprina* are temperature dependant. The assumption of a linear relationship for the former permits identification of a developmental zero and thermal summation by integration of the area under the curve of environmental temperatures and above the developmental zero line to estimate age/state of development in day degrees (or other unit-time degrees) (Kitching 1977). Vogt et al (1974) identified a developmental zero of 8.2^{0}C and defined 6 stages in the first overian cycle and five in subsequent cycles. Woodburn et al (1978) give the following estimates for the first five stages of the first overian cycle:

Table III: *Mean female age in day-degrees at completion of each stage of egg development during the first ovarian cycle*

Stage	Mean ± s.d.
0	31.3 ± 7.7
1	41.0 ± 7.9
11	53.5 ± 11.5
111	68.7 ± 10.4
1V	74.8 ± 8.4

Activity - temperature relationships are given in note 1.

There will always be a range of heat energies around an optimum (range) which are positively beneficial for an animal. In *L. cuprina's* case the optimum will be about 26.7^{0}C because it is the lowest temperature, and hence the slowest 'ageing' rate, still allowing maximum acitivity. The upper limit of the positively beneficial range will be about 38^{0}C because at higher temperatures the animal becomes rapidly less active while it is ageing ever more quickly; the lower limit is more difficult to determine because while activity quickly decreases below 26.7^{0}C the animal will be ageing more slowly. This beneficial range of heat energies constitutes a set of resources on the envirogram. Outside of this range the animal will become increasingly disadvantaged until the upper and lower death points are reached. We have found no information concerning these points but for our purposes it is sufficient to note that if a particular heat energy object is not a resource then it is a malentity. That is, notwithstanding the following possible curious result. It depends on the position of the lower death point: if that point is 8.2^{0}C (calculated developmental zero) or above the conclusion that all non-resource heat energies are malentities will clearly follow. But if the death point is below 8.2^{0}C then for the range between death point and 8.2^{0}C the animal will show no activity but also will not age. Clearly, there is no advantage to the animal but unless the situation 'stresses' the animal in some way (and that is difficult to see if the animal is not ageing) then there will also be no disadvantage. The range of heat energies concerned would satisfy neither the resource nor the malentity definition - formally, at least, it would not be in the animal's environment.

The modifiers for "heat energy" as both resource and malentity will be the same as those discussed in note 1 and represented on the environment as modifiers of "heat energy" as a second-order modifier of resources (first-order modifier being "subject animal (activity)").

7. Only adult blowflies qualify as potential mates under the mates definition because at any particular time "t" only adults, just then, have a probability above zero of producing viable offspring (this is a simplification; for the definition and fuller discussion see the General Introduction). Consequently, in the three non-adult envirograms the null set, {∅}, appears in the mates section. In addition, given the probablistic component of the definition of a mate we are concerned not only with all the factors that contribute to mating success but also with lifetime fecundity - the latter measured by the number of viable fertilized eggs laid by our subject female.

All the available adult male *L. cuprina* are potential mates for our female. They fall into two classes: natural members of the population and the mutants released by the C.S.I.R.O. (see note 8). With the latter exception all modifiers will be the same for both classes and together they will determine the mating success of the relevant male - female pairing. Several authors comment that the ratio of the sexes is 1:1.

Following the approximately 31.4 day-degree teneral period our female must do 3 things to produce viable eggs:

(i) find protein to begin maturing eggs;
(ii) mate with one of the available males; and
(iii) find an oviposition site

(i) Protein: Note 2 gives details of sources, normal utility to the fly and factors effecting availability. However, the shortage or absence of protein can have rather drastic effects on mating success. It has been shown that virgin females must find protein within 3-4 days of emerging before they will readily accept males; older virgin females remained reluctant to mate even after they were supplied with protein. Tillyard and Seddon (1933) comment that the females ovaries will not mature at all unless protein is obtained within the first 10 days of adult life. Kitching (1981) notes that females with access to an inadequate amount of protein will mature less than a full clutch of eggs. He says that this occurs in a small percentage of cases in the wild. In addition, delays in finding protein, though not long enough to give the above drastic results, are important (see below). Nevertheless "protein (food)" is a first order modifier of mates.

Once sufficient protein has been obtained ovarian development is temperature dependant with a developmental zero of $8.2^{0}C$ identified by Vogt et al (1974) and Woodburn et al (1978).

(ii) Mating: Once mated, females will not readily mate a second time. Thus, characteristically, all of the progeny of a female (i.e. produced over several cycles - see below) will be sired by one male. Nevertheless, any male ("other males") that manages to mate with a previously mated female will replace the original male as sire of subsequent progeny - as such, he is a first-order modifier of the mating success of the original pairing.

Several authors comment that mating occurs on or around feeding sites which act as 'centres of attraction' for both sexes and hence as "mating concourses" (1st-order mod). Usually protein sites are mentioned though it would seem that meetings could occur at carbohydrate sites as well. Perhaps the greater abundance of carbohydrate sites means that a male is more likely to meet more females at protein sites - and so this strategy has evolved. Kitching (1981) notes that there is good evidence for mating delays - obtained by comparing morphological age criteria with reproductive state and an ideal (i.e. heat driven) development. Further good, though circumstantial, evidence is provided by trapping results, wherein significant proportions (averaged at 5% over a year) of unmated though fully gravid females were caught. Foster et al (1975) confirms this. A shortage of mating concourses is considered to be the reason and as with the 'protein delays' (above) mating delays are important (see below).

(iii) Oviposition: (Most details are given in note 3) The oviposition of a clutch of eggs ends a cycle of ovarian development. Norris (1965) comments that eggs, not oviposited within the first five days after maturation, may degenerate and become non-viable. This is not the only reason that delays in oviposition are important (see below).

Each time a female oviposits she can begin a new cycle of ovarian development - she may even feed on the protein site just utilized for oviposition to begin maturing the next clutch of eggs. As mentioned above mating need not occur in these later cycles. Oviposition will follow; and so on, through succeeding cycles. Thus, we could determine the lifetime fecundity of a female *L. cuprina* by knowing:

(a) the clutch size she lays

and (b) the number of clutches laid during her life

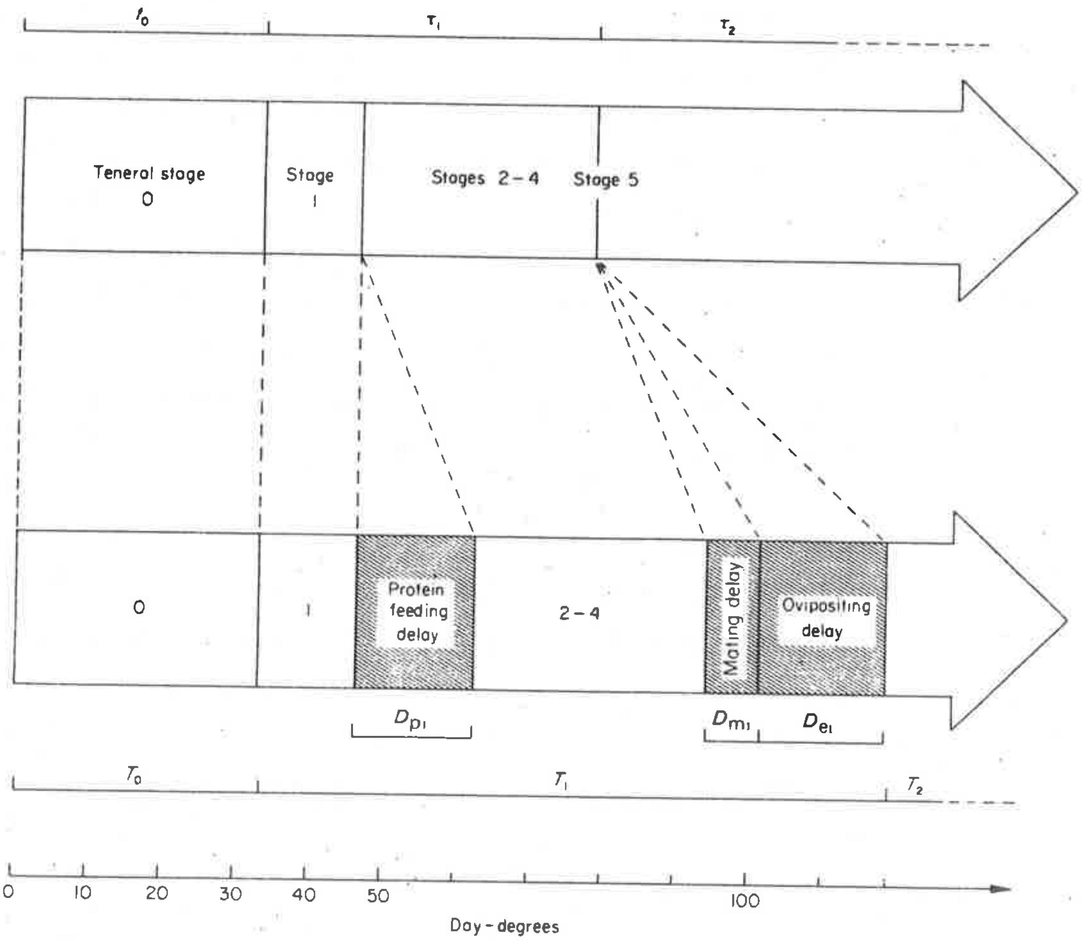
(a) Clutch size: Foster *et al* (1975) reports that clutch size is a linear correlate of the size of the adult female fly as indicated by its head width. They give the equation:

$$Y \text{ (clutch size)} = 172.64x - 298.67$$

where x is the head width in millimetres

Presumably, this is for ideal conditions. Several factors are known to influence adult size (and hence clutch size): the larval medium, the density and species composition of the larvae on the medium during the feeding phase, and the length of time that a larva is permitted to feed (for all, see notes 18, 19 and 20). Although it is not formally true, for reasons similar to those alluded to in note 16 when discussing a similar case, we show "larval medium (of subject female)" and "larval competition" as first-order modifiers of notes. From the above equation Kitching (1977) gives a clutch size of 220 based on an average head width of 3.00 mm. Shanahan (1965) gives a range of clutch size 70-260 while Kitching (1974) gives 120-280.

(b) Number of clutches: this will be a further function of the length of each ovarian cycle and longevity. Kitching's (1977, 1981) results indicate a median longevity of approximately 400 day degrees for females under laboratory conditions with each of the ovarian cycles lasting approximately 42.2 day degrees. Discounting the teneral period this would allow *L. cuprina*, potentially, about 9 ovarian cycles (see case 1, table below). Kitching comments that he has observed up to 7 or even more in the ideal laboratory situation. Cases 2, 3 and 4 on the table consider successive rates of mortality in the field overlaid on case 1 and he argues that field longevity will have a median of approximately 170 day degrees - corresponding to just over 3 oviposition cycles (case 4). Thus, all those factors which shorten the life and lower the fecundity of our female to below the potential maximum will be first-order modifiers of any mated pair - in short, these modifiers will be all the "predators and malentities" appearing on the envirogram. Given that these factors reduce field longevity to the median given above any factor which serves to increase the length of ovarian cycles (ie. over the ideal temperature dependant time) will reduce actual fecundity. These factors fall into two classes. Firstly, covered above, shortages of protein, males and mating concourses, and oviposition sites will all tned to lengthen ovarian cycles. The second class relates to the flies ability to search for and find the above requirements. As Kitching (1977) remarks "the crucial point is that when environmental conditions are such as to impair activity the insect will be less able to search for and exploit resources in the field. When these resources are essential to the developmental progress of the animal this will cause delays and consequent reductions in fecundity over the lifetime of the individual concerned". The range of modifiers captured by the above generalization has wider application on the envirogram and details are given in note 1. Thus "subject animal (activity)" will be a modifier (2nd-order) of "protein (food)", "mating concourses" and "oviposition site" and the higher order modifiers (given in note 1 and on the envirogram) will determine, in conjunction with the availability of sites, whether delays occur. Kitching summarizes what he calls the time/resources/fecundity mechanism in the following figure.



> The upper arrow shows the undelayed progress of ovarian development when only heat input is limiting; the lower arrow indicates the course of development with the delays discussed above. The symbols are those used by Kitching (1977) and refer to equations used in that paper.

The last three cases on the table give field measurements. Presumably the difference between them and case 4 indicates the extent of the delays encountered in each of the years. LPF means lifetime potential fecundity and LAF, lifetime actual fecundity - both are calculated from the numbers of ovipositions using 220 as clutch size.

TABLE 2: Estimates of the mean numbers of ovipositions for *Lucilia cuprina* (see Fig. 4 and text) (Kitching, 1981).

Case	Situation	Number of ovipositions	LPF or LAF
Potential			
1	Laboratory-type survival	8.96	1971
2	Natural survival case 1	7.37	1621
3	Natural survival case II	5.54	1219
4	Natural survival case III	3.34	735
Actual			
5	Season 1972-73, n = 2346	0.600	132
6	Season 1973-74, n = 3168	0.451	99
7	Season 1974-75, n = 1525	1.001	220

Foster *et al* (1975) comment that the occurrence of more than three ovarian cycles in the wild is unusual (unpublished data). Many authors give normal time (days etc.) estimates of longevity, cycle length etc., but the present authors believe that in this context the day-degrees measurements provide more significant generalizations. In the laboratory males live significantly shorter lives than females. Finally, several authors quote 1000 eggs as an estimate of lifetime fecundity but the figure seems to be unpublished and is probably a laboratory result.

8. Kitching (1981) reports that work is under way by researchers in CSIRO to develop flies with deleterious mutant genes and rearranged compound chromosomes. These new strains are to be released in the field to lower the fecundity and viability of the native populations. Thus, the CSIRO is a first order modifier of "mutant male adult *L. cuprina*" that may be selected by our subject female as a mate (also see note 7). Note that if these mutants or any mate for that matter are in fact sterile then they do not satisfy the mates definition but will appear on the envirogram as a malentity (see the General Introduction for discussion). γ-rays appear as a first-order modifier of 'mates' since potential mates are removed by the action of the γ-rays from the environment.

In the work presently (1982) being undertaken by Mr Samrit Singh-Asa (Entomology Department, University of Queensland) on the effect of irradiation by γ-rays, the pupae have been irradiated when 5 to 6 days old, using a ^{60}Co source and a dose rate of 3.5 to 2.3 Krad/min. The irradiation appears to have no effect on the rate of pupal emergence, irradiated males can compete on equal terms with non-irradiated males as mates and the percentage of eggs which hatch drops off markedly as the dosage is increased (Singh-Asa, pers. comm.).

Another present line of research is into the chemical control of behaviour. If ovipositing in the presence of the complex compound (1,1-bis-(p-ethoxyphenyl)-2-nitropropane) a gravid female *L. cuprina* will lay substantially fewer eggs. If the compound is placed on a susceptible sheep protection will last up to 8 weeks. Again this chemical is a first order modifier of any mate for our subject female because if it is present the likelihood of the pair producing viable offspring is reduced. Also, for reasons touched on at the beginning of note 3, the chemical will be a malentity for our subject female.

9. In various cases with different animals, it is probably acceptable to classify "collectors and research workers" as either malentities or predators of the subject animal.

Here we have calssified them as predators, thus assuming an interpretation of the primitive symbol 'H(research worker)' in the defining equation for predators, which allows it to increase because the human gains some benefit from the action of trapping a blowfly.

For fuller discussion and the difficulty of interpretation of 'H(human)' generally, see the General Introduction to this series (1983 version).

10. Few predators of adult *L. cuprina* are mentioned in the literature. Several authors comment that some blowflies must be eaten by insectivorous birds: only one observation is recorded, *Rhipidura leucophyrs*, the willie-wagtail. Similarly, several authors comment that generalist insectivores like predacious wasps such as *Sericophorus* spp., asilids and dragonflies must also take some.

Foster *et al* (1975) comment that during the teneral period (i.e. before flight muscles are fully operational) adults are at much greater risk of predation by non-flying insectivores, though they name none. Norris (1959) names ants but it is not clear if he means as predators of adults.

Tillyard and Seddon (1933) report that adult blowflies suffer from fungal diseases, the best known of which is *Empusa muscae*. They also note that adults are attacked by bacterial diseases but no further details are given. Norris (1950) reports that certain weather conditions increase the incidence of both the above but again gives no details.

11. Tillyard and Seddon (1933) discuss many oils, pastes, powders and emulsions applied to sheep in various ways in attempts to control blowflies. Most of the chemicals have fallen into disuse, though the methods of application are still used - some are listed in note 5. The discussion below is confined to the effect of these chemicals on adult flies but it is clear that *L. cuprina* immature stages will also encounter these malentities. Note 17 gives some details.

For a time DDT and BHC were widely used. Shanahan (1965) reported that jetting with these chemicals could provide 6 weeks protection against body strike and 10-14 weeks protection against poll strike in rams. Dieldrin and Aldrin were also used briefly and the same author reported that jetting with them provided 14 weeks protection against body strike and 6 weeks against breach strike. But by late 1957 field populations of *L. cuprina* had developed almost total resistance to Dieldrin and Aldrin. Apparently there had been a resistant gene already present at high frequency in the population when the use of these chemicals commenced. Subsequently, various organo-phosphate chemicals have been widely employed - Nemacide, Nankor, 5.1751 and, in particular, Diazinon. Resistance to the organophosphates took some time to develop. Foster *et al* reports that it first appeared in 1965 and that by 1974 they gave as little as one weeks protection in some areas. Kitching (1981) reports continuing and developing resistance in both larvae and adults but he also notes that at the time of writing the only treatment at all effective is the application of organophosphorous diazinon to the body and breach (see note 1 - variable resistance).

On the assumption that resistance is genetically based, we include "parent(s) with resistant gene(s)" on the envirogram as a first-order modifier of "chemicals". Strictly speaking this is incorrect, in the present generation the relevant gene is part of our subject animal and anything to do with a parent belongs on an envirogram at some time t, before the present. Uncontentiously, "man" as maker and user of these "chemicals" is also a first-order modifier. Finally, any enviromental factors which contribute to the dissipation of the chemical's potency over time will also be first-order modifiers - these will include, at least, "wind" and "rain". Note 8 records some current CSIRO research with chemicals.

12. Many authors note that rain causes a reduction in blowfly activity (see note 1). Kitching (pers. comm.) commented that heavy rain may act directly as a malentity for blowflies and may impair their flight ability. However, he added that the lack of reports of blowflies on the wing during rainy weather may also be an artefact of entomologists seeking shelter. Norris (1959) reports that blowflies use sheltered cavities behind "bark", or around "stones", for protection in stormy weather - both are first-order modifiers.

It is also frequently reported that wind depressed blowfly activity, particularly if strong (see also note 1). The modifiers reported by Norris clearly cover "wind" also and the inference that it is a a malentity seems justified. However, it was also commented in note 1, that a certain amount of wind (kinetic energy) is almost certainly beneficial to *L.cuprina*. So we propose that on this energy continuum, as with heat energy that there will be a certain range of kinetic energy (wind) which constitutes resources and that the complement of that range will constitutes malentities.

Also in note 1 there were comments concerning the effect of humidity ("moisture (in air)") on *L. cuprina*. Again it seems almost certain that there will be a beneficial range of humidities (resources) and a progressively debilitating range (malentities). In both cases, the modifiers will be those given in note 1.

Finally, the suggestions above have been that the objects concerned are direct malentities, but the objects also qualify as malentities for the following reason: all, at certain values (where applicable) are negative modifiers of "subject animal (activity)" in that they can prevent *L. cuprina* from foraging or mating etc. As the cause of such delays in the animal's 'working schedule' all, at the relevant values, satisfy the definition of a malentity.

13. A trap constitutes a malentity in the environment of an individual fly because it is an inanimate object which reduces the fly's life expectancy and possibility of producing offspring. The use of traps has declined in modern times, though at times in some areas traps have been widely used in an attempt to control blowflies - i.e., in general, not just *L. cuprina*. There has been considerable debate over the effectiveness of traps as an agent of control, though Mackerras (1936) demonstrated that a high intensity of traps (one per 100 acres) could reduce 'strike' by up to 50%.

Tillyard and Seddon (1933) give details of traps and records of phenomonally high catches (without specifying the species involved). Various baits are reported by various authors - the only point of real interest is that baits in the early stages of decomposition will attract primary flies (see note 20) like *L. cuprina*, while increasing percentages of secondary flies will be attracted as decomposition advances. Consequently, traps that are not cleaned and re-baited frequently may favour primary flies (*L. cuprina*) by reducing the damaging effects of secondary larval mediums (see note 20). The appearance of "traps" on the larva envirograms refers to this possibility.

"Bait", generally, is a first-order modifier of traps and the chemical 'Bromoform' which increases the attractiveness of (any) bait to *Lucilia* spp. will be a second-order modifier. Though man modifies all components of this chain we place him only at the end, as a third-order modifier.

"Other blowflies" accumulated in or around a trap and the activity of "larvae" resulting from oviposition on the bait will both tend to attract further flies and are thus first-order modifiers (Norris 1965).

Blowflies were attracted to dark coloured traps and repelled by light coloured ones under hot conditions, while the reverse was true under cool conditions (Norris 1965). Thus, "colour" as a first-order modifier and "heat energy" as a second-order modifier. These experimental results were foreshadowed by Tillyard and Seddon's earlier advice on the placement of traps: they argued that the shade given by "trees and shelter" (1st-order modifier) would be sought by flies in hot weather (2nd-order modifier) while open, sunlit spaces would be favoured when cooler (see note 1) - and that traps should be placed accordingly. In the latter (cooler case), the appropriate "heat energy" as a second-order modifier would remove "trees and shelter" from the envirogram.

In experiments in Canberra, it was found that of a line of traps the one most to windward would always catch more flies (Tillyard and Seddon 1983). Blowflies tend to move with the wind (see note 1) so presumably they tend to be attracted by the first trap they come across. Thus, "kinetic energy (wind)" as a first order modifier.

Tillyard and Seddon also note that all adult blowflies are attracted to light sources and they comment that this is important in the construction of traps. Although they do not give further details we have included "light energy" as a first order modifier.

Finally, Kitching (1981) shows that adult female *L. cuprina* at different stages of development show different propensities for being trapped. Given that most baits are made of protein of some sort, the catches in traps tend to be made up predominantely of protein motivated flies - i.e., young, post-teneral flies requiring protein to begin egg maturation and fully gravid flies seeking purulent flesh for oviposition. No comments are made regarding males but given that their protein consumption rises to an early peak and then dwindles it would seem likely that they would be trapped according to a similar pattern.

14. Kitching (pers. comm.) reports that adult *L. cuprina* take up "oxygen" (resource) through their tracheae. He suggests that as with other insects, consumption will be modified by activity ("subject animal (activity)" - 1st-order modifier) - i.e., not like other adult resources in that a search is needed but that activity itself requires oxygen. In turn the principal modifier of activity is "heat energy" (2nd order; see note 1).

L. cuprina larvae take up oxygen through pairs of spiracles, both anterior and posterior; the same modifiers apply. Tillyard and Seddon (1933) report that at times larvae drown (see note 19). It seems clear that lack of oxygen is the cause - thus "water" as a first-order modifier of oxgyen.

15. As a corollary to our comments in note 1 concerning the role of an independent moving organism's activity, a *L. cuprina* egg, not capable of independent movement, has its entire envirogram modified either by inanimate forces of nature or those in combination with the movement of the sheep upon which it was laid. In short, the entire envirogram is modified by the "oviposition site" chosen by its female parent.

The egg's first requirement or resource is a "substrate" to which it is anchored by a sticky secretion (1st-order modifier) exuded by the "female parent" (2nd-order modifier) at oviposition. The only other resources are sufficient heat energy and sufficient humidity to reach hatching.

We have found little information on egg temperature tolerances: Waterhouse (1947) found, in the laboratory, that eggs kept and hatched at 104°F gave stunted larvae and that at 100°F the larvae grew quickly upon hatching but none pupated. However, in a batch and fed for 3 days at 104°F and then removed to 75°F all pupated and produced adults. Clearly an egg's upper heat tolerance limit is higher than a larva's and given Waterhouse's first result we presume that it will be below 104°F. We have no information on the lower limit although as usual there will be a range of "heat energy" resources and a range of malentities. Waterhouse also gives the following information about the temperature conditions on sheep:

FLEECE TEMPERATURE:	Summer,	diffuse light	approx. 100°F
		bright sunlight	approx. 107°F
		highest recorded	approx. 114°.5 F
		wet fleece	approx. 50°F lower
	Winter,		approx. 80°F

SKIN TEMPERATURE: Variable but generally above 90°F

All the "heat energy" modifiers from the adult envirogram (and note 1) will be operative here also. Both sheep (figures above) and carrion (see note 18) have characteristic latent heat energy ("heat energy (substrate)") which will be a first-order modifier. In addition, we can see from Waterhouse's figures the importance of "moisture (on substrate)" which will also be a first-order modifier. Clearly an egg would be in difficulties in summer on a dry fleece on a sheep standing in bright sunlight. Finally, both "heat energy (substrate)" and "moisture (on substrate)" will be modified (2nd-order modifier) by oviposition site, and "moisture (on substrate)" will also be modified by the same modifiers as on the adult envirogram and in note 3.

Given the above it is not surprising that several authors note the importance of humidity ("moisture (in air)") for egg survival. Foster *et al* (1975) comment that for temperatures between 25-30°C any relative humidity above 70% produces no ill effects; however, outside this temperature range, humidities below 90% cause marked reductions in both development rates and hatching success. Thus "heat energy" is a first order modifier. Norris and other comment that such mass oviposition may benefit the species if humidities are unsuitable for egg survival as eggs near the centre of the mass may be protected from desiccation. Again, there will be a range of moisture (in air) resources, and malentities. "Other eggs" as modified by "female parent and other *L.cuprina* females" will be a first-order modifier - particularly of the malentities (as with the adult envirogram) the principal modifier of "moisture (in air)" will be "moisture (on substrate" which in turn will be modified by "oviposition site" and the other modifiers from the adult envirogram and note 3.

Tillyard and Seddon (1933) record the hatching time as 1-2 days except in very cold weather but Foster *et al* (1975) quote 8-12 hours. In simulated strikes with constant moistening the latter recorded a hatching level of 70.6% ± 7.4%.

16. There is considerably more information concerning the predators and parasites of *L. cuprina*'s immature stages than for adults, though various authors disagree on minor points.

Any known predator of any particular stage (i.e. EGG, LARVA, PUPA) will appear on the relevant envirogram though many factors will determine the likelihood of a particular individual being attacked. Most important of these is the oviposition site chosen by the female parent; many authors comment that virtually all blowfly predators use carrion as a 'cue' resulting in a steady build-up in the number of predators at a "carrion" site and their virtual absence from "living sheep" sites.

Clearly, oviposition site will be a first-order modifier for any predator - indeed oviposition site modifies every aspect of object on every immature stage envirogram (see also note 14). While all of *L. cuprina*'s immature stage predators are more successful on carrion we will show "carrion" as a modifier only for those predators not present on live sheep (Thus, if "carrion" does not appear the predator will attack immature stages on or from live sheep - albeit infrequently in most cases).

With the exception of the predacious secondary blowfly larvae and the very occasional Hymenopterous parasite all of the organisms mentioned below apply only when carrion is the site (Tillyard and Seddon, 1933):

Ants: Only *Iridomyrmex detectus*, the meat ant, is mentioned specifically but Tillyard and Seddon (1933) comment that the species is relatively rare in sheep areas. They add that the species prefers carcasses in bright sunlight, thus "light" is a first order modifier. Kitching (1981) refers to the ubiquitous, omnivorous ants and several authors comment that ants will attack both eggs and larvae. Waterhouse (1947) notes that ants make their main attacks (most attacks?) on larvae that are leaving or have left the carcass. Ants arrive at a carcass very early, often before *L. cuprina* - *Lucilia* spp. tend to be the first of the blowflies. (Fuller (1934) comments that a small brown ant, *Pheidole* sp. is seen occasionally on carrion but does not touch other insects - this raises the possibility that ants compete with *L. cuprina* larvae for food on carrion; thus "(ants)" are second-order modifiers of "carrion").

Beetles: Tillyard and Seddon (1933) comment that there tends to be a similar though less pronounced succession of beetles on carrion - they give the following table:

STAGE	FAMILY	SPECIES
1. Primary stage		
(a) Autolytic period	None	None
(b) Early bacterial period	STAPHYLINIDAE	*Creophilus erthyrocephalus* Fabr. (Red-headed devil's coach horse)
		Aleochara speculifera Er.
		Aleochara guerini Bern. & Sch.
		Homalota sordida Marsh
		Philonthus subcingulatus Macl.
		Philonthus nigritulus Grav.
		Philonthus politus Linn.
II. Secondary Stage	HISTERIDAE	*Saprinus cyaneus* Fabr.
		Saprinus australasiae Blkb.
		Saprinus sinae Marsh.
		Carcinops 14-striatus Steph.
		Gnathoncus ripicola Marsh.
III. Tertiary Stage	SILPHIDAE	*Ptomaphila lachrymosa* Schr.
		Choleva australis Er.
		Choleva sp. indet.
	CLERIDAE	*Necrobia rufipes* de Geer
	SCARABAEIDAE	*Onthophagus australis* Guer.
		Onthophagus nitidior Blkb.
	TROGIDAE	*Trox candidus* Harold
	CARABIDAE (predates on other beetles)	*Carenum* sp. indet.
		Phorticosomus sp. indet.
IV. QUARTERNARY STAGE	DERMESTIDAE	*Dermestes vulpinus* For.
		Dermestes cadaverinus Fabr.
		Trogoderma sp. indet.

Tillyard and Seddon regard only the primary and secondary beetles as relevant for *L. cuprina* but Fuller (1934) feels that the tertiary stage families Silphidae and Cleridae may occasionally be present in time to affect *L. cuprina*. Kitching (1981) also mentions the Silphidae. Except where disagreement is noted the order of arrival at the carcass is assumed to be down the table). Staphylinidae: includes rove beetles and devil's coach-horses. The large red devil's coach-horse, *C. erythrocephalus* predates both larvae and puparia of blowflies as do the larvae of the species. However, both adults and larvae will only attack *Chrysomyia* spp. when no primary, maggots or puparia, are present. Waterhouse (1947) comments that an adult of this genus (i.e. *Creophilus*) will consume 3 fully grown blowfly larvae per day. *C. erythrocephalus* is also recorded from offal heaps and piggery waste; if *L. cuprina* does not occur at such sites, which seems likely for piggery waste, then the availability of such sites would tend to reduce the predation of *L. cuprina* - thus "(piggery waste" is a first-order modifier. *Creophilus* spp. arrive at a carcass at about the same time as the primary blowfly *Calliphora augur* - i.e., a little after *L. cuprina*. (This may mean that for a time only *L. cuprina* larvae are available; as such this genus - perhaps family - will modify (2nd-order modifier) inter-specific compeition or a carcass; they will also modify primary intra-specific competition (see note 20) but not secondary intra-specific because of their distaste for *Chrysomyia* spp. *Creophilus* spp. are numerous in spring, abundant in summer, declining in number during autumn and absent by mid-winter; thus, the genus will always be active when *L. cuprina* is. Just as *Creophilus* spp. are becoming less active the smaller staphylinids *Philonthus politus*, *Aleochara haemorrhoidalis* (not on above table), and *Homalota sordida* are becoming more abundant. The first two named arrive at the carcass at about the same time as *Creophilus* spp. and predate eggs and young larvae. The last named appears very early at the carcass, about the same time as *Lucilia* spp. - no further details are given. Given that the smaller staphylinids are not present during the warmer parts of the year "heat energy" will be a first-order modifier.

Histeridae: Fuller (1934) comments that *Saprinus australasiae* and *S. cyaneus* are ecologically inseparable and that *S. sinae* and *Gnathomcus ripicola* probably have similar habits. Tillyard and Seddon (1933) consider that *Saprinus* spp. arrive at the carcass significantly after *Creophilus* spp. while Fuller (1934) reverses the order. Adults of the genus will attack both puparia and larvae of all blowfly species, though they prefer "puparia" (which are thus first order modifiers or the larva envirogram), and will only eat *Chrysomyia* spp. when no primary larvae or puparia, are available. Woodhouse (1947) reports that an adult of the genus will eat one fully grown blowfly larva per day. In fact the genus will predate any "non-blowfly soft grub, maggot or pupa" which are thus first-order modifiers. Fuller (1934) reports that the genus is found as often in "rotting vegetable matter" as in carrion so this too is a first-order modifier. *Saprinus* spp. larvae also predate blowfly puparia. Despite the disagreement about the timing of the histeridids arrival at the carcass it seems likely that they would effect blowfly larval competition in a way similar to the staphylinids. Also like *Creophilus* spp., *Saprinus* spp. are active at all times of year that *L. cuprina* is active.

Silphidae: *Ptomaphila lachrymosa* predates blowfly larvae. The species is numerous in spring and very common in summer though less so than *Creophilus* spp. and *Saprinus* spp. The species probably arrives at the carcass too late to be more than an occasional predator of *L. cuprina* so its effects on competition will be small. As *P. lachrymosa* is absent in the cooler months while *L. cuprina* is still active, "heat energy" is a first-order modifier.

Cleridae: *Necrobia rufipes* will not attack blowfly larvae or puparia under experimental conditions but it has been found to devour blowfly eggs. The species is present in spring and abundant in autumn; again "heat energy" will be a first-order modifier.

Hymenopterous parasites: Tillyard and Seddon (1933) give the following list:

None of the other Hymenopterous parasites native to Australia exercise any appreciable control of blowflies. The following is a complete list, arranged in the order of super-families and families:-

Super-family CHALCIDOIDEA:

Family CHALCIDIDAE:

1. *Brachymeria calliphorae* (Frogg.)
   (= *Chalcis calliphorae* Frogg.).
2. *Dirrhinus sarcophagae* Frogg.

Family ENCYRTIDAE:

3. *Tachinaephagus zealandicus* Ashmead
   (= *Stenoterys fulvoventralis* Dodd,
   = *Australencyrtus giraulti* J. & T.).

Family PTEROMALIDAE:

4. *Mormoniella vitripennis* Walk.
   (= *Nasonia brevicornis* G. & S.).
5. *Spalangia obenabooi* Girault
   (= *S. muscidarum* J. & B. nee Rich.).
6. *Pachycrepoideus dubius* G. & S.

Super-family PROCTOTRYPOIDEA:

Family DIAPRIIDAE

7. *Hemilexomyia abrupta* Dodd.
8. *Trichopria* sp. indet (possibly *T. quadrata* Dodd).
9. *Spilomicrus* sp. indet.
10. *Paraspilomicrus froggatti* J. & T.

Family BETHYLIDAE:

11. *Parasierola* sp. indet.

(Note - The introduced parasite *Alysia manducator* Panz., belonging to the family BRACONIDAE, is not included in the above list, as it is uncertain whether it has become established in Australia.)

Kitching (1981) confirms that *Alysia manducator* was never established in Australia. Tillyard & Seddon give almost no details concerning which blowfly species the above will attack. Many authors maintain that the pteromalid *M. vitripennis* is an occasional predator of *L. cuprina* (see below). Kitching (1981) and Fuller (1934) mention chalcids and *B. calliphorae* respectively so we presume that the family is known to attack *L. cuprina*. Fuller also comments that the only records for the family Diapriidae arefrom the Calliphoridae blowflies (this family includes *L. cuprina*) but adds that *H. abrupta* apparently attacks only *Calliphora stygia*. *M. vitripennis* visits the carcass early and waits for puparia to parasitize. This insect cannot burrow in "soil" (1st-order modifier) very well so it is most often successful against the sedentary and shallow puparia of the secondary flies *Chrysomyia rufifacies* and *Microcalliphora varipes*, and thus modifies secondary inter-specific competition on larval mediums. Tillyard and Seddon comment that the species may occasionally succeed against puparia from live sheep - perhaps it has adapted to *C. rufifacies'* habit of pupating in the wool of struck sheep. The same authors calculate that in total terms, at most 4% of blowfly puparia will be available for attack by *M. vitripennis*, though Waterhouse (1947) noted that between November and March two-thirds of all secondary puparia (*C. rufifacies* and *M. varipes*) were parasitized by the species. Tillyard and Seddon comment that puparia are immune from attack during two periods: the first day and the last two days of puparial life - eggs laid during these periods fail to prevent emergence. Fuller (1934) reports that *B. calliphorae* can burrow in soil well and that the species attacks maggots (larvae) - one parasite developing in each. This species in common at the end of summer and in autumn so if it attacks *L. cuprina*, "heat energy" will be a first-order modifier - because the latter is active at other times of the year.

Vertebrates: Fuller (1934) reports that Jew-lizards, *Amphibolurus barbatus*, were seen devouring blowfly larvae both on and wandering from a carcass. She adds that on two occasions magpies, *Gymnorhina tibicen*, have been observed siezing maggots wandering away from carcasses.

Blowfly larvae: This section should be read in conjunction with note 20. All of the blowfly larvae that predate the larvae of *L. cuprina* will also be competitors in one way or another, however the predacious larvae will also modify competition by reducing the numbers involved. Whenever the following appear on the envirogram as either predators or modifiers of competition they will in turn be modified by the same modifiers set out in note 20.

Easily the most important of the predacious blowfly larvae are the large and voracious larvae of *Chrysomyia rufifacies*. It is stronger than other maggots and has sharp, strong mouth-hooks which it uses in predating other maggots. On both carrion and living sheep it takes no notice of other maggots until it accidentally touches one when it quickly curls and bites - the prey struggles violently and occasionally escapes. However, if the escapee is punctured, other maggots (see below) will gather around and devour it. *C. rufifacies* larvae prefer a mixed diet of meat and other larvae but will develop satisfactorily on either alone. For the reasons given in note 20 *L. caprina* larvae will fare better against *C. rufifacies* on live sheep. It is not recorded whether *C. rufifacies* is cannibalistic but on the above information the species will be a modifier of both intra-specific and primary inter-specific competition. *C. micropogon* larvae are also recorded as predators of *L. cuprina* larvae and will modify competition in a similar way. Fuller (1934) reports that Froggat (1981) recorded the larvae of the secondary blowfly *Microcalliphora varipes* as predacious but that she was unable to verify this. She also reports that she was able to confirm Froggat's record that the larvae of the tertiary blowfly *Peronia rostrata* are occasionally predacious. The latter would only rarely be encountered by *L. cuprina* larvae.

All the above are included there because they do, or may, initiate predatory attacks on other larvae but in fact larvae of all blowfly species will engage in predatory bouts on injured larvae - usually following uncompleted attacks by "*C. rufifacies*" (first-order modifier). However, healty larvae will attack any dead, injured or debilitated individuals - Norris (1959) reports that *L. cuprina* larvae hatching on sheep, in adverse conditions will feed on eggs and less hardy individuals until they attain second instar and are vigorous enough to attack the living tissue. Thus, any "malentity(s)" which is sufficiently injurious or any "predator(s)" which damages but fails to kill a larvae will be a first-order modifier of all blowfly larvae as predators. In addition, hot ("heat energy") dry ("moisture (in air)" conditions will modify larvae as predators of eggs. In *L. cuprina's* case, predation of eggs by larvae will usually be by siblings or others of the species as modified by the tendency of "other female *L. cuprina*" to oviposit together (see note 15), though occasionally other primary larvae may be involved.

17. The removal of carcasses by "man" makes man a first-order modifier of the oviposition site "carrion". Generally more important though is the effect that man's activities have on the larval environment.

Carcasses in sheep-grazing areas are invariably flyblown when found; and, given that *L. cuprina* is the earliest blowfly visitor to larval media the timing of any treatment will be paramount in determining any effect on our subject species:

The burning of a carcass while it is occupied by *L. cuprina* eggs and larvae will kill those individuals ("fire" as a malentity on both envirograms). However, it is more likely that by the time a carcass is discovered most of the primary larvae (inc. *L. cuprina*) will have developed and departed. In this event the burning of the carcass will favour *L. cuprina* by killing the secondary larvae still present and resulting in decreased secondary inter-specific competition for later generations (see note 20).

Another tactic, carcass burial, is more directly favourable to *L. cuprina*. Any larvae present will continue to develop and are able to pupate deep in compact soil and emerge without suffering ill-effects (see note 22). Even better, later blowfly visitors will not be able to oviposit on the carcass so again secondary inter-specific competition will be decreased, though this time for the present generation. In addition, larval predators will not be able to 'cue' onto the carcass (see note 16). Tillyard and Seddon (1934) report:

The following are the results of some experiments carried out on the burial of carcasses at Canberra by Miss M. Fuller (1932b):-

Experiment 1. In October, the carcass of a sheep was divided into halves, each weighing 15lb. One half was left exposed to ordinary blowfly attack for two days, then placed in a clean oil-drum in the insectary, and buried under 2 feet of fairly loose soil. The other half was left exposed for five days, and then placed in a similar drum in the insectary but not buried. The flies which emerged from each half were counted and classified, with the following result:-

	Primary Flies				Percentage of Primary Flies	Secondary & Tertiary Flies		
	C. stygia	*C. augur*	*L. sericata*	*L. cuprina*		*Ch. rufifacies*	*M. varipes*	*P. rostrata*
					%			
Buried	5,667	1,323	234	16	100	Nil	Nil	Nil
Unburied	816	1,698	35	Nil	70	222	189	604

This experiment demonstrates the effect of competition and burial on the primary maggots.

Experiment 2. Two cats were killed and left exposed for two days. The carcass of one cat was then buried, while the other was simply brought into the insectary, and left unburied. The flies which emerged from each were collected and classified, with the following results:

	Primary Flies		Percentage of Primary Flies	Secondary Flies
	C. augur	*L. sericata*		*Ch. rufifaries*
			%	
Buried	5,270	106	99	29
Unburied	5,443	108	85	1,072

From this experiment we conclude that burial greatly interferes with the emergence of the secondary flies.

Experiment 3. In February, two cats were killed and exposed for two days. One of these was thoroughly poisoned by using the solution of arsenic recommended by W.W. Freggatt (see below); the other was left unpoisoned. Both carcasses were buried in the insectary cubicles at the end of the second day, and the flies which emerged from them caught and classified, with the following results:

	Poisoned Cat	Unpoisoned Cat
Total number of flies	Nil	6,300 (all except 71 flies were primaries)

However, unlike fire, burial will at least remove a protein site - thus affecting adults in a number of ways.

The most effective, though still not ideal, tactic is to poison the carcass. This will kill *L. cuprina* eggs and larvae (like fire) and has the added advantage of killing feeding adults - i.e., "chemical" as malentities for egg, larva and adult - see also note 11. But again primary flies are likely to be less affected than secondary ones and the result will, like fire, modify secondary inter-specific competition for later generations.

"Carrion" will be a first-order modifier for all the malentities mentioned. "Soil" as modified by "man" (i.e., carcass burial) will modify secondary inter-specific compeition on the larva envirogram, while the effect of fire and chemicals on future competition would be shown on envirograms drawn for the secondary competitors.

18. *L. cuprina* larvae like the adults of the species are capable of independent movement (the parallel comments at the beginning of note 1 apply here also). However, because of their limited mobility their envirogram like that of the egg of the species, will be modified in most respects by the oviposition site chosen by their female parent. Thus, "subject animal (activity)" will modify (1st-order) most resources and in turn will be modified, or constrained, by "oviposition site" (2nd-order) and all the attendant modifiers from note 3 and the adult envirogram.

The following are the results of some experiments carried out on the burial of carcasses at Canberra by Miss M. Fuller (1932b):-

Experiment 1. In October, the carcass of a sheep was divided into halves, each weighing 15lb. One half was left exposed to ordinary blowfly attack for two days, then placed in a clean oil-drum in the insectary, and buried under 2 feet of fairly loose soil. The other half was left exposed for five days, and then placed in a similar drum in the insectary but not buried. The flies which emerged from each half were counted and classified, with the following result:-

	Primary Flies				Percentage of Primary Flies	Secondary & Tertiary Fl		
	C. stygia	*C. augur*	*L. sericata*	*L. cuprina*		*Ch. rufifacies*	*M. varipes*	*P. rostr*
					%			
Buried	5,667	1,323	234	16	100	Nil	Nil	Ni
Unburied	816	1,698	35	Nil	70	222	189	60

This experiment demonstrates the effect of competition and burial on the primary maggots.

Experiment 2. Two cats were killed and left exposed for two days. The carcass of one cat was then buried, while the other was simply brought into the insectary, and left unburied. The flies which emerged from each were collected and classified, with the following results:

	Primary Flies		Percentage of Primary Flies	Secondary Flies
	C. augur	*L. sericata*		*Ch. rufifaries*
			%	
Buried	5,270	106	99	29
Unburied	5,443	108	85	1,072

From this experiment we conclude that burial greatly interferes with the emergence of the secondary flies.

Growth rates and activity are primarily dependant on temperature ("heat energy" - 2nd-order). Other second-order modifiers will include "moisture (in air)" (see note 21) and "light energy". Tillyard and Seddon (1933) report that all blowfly larvae are strongly repelled by light - it seems highly likely that this response is connected with eitehr or both heat energy and humidity but lacking details we include it provisionally as a second-order modifier. It is also noted that most larvae, when preparing to pupate, will leave the medium at night.

Most of Waterhouse (1947) concerns temperature conditions during larval development. Again, we will see the characteristic division of heat energies into resources and malentities and the same modifiers will apply to the two just mentioned and "heat energy" as a modifier of activity. All the modifiers from notes 1 and 6, and the adult envirogram will again apply with the addition, as for the egg, of "heat energy (substrate)" as a modifier of the next highest order. This in turn, because of the different thermal characteristics of (i) carrion and (ii) live sheep, will be modified by "oviposition site".

(i) carrion: Waterhouse gives the following graph as typical carcass temperature curve. The body temperature of the animal will fall to near ambient soon after death. Within 2 days, the development of larvae begins slowly, causing the temperature to rise - the process is self-accelerating; as the temperature rises larval development becomes more rapid and activity far greater - this results in further heat production and equilibrium is soon reached between air and carcass temperature. Later the same author adds that while the mechanism has not been investigated there is good evidence that larvae produce the high temperatures - although bacteria probably play a part - thus we include "larvae" and "bacteria" as modifiers of "heat energy (substrate)". In summer, the maximum carcass temperature recorded was 121.5°F and a daily average of 115°F was recorded more than once. At temperatures like this many larvae both fully grown and immature would leave the carcass - some would find their way back onto cooler portions but the majority perished. It was noticed that primary larvae were the first to leave the carcass under such circumstances and it has been shown in England that the order of resistance of prepupae and pupae (of English blowflies) to high temperature is correlated negatively with the order of seasonal succession. If the same holds true in Australia then *L. cuprina* will be the fly most affected by high temperature. On a carcass, all larvae but the first few to develop will be exposed to these high temperatures - but the favoured few would most often be *L. cuprina*.

(ii) live sheep: Some details concerning the temperature conditions on live, healthy (i.e. unstruck) sheep have been given in note 15. During the course of a strike as the area of skin becomes progressively inflamed and exudation begins the skin temperature of the sheep will rise to about 5-10°F above normal after 24 hours - i.e. about 95-100°; and then progressively as follows:

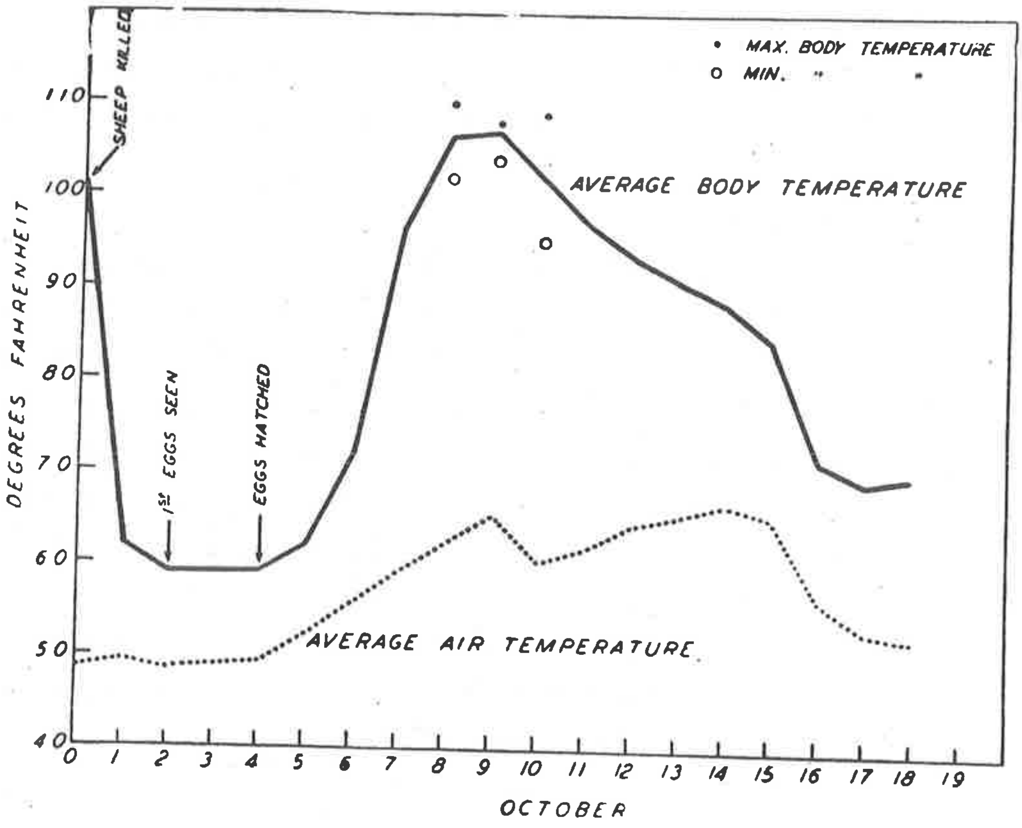


FIG. 1.—Graph showing the body temperature of a dead sheep infested with blowfly larvae and the air temperature over the same period.

after 48 hours, skin temperature about 7-13°F above normal,
i.e., 97-103°F; rectal temperature about
102-106°F
after 72 hours, skin about 102-105°F
rectal about 106-108°F

Once skin temperature has risen above 100°F primary larvae begin to show a tendency to leave the skin - however, unlike a carcass they can usually find a cooler place in the fleece where they can feed among the exudate matted fibres - thus "wool" as a modifier of "heat energy (substrate)". It is suggested that the 5-10°F cooler conditions encountered in a typical strike and available retreats in the wool are important factors which contribute to *L. cuprina*'s greater success on live sheep larval mediums.

There are several theories about how elevated temperatures affect blowfly larvae. Waterhouse (1947) gives details.

Finally, several authors comment on English work which showed that an animal that dies because of strike and thus provides a 'myiasis carcass' seems to favour the species causing the myiasis. It is suggested that the temperature trend of such a carcass will follow a different (and more favourable) course from that of an animal dying from other causes. Thus, such carcasses may produce more *L. cuprina* than is usual from carrion.

19. Clearly, the principal food for *L. cuprina* larvae is "protein (in animal tissue)" whether from the copious, protein rich, serous exudate from ulcerated skin in struck sheep or the liquids in dead and decaying flesh. However, Tillyard and Seddon (1933) report cases where larvae on live sheep can live in the wool away from the skin or on substances on the surface of the skin (i.e., strike need not occur); there are also the more unusual oviposition sites mentioned in note 3 - but we have found no details regarding larval nutrition except on animal tissue in the conditions mentioned above. Irrespective of the larval medium the oviposition site chosen by the female parent will be a first-order modifier; because of important differences that will become clear we resolve oviposition site into the twin first-order modifiers "carrion" and "living sheep". As on the adult envirogram (cf. note 3) we can show *L. cuprina*'s preference for living sheep by making

"living sheep" (2nd-order modifier) a modifier of "carrion" - if the former is present the latter drops off the envirogram. Unless otherwise stated modifiers mentioned below will modify both "carrion" and "living sheep".

Digestive fluids in the larva's gut break down the imbibed liquid and finely titurated particles of fat, protein and fibrous tissue; Tillyard and Seddon (1933) suggest that the same fluids, voided in the excreta, may help to liquify tissue for later consumption - thus, "digestive fluids (in excreta)" as a second-order modifier. "Bacteria" (2nd-order) also probably play a part in liquifying food; the same authors suggest that "bacteria" (1st-order) when ingested, may be important in supplying "vitamins".

The second last paragraph of note 16 records the conditions under which blowfly larvae, not normally predacious, will attack other blowfly larvae. Under the same circumstances (i.e., the same modifiers) "other blowfly larvae" will appear on the envirogram as a food resource.

Shanahan (1965) comments that, after hatching, larvae will normally feed for about 4 or 5 days before deserting the medium to pupate. Given that growth rates are heat dependent (see note 18), a unit-time-degrees measurement would be more satisfactory. The amount of time a *L. cuprina* larva will spend feeding will depend on the temperature conditions on the medium (see note 18), whether the medium remains nutritionally suitable (below) and whether or not competition with other blowfly larvae drives our subject larva from the medium (see note 20).

The conditions affecting the nutritional suitability of "carrion" are, principally, ambient temperature ("ambient heat energy") and humidity ("ambient moisture (in air)") - both second-order modifiers. The following quotation comes from Fuller (1934):

> "It has been observed that extremely high humidity, along with high temperatures in summer, may render a carcass unavailable to some blowflies. A dead cat was noticed to liquefy and putrefy overnight and it did not harbour maggots of the blowflies present at that time. On the other hand, when the temperature is high, and the humidity very low, the carcass loses moisture too

> rapidly, and much of the food becomes unavailable to larvae, thus greatly intensifying competition and causing a higher larval mortality. I.M. Mackerras has observed a much more extreme condition, in the far western districts of Queensland, the intense dryness of summer producing an effect somewhat comparable with mid-winter conditions in Canberra. The carcass becomes so desiccated that it is practically unavailable as food for maggots. The result is that flies are scanty and are not prolific owing to the lack of protein foods, so that the larval food which is available is not overcrowded and there is no competition".

It should be noted that any effect of high temperature which shortens the duration of the suitability of a carcass will be offset to an extent by the increased activity and growth rates of the larvae. In addition, Tillyard and Seddon (1933) note that in cold weather (still "ambient heat energy") larvae may cease to feed and/or that the carcass may fail to reach the secondary, liquifying stage of decomposition (i.e. mummification). A carcass that becomes too dry, whether by high or low temperatures, can be restored to a suitable state by "water (rain)" (3rd-order). However, Waterhouse (1947) reports that rain (1st-order) can reduce the food supply by leaching juices from the carcass. He adds that heavy rain will wash larvae out of a carcass and that large numbers will drown - thus "water (rain)" as a malentity modified (1st-order) by "kinetic energy (rain)"; carcasses sheltered by "trees etc." (2nd-order) would tend to be protected from this. Finally, both ambient temperature and humidity will be modified by the factors discussed in notes 1 and 3 (and on the adult envirogram). All of the above will also modify the nutritional suitability of "live sheep" though to a much lesser extent: it is true that the larvae have, in addition, to contend with the self-heating powers of the sheep (whatever they may be) but this is more than offset by the more controlled and continuously available protein and moisture from the myiasis wound.

There is a direct relationship running from the amount of food a larva can ingest through puparial weight and adult female size to fecundity (see note 7). The following figure is from Norris (1959):

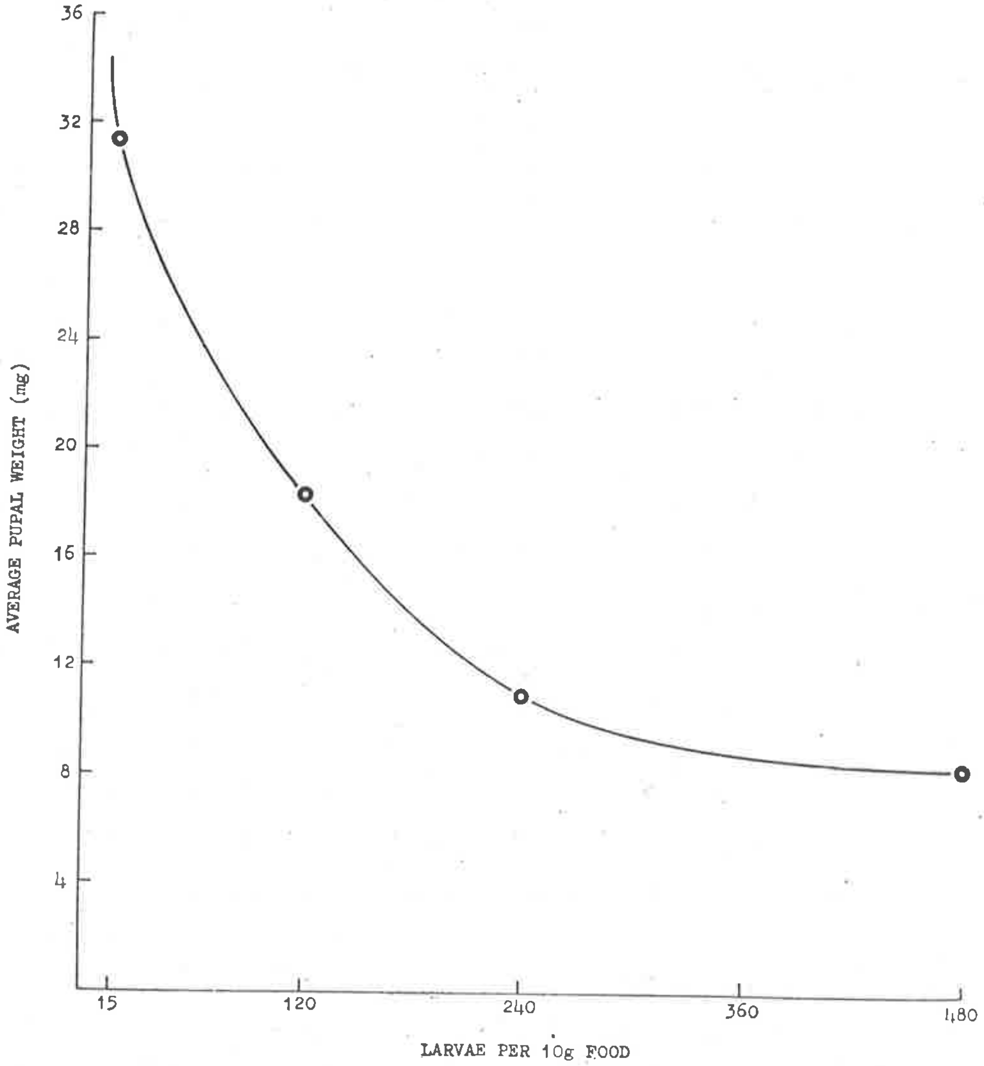


Fig. 3. Relation between puparial weight of *Lucilia cuprina* and the amount of food provided per larva (after WEBBER (1955)).

20. From the literature we have seen we have compiled the following list of Australian blowfly fauna:

PRIMARY FLIES: *Lucilia cuprina* (Wiedemann)
L. sericata (Meigen)
Calliphora stygia (Fabricius)
C. australis (Boisduval)
(= *C. albifrontalis* (Malloch))
C. fallax (Hardy)
C. augur (Fabricius)
C. nociva (Hardy)
C. vicina (Robineau-Desvoidy)
(= *C. erythrocephala* (Meigen))
C. tibialis (Macquart)
SECONDARY FLIES: *Chrysomyia rufifacies* (Macquart)
Ch. micropogon (Bigot)
Microcalliphora varipes (Macquart)
Sarcophaga froggati (Taylor)
S. hardyi (J & T)
S. misera (Walker)
TERTIARY FLIES: *Peronia rostrata* (Robineau-Desvoidy)
Musca hilli (Johnston and Bancroft)
(= *Biomyia hilli*)
M. domestica (Linneaeus)
Fannia australis (Malloch)
Muscina stabulans (Fallén)
Ophyra nigra (Macquart)
Piophila casei
Onesia accepta
(Tillyard and Seddon (1933); Norris (1959) and Fuller (1934)).

Most of the above are recorded from both sheep myiasis and carrion. The three groupings are based on the stage of putrefaction or decomposition (changing odours) that will attract females of the various species to oviposit on carrion or sheep. A primary fly is one that can initiate strike on an unaffected sheep and/or that will oviposit on a carcass before bacterial action has begun liquifying softer tissues. Secondary flies require the conditions set up by primary larvae before they will oviposit on sheep while they will utilize carrion at about the time the softer tissues are liquifying, whether or not primary flies have preceded them. It is still possible for primary flies to oviposit at these later stages. Tertiary flies will come still later. Because of these different oviposition times there tends to be a succession of species occupying both a developing myiasis and a decomposing carcass. Several authors comment that succession is similar on both sheep and carrion - the major difference being that on sheep, owing to healing action, the process may be delayed in a particular stage or reversed to earlier stages so that, for example, it would be possible (occasionally) for primary flies to follow secondary flies (i.e. after initiating myiasis for them in the first place). At any particular stage the larvae present on the medium will be in competition for the available food resources - formall only their presence and dietry overlap is required even if the resources are super abundant but in fact we have found no recorded case of a carcass not being overcrowded and while competition is less intense on live sheep again no non-competition case is recorded.

For *L. cuprina* larvae we can divide this competition into three major (i) - (iii) and one minor section (iv).

(i) Intra-specific competition - i.e. with the larvae of other primary flies.

(ii) Primary inter-specific competition - i.e. with the larvae of other primary flies.

(iii) Secondary inter-specific - i.e. with secondary larvae.

(iv) Tertiary inter-specific - i.e. with tertiary larvae. (This will occur only rarely given the length of a larval period and the time taken from a medium to become suitable for tertiary oviposition). No further notes are given.

(i) Intra-specific. This forms of competition will always occur even if only between siblings but the tendency for *L. cuprina* females to oviposit together (see note 3) will intensify the competition - thus "other *L. cuprina* larvae" as a second-order modifier and "other laying *L. cuprina* females" as a third-order. The general effect is to reduce the size of resulting pupae (and hence adult size and fecundity - see note 7), however, as numbers per unit of medium increase the resultant number of pupae and adults will fall - i.e., not just a percentage increase in mortality with approximately equal numbers surviving. This type of competition occurs equally on sheep and carrion but its effects will tend to be masked by the other types of competition.

(ii) Primary Inter-specific. This competition with "other primary larvae" is effectively an intensification of intra-specific competition - the same comments (above) regarding size and numbers apply, but generally relatively high numbers of undersized flies will be produced. Fuller (1934) conducted experiments where she placed equal numbers (i.e. 500) of larvae from several primary species on carrion and took percentage emergence of adults as a measure of competitive success. She gives the following table:

Number	*C. augur*	*L. sericata*	*L. cuprina*	*Ch. rufifacies*
	%	%	%	
1	89	56	56	Absent
2	58	57	31	Present
3	100	99	72	Absent
4	Absent	89	45	Present

Clearly, *L. cuprina* was least successful, behind *C. augur* and *L. sericata*. As usual whenever an animal appears on an envirogram the whole of that animal's envirogram will also appear, beginning with the centrum as modifiers of the next highest order. In the present case the whole of a primary fly's envirogram will determine the extent to which it comes into competition with *L. cuprina*. However, with *C. augur* and *L. sericata* we can highlight several points which we know to be of direct consequence. Firstly, we know that different species tend to oviposit on larval mediums at different times and we know that *L. cuprina* tends to be the earliest. As already noted several authors regard this as a function of the specific odours of decomposition that a species finds most attractive - thus "odour" as a third-order modifier, modified in turn by the factors on the adult envirogram and discussed in notes 1 and 7 (though applying to different species). For *C. augur*, its later oviposition time will be offset by the fact that it larviposits (i.e. no delay for hatching). The general effect here is that at least some of the *L. cuprina* larvae will be older, stronger and better able to withstand competition (Fuller apparently used larvae of equal age). Secondly, it is likely that the various primary flies will have differing geographical and seasonal distributions and any environmental factors which modify one species' distribution but not anothers will modify competition. We know that *L. sericata* and *L. cuprina* have different geographical distributions (see introductory note, p. 1) but we have not been able to find out why. Norris (1959) comments that *C. augur* is concentrated in the South-East quadrant of Australia and does not occur in the west so it appears that this species also has a narrower distribution than *L. cuprina* though again we do not know why. However, we can mask our ignorance by making "distribution factors" a third-order modifier of the competition under discussion. As for seasonal distribution Fuller's (1934) results (see note 1) have *Lucilia* spp. and *C. augur* with the same pupal dormancy temperature - i.e. 15°C. However, remarks by Tillyard and Seddon (1933) (see note 22) indicate that there will be an upper temperature above which pupae will also remain dormant. Thus, in general, "heat energy (in soil)" will modify primary inter-specific competition. Thirdly, we know of *C. augur* that it is the only primary blowfly to utilize non-animal based oviposition sites and also a greater variety of animal sites: Fuller (1934) records dead *Oncopera* sp. (Hepialidae) larvae, sour milk and fermenting grain while Norris (1959) records earthworms, snails, (both dead), other dead invertebrates and the head and nostril cavities of a living brown hawk (*Falco berigora* (Vigors and Horsfield). Thus we can show "other oviposition sites" as a modifier (3rd-order) of *C. augur* because with the availability of such sites the species is less likely to come into competition with *L. cuprina*. Clearly, there will be a multitude of other factors from the envirograms of each primary species which will affect competition.

Primary inter-specific competition is much less disadvantageous to *L. cuprina* on sheep than on carrion: firstly, because the general conditions are more favourable to the species (see, for example, note 18); and, secondly, because *L. cuprina* utilizes living sheep as an oviposition site earlier and to a much greater extent than other species - Norris (1959) reports that *C. stygia* participates in less than 10% of strikes though a slightly higher percentage of those initiated by *L. cuprina* and of 26 strikes examined by Waterhouse (1947), 16 produced only *L. cuprina* adults and the results of the other 10 are given on the following table:

Species	Month Strike Commenced									
	November					December		April		
L. cuprina	1,692	37	217	433	398	4,343	398	9,704	2,683	974
L. sericata						44				
C. stygia	31	157	11			168		573	658	448
C. augur	13	87	72	165	156	3	156		2	12
Ch. rufifacies						31				
P. rostrata						301			4	1
M. domestica								203		
Total	1,736	281	300	598	554	4,890*	554	10,480*	3,347	1,435

* These sheep died

One of the 10 involve secondary larval and 4 involve tertiary but clearly the competition (if any) was intra-specific and primary inter-specific and the success of *L. cuprina* is obvious. It is worth noting that the all of the *L. cuprina* only strikes occurred either in November and earlier or in March and later. This probably reflects the spring build up and autumn decline in the general blowfly population when because of numbers there will be less demand for oviposition sites - all of the mixed strikes occurred during the period when the general blowfly population is at its highest and is further evidence for including "heat energy (in soil)" as a third-order modifier of competition.

Despite the differences in primary inter-specific competition on sheep and carrion the modifiers of both will be precisely the same - only quantification if determined would be difficult.

(iii) Secondary inter-specific. Of the "secondary larvae" that compete with *L. cuprina*, "*C. rufifacies*" is easily the most important. Note 15 records their predation of *L. cuprina* larvae and that in consequence they modify the above (i.e. (i) and (ii) types of competition. In that context, they remove larvae whose dietary overlap with our subject individual is 100% while they, the predacious secondary larvae, gain at least a percentage of their nutritional requirement from other larvae. Thus for a given number of larvae the more of that number that are secondary the greater the amount of food available for our individual *L. cuprina* larvae. Of course, the chance of our subject being eaten will increase with the percentage of secondary larvae - but there will be a level which optimally balances the pros and cons. A consequence is that, on carrion, where the combined effects of conditions (see note 18), predators (see note 16) and all competition are most severe, if any *L. cuprina* survive then they tend to be close to the maximum size for the species. In addition to predating *L. cuprina* and competing for its food Tillyard and Seddon (1933) and Fuller (1934) both report that *C. rufifacies* larvae jostle and harrass primary larvae to an extent that their very presence seems to repel the primary larvae and drive them from the medium even while food and space are still available. However, this effect may be associated with temperature - see note 18. Whatever the reasons, at best these deserting larvae will produce stunted adults - otherwise they will perish.

Again all the factors mentioned in section (ii): heat energy, odour, distribution factors and other oviposition sites will modify secondary inter-specific competition for *L. cuprina*. Again, for the same reasons *L. cuprina* will be more successful on sheep than on carrion though the modifiers will be the same. One factor that applies specifically to *C. rufifacies* is that it shows a very strong preference for oviposition sites sheltered from the sun so, for example, if it uses a carcass in the open then it will utilize the deepest available hollows - say, between the hind legs. Thus "light energy" would modify (3rd-order) *L. cuprina* - *C. rufifacies* competition. In commenting on secondary inter-specific competition on live sheep Waterhouse (1947) notes that secondary larvae only attack a proportion of struck sheep (Norris (1959) gives 8% for *C. rufifacies*) and that this is usually only after the first generation of primary larvae have departed - it seems that the natural resistance of the sheep delays the reaching of the appropriate stage of decomposition and odour.

Fuller (1934) notes that the size of a carcass will have no effect on the extent of overcrowding and suggests that a carcass's odour will be proportional to its size and that the number of flies attracted to it will be proportional to its odour. Consistent with this she adds that a small carcass in the vicinity of a larger one will be massively overcrowded - thus "larger nearby carcass" as a modifier of all competition.

Finally, the above in conjunction with notes 16 and 18 justifies Waterhouse's (1947) comment that carrion as a larval medium will produce very few adult *L. cuprina* and held to key to why *L. cuprina* in Australia has evolved further down the road towards obligate parasitism on the sheep.

21. Blowfly larvae are particularly susceptible to desiccation so that again we will have a range of humidities ("moisture (in air)") that constitute resources and a range that constitute malentities. Shanahan (1965) suggests that the characteristic gregarious colonies of larvae ("other larvae" - 1st order) modify humidity - at least in the microclimate. All other modifiers will be as for adult oviposition sites - envirogram and note 7.

Fuller (1934) reports that dryness will cause larvae to stop feeding and enter a diapause, or, if excessive to shrivel and die - thus "moisture (in air)" is also a first order modifier of food. She adds that the effect of excessive humidity is to cause 'patching' and other "bacterial diseases" - "moisture (in air)" as first-order modifier of a predator.

22. The pupal sub-system begins when a prepupa (late third instar larva) leaves the larval medium to enter the soil. Metamorphosis into a puparium in which the pupa develops, will follow and in due course an adult will emerge.

The first essential resource is a suitable "pupation site". Many factors, all first-order modifiers, will determine the suitability of a site: Temperatures ("heat energy (in soil)") below 10°C inhibit pupation as the prepupa will go into hibernation until conditions become more fabourable and it has been suggested that high temperatures by destroying an essential hormone, may prevent pupation altogether. Foster *et al* (1975) also suggest that high humidity ("moisture (in soil)") will inhibit pupation and Tillyard and Seddon (1933) make the same suggestion for low humidities. Clearly, "water (rain)" will be a second-order modifier; Norris (1965) reports that prepupa of several British species may surface if soil becomes waterlogged and seek dry pupation sites. The "substrate" will also be a second-order modifier of both "heat energy (in soil" and "moisture (in soil)" - soil quality and permiability, in particular, will be operative factors. In addition, the "substrate" will be a first-order modifier of "pupation site" - for example, if the substrate is rock the distance to travel before pupation can occur will be increased.

L. cuprina normally pupates some distance from the larval medium (see also note 16) so, invariably, a search of some duration is involved. The prepupa's activity, and the associated modifiers will be analogous to those for feeding larvae - see note 18; and "subject animal (activity will modify "pupation site". The actual "heat energy" experienced by the animal, as modified by "heat energy (in soil)" will be the primary determinants of activity - in addition to the factors discussed above which favour hibernation (see also note 1 for emergence temperatures). Tillyard and Seddon (1933) comment that larvae that have lived in a very putrid medium are apparently affected by the "gases of putrefaction" in such a way that pupation is prevented for a considerable time; the gases will thus modify activity. The actual distance that *L. cuprina* moves before pupating is not estimated but a figure of 10 feet is frequently cited as being common for blowflies while Norris (1965) reports that *L. sericata* will move up to 21 feet away from a carcass before pupating. Smit (1931), in South Africa, reports that the same species will pupate up to 6 feet (depth) in the earth and that flies could emerge from as much as 3½ feet down without damage. Foster *et al* (1975) report a mean pupation depth of 1.5 centimetres.

In addition to the above roles and as with earlier stages both "heat energy" and "moisture (in air)" will yield ranges of resources and complementary ranges of malentities - both high and low temperatures and dryness can cause pupae to die. The waterlogging of soil which may also kill pupae lies at the other end of the "moisture (in soil)" range.

Pupal development rates increase linearly with temperature: at 15°C development will take 25 days and at 30°C only 6 days - the survival rate across this range was 94.6 ± 1.3%. (Foster *et al* (1975)). Consistent with these figures Kitching (1974) reports that in summer, when conditions cuasing hibernation are unlikely to occur, pupae will last as little as 1-2 weeks. Waterhouse (1947) found that in ideal uncrowded conditions at 75 F, 100% of *L. cuprina* larvae managed to pupate while between 95 - 100% survived to emerge successfully. However, the averages from all the field experiments conducted were 79% pupation and 45% emergence. The conclusion that there is excessive mortality in the pupal sub-system (at least for larvae from carrion) is supported from other quarters but we have found no adequate delineation of the causes.

E REFERENCES

Cragg, J.B. (1955) . The natural history of sheep blowflies in Britain. *Ann. Appl. Biol.* 42, 197-207.

C.S.I.R.O. (1973). *The Insects of Australia.* (Melbourne University Press).

Foster, G.G., R.L. Kitching, W. Vogt and M.J. Whitten (1975). Sheep blowfly and its control in the pastoral ecosystem of Australia. *Proc. Ecol. Soc. Aust.* 9, 213-229.

Fuller, M.E. (1932). Notes on the effect of carcass burial on blowflies. *Jour. Coun. Sci. Ind. Res. (Aust)* 5, 162.

Fuller, M.E. (1934). The insect inhabitants of carrion: a study in animal ecology. *Bull. Coun. Scient. Indust. Res. Aust.* No. 82.

Gilmour, D., D.F. Waterhouse and G.A. McIntyre (1946). An account of experiments undertaken to determine the natural population density of the sheep blowfly, *Lucilia cuprina* (Wied.). *Bull. Coun. Scient. Indust. Res. Aust.* No. 195.

Holdaway, F.G. (1932). Fly strike of sheep a natural phenomenon. (Unpublished).

Kitching, R.L. (1974). Controlling sheep blowfly. *Aust. Nat. Hist.* 18, 122-127.

Kitching, R.L. (1977). Time, resources and population dynamics in insects. *Aust. J. Ecol.* 2, 31-42.

Kitching, R.L. (1981). A resource-limited specialist species. Chap. 10 in *The Ecology of Pests: Some Australian Case Histories*, Eds., R.L. Kitching and R.E. Jones (C.S.I.R.O. Australia, Melbourne), 193-214.

Kitching, R.L. and J.A. Roberts (1975). Laboratory observations on the teneral period in sheep blowflies, *Lucilia cuprina.* (Diptera: Calliphoridae). *Entomol. Exp. Appl.* 18, 220-225.

Mackerras, I.M. (1936). The sheep blowfly problem in Australia: results of some recent investigations. *Pamph. Coun. Scient. Indust. Res. Aust.* No. 66.

Morley, F.H.W., A.D. Donald, J.R. Donnelly, A. Axelson and P.J. Walker (1976). Blowfly strike in the breech region of sheep in relation to helminth infection. *Aust. Vet. J.* 52, 325-9.

Norris, K.R. (1957). A method of marking Calliphoridae (Diptera) during emergence from the puparium. *Nature* (Long.) 180, 1002.

Norris, K.R. (1959). The ecology of sheep blowflies in Australia. In *Biogeography and Ecology in Australia*. Eds. A. Keast, R.L. Crocker and C.S. Christian (Junk: The Hague) 514-544.

Norris, K.R. (1965). The bionomics of blowflies. *Annu. Rev. Entomol.* 10, 47-68.

Roberts, J.A. and R.L. Kitching (1974). Ingestion of sugar, protein and water by adult *Lucilia cuprina* (Wied.) (Diptera: Calliphoridae). *Bull Entomol. Res.* 64, 81-88.

Shanahan, G.J. (1965). A review of the flystrike problem in Australia. *J. Aust. Inst. Agric. Sci.* 31, 11-24.

Smit, B. (1931). A study of the sheep blowflies of South Africa. *Rep. Div. Vet. Serv. Anim. Ind. Onderstepoort* 17, 299-421.

Tillyard, R.J. and H.R. Seddon (Eds. (1933). The sheep blowfly problem in Australia. Report No. 1 of the Joint Blowfly Committee. *Pamph. Coun. Scient. Indust. Res. Aust.* No. 37.

Vogt, W.G., T.L. Woodburn and M. Tyndale-Biscoe (1974). A method of age determination in *Lucilia cuprina* (Wied.) (Diptera: Calliphoridae) using cyclic changes in the female reproductive system. *Bull. Entomol. Res.* 64, 365-370.

Waterhouse, D.F. (1947). The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly, *Lucilia cuprina*. *Bull. Coun. Scient. Indust. Res. Aust.* No. 217.

Woodburn, T.L., W.G. Vogt and R.L. Kitching (1978). Estimation of age of females in field populations of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) using ambient temperature and solar radiation. *Bull Entomol. Res.* 68, 251-261.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XIX THE MONARCH BUTTERFLY *(Danaus plexippus)*

by

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ABSTRACT

The precise environment of the Monarch Butterfly *(Danaus plexippus)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * * *

A general introduction to the whole series of reports on the precise enviornment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A. INTRODUCTORY NOTE

Danaus plexippus is known by the common names of Monarch, Wanderer and more rarely, 'the black-veined brown butterfly'. *Danaus plexippus* arrived in Australia from North America where it originated. It was first sighted in Cardwell (Queensland) in 1870. By 1871 30 specimens had been captured in Brisbane. The butterfly is now found on the eastern coastal strip of Australia from Cape York to northern New South Wales. There are also small populations around Sydney and in parts of Victoria and South Australia. The envirograms are drawn for individuals in the south-east Queensland study area used by Dr Myron Zalucki (Zalucki, 1981a).

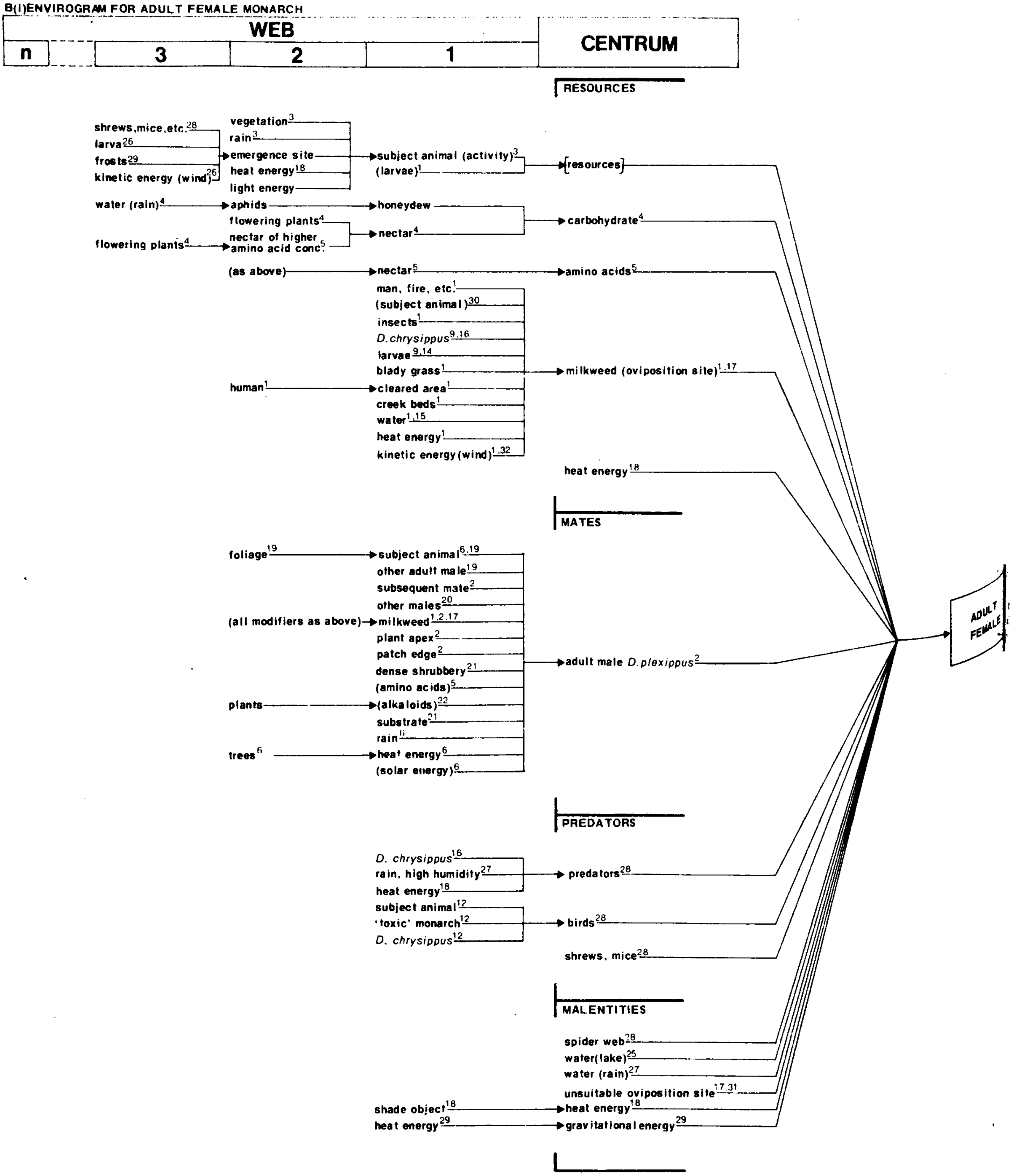
On emergence from the egg the average larval size is 1.9mm (range 1.7 to 2.0mm). The larva passes through five instars before pupating.

On average, adult *D. plexippus* live 330 day-degrees, with some individuals surviving to 580 day-degrees and above. This is a life-span of about 4 weeks in normal summer temperatures in south-east Queensland and about 3 months in normal winter temperatures in the same area.

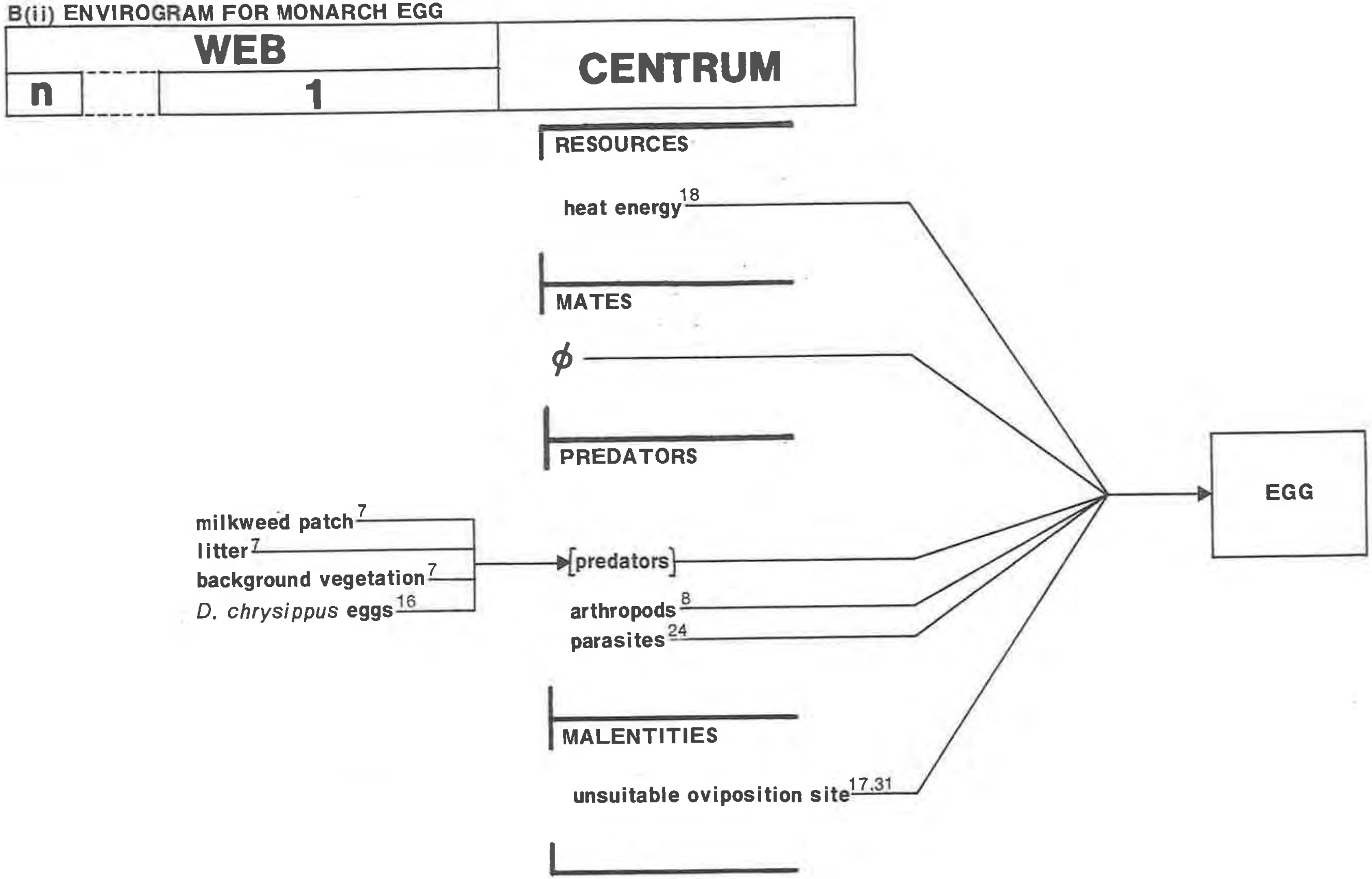
The butterfly has been reported as flying at speeds up to 40 km per hour. Mean flying speeds are 1.43m/sec for females, 2.38 m/sec for males. The species is known for its ability to fly long distances.

We have pleasure in thanking Dr Myron Zalucki who lent us an early copy of his thesis from which we obtained much of the material contained in this report. Dr Zalucki also assisted us with many helpful comments.

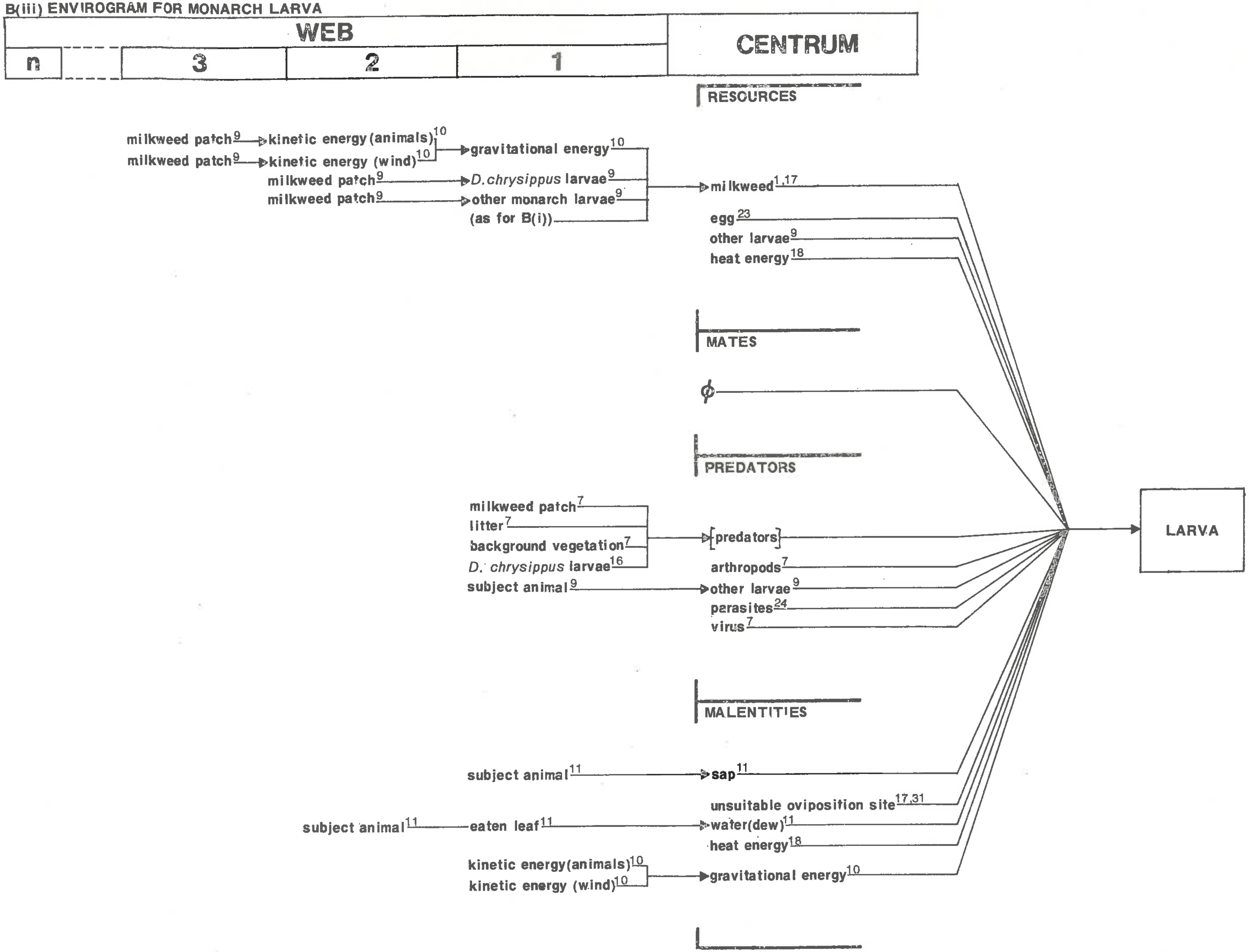
B(I)ENVIROGRAM FOR ADULT FEMALE MONARCH



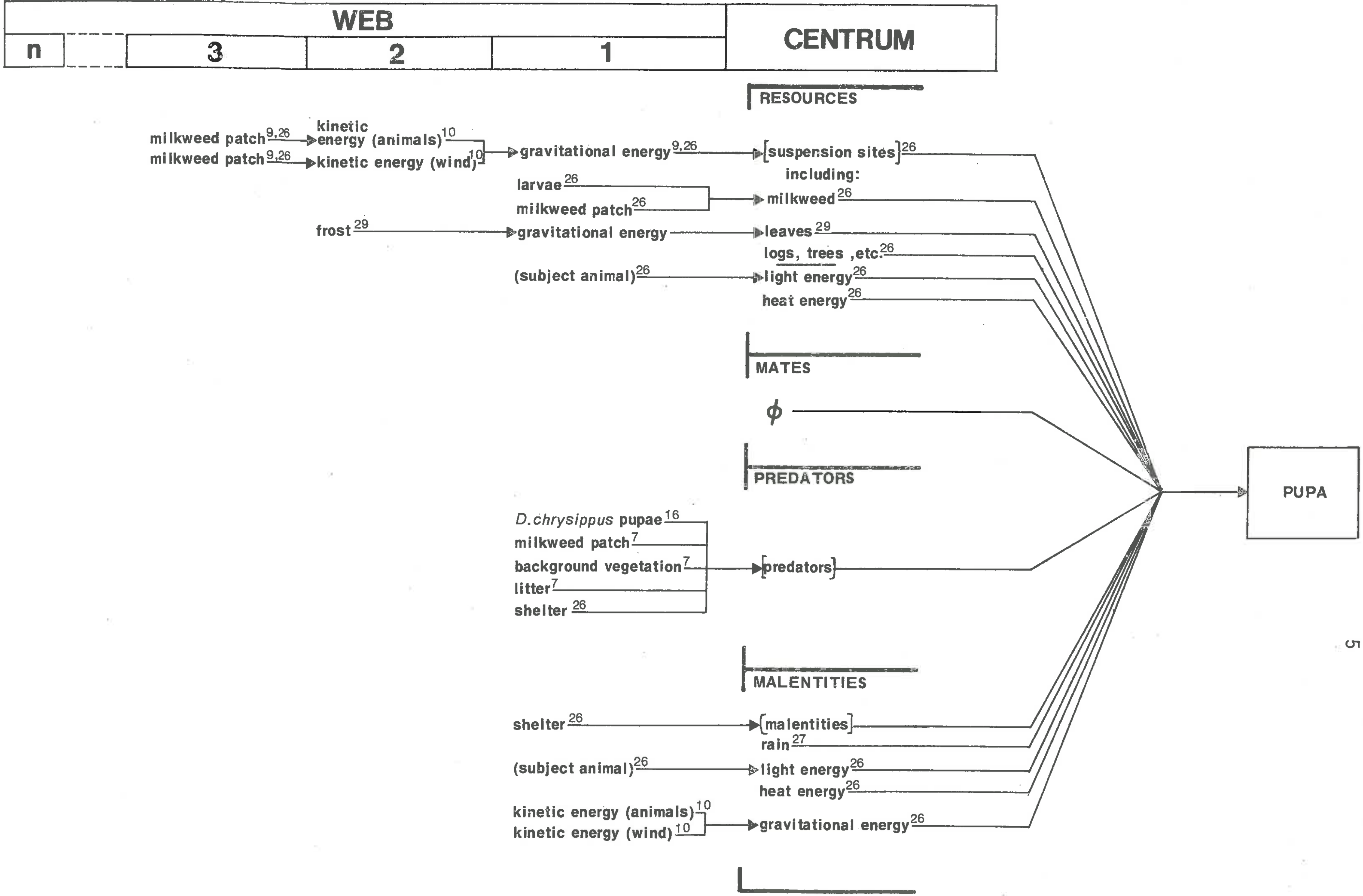
B(ii) ENVIROGRAM FOR MONARCH EGG



B(iii) ENVIROGRAM FOR MONARCH LARVA



B(iv) ENVIROGRAM FOR MONARCH PUPA



C. NOTES ON THE ENVIROGRAM

1. The Monarch lays its eggs exclusively on plants belonging to the family Asclepiadaceae, represented in south-east Queensland by three species, all commonly called milkweeds. Thus milkweeds will be both a first-order modifier of mates and, in consequence, a resource for adults (see General Introduction) and a food resource for larvae. An informal version of the defining equation which classifies milkweeds as a first-order modifier of mates is:

$$\text{Milkweed } \mathrm{Mod}'_t \text{ female} =_{\mathrm{Df}} (\exists \text{ male}) \; [\{\xi_t \text{ milkweed female} \supset \text{male } \mathrm{Mat}_t \text{ female}\} \;\&\; \{\sim\xi_t \text{ milkweed female} \supset \sim \text{male } \mathrm{Mat}_t \text{ female}\}]$$

The three south-east Queensland Asclepiadaceae are, in order of preference to the Monarch (assuming plants of equal ages): *Asclepias curassavica* L., *A. fruticosa* L., and *A. physocarpa* (E. May) Schlect. *A. fruticosa* L. predominates in the region; it occurs in patches of various sizes ranging from single isolated plants to entire paddocks. Milkweeds grow 1 to 2m in height and are often taller than background grasses. Two other Asclepiadaceae were offered as host plants in an experiment by Zalucki (1981a): the rubber vine *Cryptostegia grandiflora* R.Br and the moth plant *Araujia hortorum* Fournier. About 1% of eggs were laid on the latter and none at all on the former. The host species *Calotropis gigantea* also occurs in Australia (but not in south-east Queensland). In the Camden area (in N.S.W.) the milkweed *Gomphocarpus fruticosus* is the main food plant. Orrell (1970), in South Australia, reports *D. plexippus* larvae feeding on the crown plant *Calotropis procera* and the button orchid *Asclepias dischidia.* Urquhart (1960) gives an extensive list of host plants for various regions of the United States.

Milkweed is officially declared a 'noxious weed' in south-east Queensland, since in a drought cattle will feed on it and may get sick, so under some circumstances the plants are controlled by man, who is thus a first-order modifier of the subject animal. Fire, the activities of cattle and activities of humans not primarily directed against milkweed will have similar effects.

A map of milkweed patches drawn up by Zalucki (1981a) shows that there is a strong association between the plant and roads and urban areas; it is a weed of cleared areas and is thus found near settlements, roads, farms with cleared paddocks etc. In this sense man is a modifier of 'cleared areas' and thus also a second-order modifier of the subject animal. The distribution of the plant is characteristically one of a large circular patch surrounded at irregular distances by patches which tend to be successively smaller. Otherwise milkweed patches follow creek beds. These patches present a greater circumference-to-size ratio than circular patches (see n. 2 re patch edge). In addition the plant shows strong 'clumping' - areas of high patch density alternating with areas almost devoid of patches.

The plant succession is not yet well-known. It is known, however, that blady grass can choke out milkweed.

The plant requires a fair amount of moisture and cool weather though it dies back at about 0°C.

Milkweeds are pollinated by insects and the seeds are wind-dispersed.

Notes 13 and 17 deal with the Monarch's egg-laying behaviour.

2. The ratio of females to males is about 1 at birth.

In south-east Queensland, the Monarchs fly and breed all year, though there is a distinct increase in breeding during February to April.

Pliske (1974) comments that males seeking mates place themselves in good vantage positions, usually in the sun, and often on the terminal branches of trees or the apices of tall shrubs. From such a position the males will punsue females that happen by. It seems clear from Zalucki (1981a) that males seek females by patrolling milkweed patches. His analysis of the animal's movements shows that there is a strong tendency for both females and males to patrol patch edges and that this is where matings are most likely to begin. Female Monarchs can mate many times. Up to 4 spermatophores have been found on older females. There is at least the possibility of a male which has mated a virgin female being superceded by a subsequent male (as a mate). Pliske found that maximum mating activity occurs between 10 am and 4 pm and that a single mating can least 2 to 14 hours. (For further mating behaviour see notes 19, 20, 21, 22). Other notes concerning the modifiers of mates are 6, 17, 18.

3. The Monarch is a strong flier capable of long-distance movement. It has been reported as capable of flying at 40 km/hr. Zalucki (1981a) reported mean flying speeds of 1.43 m/sec for females and 2.38 m/sec for males. Both sexes characteristically fly at about the height of the top of milkweed plants i.e. 1-2 m.

Weather conditions affect adult flying activity, in particular overcast and rainy weather depress activity (Smithers, 1972). For the former we are unsure whether light energy or heat energy is the affective object. The animal does not fly at night, which suggests that light is the operative factor, but see n. 18 , last paragraph.

Anything which affects the functioning of the butterfly's wings will limit its ability to find resources, avoid predators etc. Damage to the wings is not infrequent during late pupal development and the period immediately following emergence (see notes 18, 26, 27, 28 and 29). In addition, females' wings occasionally become tattered when searching through vegetation for oviposition sites (Urquhart, 1960).

4. Adult Monarch activity is fuelled by carbohydrate. The principal source is nectar from flowering plants, though extra-floral plant sources are also used. The butterfly has catholic tastes (but see n. 5); the following are reported: eucalypts, flowering milkweeds, Scotch thistles, *Xanthorrhoea* spp., *Lantana* spp. and *Ageratum hortorum*.

Another source of carbohydrate is honeydew from aphids which the Monarch is most likely to take in dry weather (Zalucki, pers. comm.).

5. All nectars contain amino acids. The Monarch will select those nectars with higher concentrations. The amino acids are used in egg production. The Monarch can store these amino acids for use when needed.

6. The number of eggs laid by a female Monarch was found by Zalucki (1981a) to be well represented by:

$$E_i = Atx^B e^{-Cx}, \quad \text{where}$$

E_i is the number of eggs laid on day i,
t is the number of day-degrees on day i,
x is the age of the female, in days,
and A, B and C are constants.

While this equation does not justify causal inferences it seems that the heat energy actually experienced by the animal (as approximated by the ambient temperature) and the age of the female modify the number of eggs laid. Zalucki summarizes the effect of the female's age as follows: egg production rises rapidly from no eggs 45 day-degrees after emergence to a peak of about 60 eggs per day at about 175 day-degrees and then declines slowly to 5 eggs per day after 580 day-degrees. In addition, larger females produce more eggs. As for temperature effects generally speaking there is increased egg production with increased temperature; from an average of about 50 eggs/female/day at 20°C to about 70 eggs/female/day at 25°C.

Zalucki also reports that egg-laying tends to decrease progressively with solar radiation below 500L; oviposition is decreased on cloudy days and very rare on rainy days. We are unsure if this correlation is because of the contribution that radiation makes to the heat energy actually experienced by the animal (For this and other details regarding heat energy see Paper No. XIII on *Lucilia cuprina*) or because of a behavioural adaptation.

The butterfly takes anything from 3 to 15 seconds to lay an egg (average time 6 to 7 seconds) from the moment of alighting to take-off. During peak production a female is capable of maturing about 70 eggs per day.

The average egg weight for the Monarch is .54 mg (Orrell, quoted by Urquhart, 1960).

According to Urquhart (1960), in the U.S.A., it is quite likely that a female Monarch is capable of laying more than 400 eggs during her lifetime.

7. Zalucki (1981a) recorded a variety of arthropod predators of the larvae and pupae:tachinids, various spiders, assassin bugs, coccinelids, cockroaches, mantid nymphs and ants. Also wasps were observed stinging and collecting larvae; two vespids which were identified were *Ropolida revolutionalis* (Saussure) and *Polistes variablis* (F); a sphecid of *Chlorion* sp. was also observed. Urquhart (1960) recorded in addition (in North America) three unnamed species of fly (incidence below 2%) several birds including the catbird, the black phoebe and the black-billed cuckoo (all rare) and some predacious insects which attacked only very small larvae - pentatomid bugs and the larvae of aphid lions. Also in North America lace-wing nymphs (Chrysopidae) predate larvae.

Another cause of larval mortality is from unidentified viruses; the percentage infected in Australia is unknown but in North America it can be high (Zalucki, pers. comm.). Other causes of larval mortality are dealt with in notes, 9, 10, 11, 33 and 34.

Zalucki (1981a) found that about twice as many adults are produced from eggs laid on single plants than from eggs laid on plants in larger patches. In larger patches the predation of all immature stages is significantly higher and it is suggested that predators are more easily able to cue onto a large patch and that such patches can maintain breeding populations of predators. For this reason we have recorded 'milkweed patch' as a first-order modifier of predators on egg, larva and pupa envirograms. As an example of the above it has been shown that parasitism of larvae by the tachinid *Sturmia convergens* is twice as high on plants within a patch as opposed to single plants; the mortality actually occurs in the pupal stage.

Zalucki (pers. comm. and 1981a) reports that there seems to be an increase in the number of predators of all immature stages in proportion to the amount of litter. He adds that the composition of background vegetation is also important.

Parasitism accounts for the major losses occurring in the pupal stage. There is a tendency for greater survival of larvae and pupae in winter and it is suggested that this is because of decreased parasitism.

8. Ladybugs and cockroaches have been observed eating Monarch eggs, and ants have been seen carrying eggs away. Orrell (1970) reports seeing the bush cockroach *Calolampra irrorata* devouring eggs and the common brown louse ant *Pheidole megacephala* carry off eggs.

Typically, from two-thirds to three-quarters of eggs do not hatch, and the number of live adults resulting from 1000 eggs is less than 50. (Zalucki, 1981a). We do not, however, know how much of this loss is due to predation.

9. The Monarch larvae are occasionally cannibalistic. Small larvae will sometimes drop on threads to avoid large larvae, thus acting as first-order modifiers in their own environment. Orrell (1970) reports seeing late instar larvae giving each other savage bites when passing on a leaf. However such encounters are by chance in that larvae do not actively seek other larvae as food.

D. chrysippus also use milkweed as host plants. Although species competition with *D. plexippus* larvae in south-east Queensland is negligible, because of the abundance of milkweed, the larvae may compete locally on some plants, with V-instar Monarch larvae, in which case the plants may be defoliated. The two species may also consume each others early stage larvae.

The greatest danger of defoliation is from other Monarch larvae as *D. chrysippus'* laying habits differ from the Monarch (see n. 16). Zalucki (pers. comm., unpublished data) reports that approximately 6 V-instar larvae are required to defoliate an average milkweed - i.e. defoliation is a rare event. If the plant on which it is feeding is defoliated a larva will usually die unless it can locate another milkweed. The chance for the larva doing this increases with patch size. Note that this patch effect tends to counteract the effect reported in n. 7.

10. Urquhart (1960) once observed 12 larvae dislodged from a plant when his dog brushed against it. The fallen larvae were scattered; during the following two hours 2 of them regained a position on the same

plant and another one located a small plant 5 feet away. It seemed likely that the other 9 perished.

In the above case gravitational energy as modified by kinetic energy (animal) has removed the larva from the plant. Kinetic energy (wind) may fulfil the latter function; or the larva may simply fall. We have classified gravitational energy as both a malentity, because of the damage the larva may suffer in the fall and as a first-order modifier of milkweed as a food resource.

Larger larvae are better able to relocate themselves and for reasons given in n. 9 survival chances increase with patch size.

There is, however, some evidence of later larval instars migrating from their original plants onto others i.e. not following accidental dislodgement but apparently deliberately.

11. Larvae may be drowned in, or poisoned by, the sap of the milkweed. Orrell (1970) reported that for the first 6 or 7 days the larvae nibble tiny circles in the surface of their leaf, without penetrating its membranes. During the first 2 days several larvae were found 'bogged down' in the milky latex secreted by the food-plant, particularly in young leaves. Orrell also found after a heavy dew the shallow 'circle-dishes' chewed by the larvae filled with water and several larvae drowned.

    Larvae will be poisoned only rarely when they happen to bite leaf veins on milkweed plants which contain substantially more poisonous sap than is the norm. Generally only early instar larvae are affected in this way.

12. The Monarch has partial immunity to bird predation due to its bright 'warning' colouration associated with the toxic cardiac glycosides which they contain. The situation in Australia is not well understood however in North America it seems that birds which are usually insectivores learn to avoid the Monarch. However some birds are partly resistant to the toxin and eat some parts of the butterfly. The situation is complicated by variation in the toxicity of Monarchs.

Orrell (1970) reports that laboratory tests with Monarchs showed that butterflies reared from "non-poisonous" milkweeds were eaten with gusto by birds; while those raised on milkweeds with high cardiac-glycoside content were mouthed and rejected - the same birds when offered another 'non-poisonous' Monarch rejected it. Thus our subject animal (whether or not it contains cardiac-glycosides) will have any bird that has had a previous encounter with a "toxic" Monarch removed from its environment. It is also suggested that any other butterflies with bright colouration and containing cardiac-glycosides will contribute to the avoidance of the Monarch by birds - thus *D. chrysippus*, among others, is a first-order modifier. There are a few cases reported of birds predating Monarchs (see n. 33) and Zalucki (pers. comm.) reports that Monarchs with beak-shaped segments missing from their wings are not uncommon.

13. Female Monarchs tend to disperse their eggs over a locality - i.e. among many plants and many patches of plants. Because of the distribution of milkweeds (see n. 1) a female leaving a small patch will most likely encounter another similarly-sized patch within a short time. On the other hand, if she leaves a large patch she is most likely to encounter next a small patch. Patch size had a significant effect on the number of eggs laid per plant; no. eggs/plant tended to decrease as patch size increased (about 3-10 eggs/plant for single plants down to about 2 eggs/plant for patches of 20m diameter). (Zalucki, 1981a).

Zalucki also found that eggs were not evenly distributed within a patch - more eggs were laid on plants at the edge of patches than on plants within the patch. The larger the patch the more marked is this "edge effect".

In a field experiment a patch of low density was preferred by the Monarch to one of high density (Zalucki, 1981a). Urquhart (1960) reported that eggs are seldom laid in the vicinity of trees and that they prefer open areas away from shade. This may be connected with the effect of solar radiation on oviposition (see n. 6).

Increasing patch size has been shown to correspond with increasing egg and larval mortality (see n. 7).

14. The presence of Monarch eggs on a milkweed has no apparent effect on subsequent egg-laying - neither attracting nor discouraging. However, the presence of Monarch larvae may act as a mild deterrent.

15. As in many plants maturation in milkweeds seems to be accelerated by a reduction in water supply. Thus drought conditions can reduce the population of Monarchs in two ways:

    (i) causing a reduction in oviposition by making the milkweeds less attractive (see n. 17), and

    (ii) making milkweeds less suitable as food for young larvae. (Smithers, 1972).

16. *Danaus chrysippus* also uses milkweeds as primary host plants and its larvae are thus first-order modifiers of this resource. *D. chrysippus* is much more likely to penetrate forest and wooded areas than the Monarch. It seldom utilizes single milkweed plants much preferring patches of some size in which to lay its eggs, which again differs somewhat from Monarch behaviour (see n. 13). In addition *D. chrysippus* is absent from the Monarch's S.E. Queensland range during winter. For all these reasons the amount of interaction between the species is moderate. Apparently the predators for the two species also coincide so that *D. chrysippus* acts as a modifier of predators on all envirograms.

    Notes 9 and 12 also mention some aspect of *D. chrysippus'* interaction with the Monarch.

17. Differences of species (see N. 1), age, size and general plant health have been shown to influence the Monarch's laying behaviour on milkweeds. In addition "particular leaf" and its position on the plant have been shown to be important (For patch effects see n. 13).

    In general younger plants are preferred and provided that they are not too old tall plants receive significantly more eggs than shorter plants. Milkweeds with new leaf growth are preferred to those without and plants with wilted leaves are avoided (see n. 15).

Only rarely will more than one egg be laid on any one leaf. More eggs are laid under the leaf than on the upper surface and stem. The tables below are from Zalucki (1981a):

TABLE 2A

Eggs per Leaf

	Singles	Two	Three	Four	Total
Number	1503	71	18	2	1594
%	94.29	4.45	1.13	0.13	100.00

TABLE 2B

Where Eggs are Laid

	Lower Leaf Surface	Upper Leaf Surface	Plant Stem	Total
Number	1537	52	5	1594
%	96.42	3.26	0.32	100.00

Zalucki also found that 75% of eggs were laid on the upper half of the host plant, with a marked mode at between 80% and 90% of the height. 87% of eggs were laid on middle-aged leaves (50 - 140mm).

All of the factors mentioned in the first paragraph of this note have been shown to influence the prospect of an individual surviving from egg to adulthood. In general an egg will be laid in a position which is positively beneficial to its chance of survival. Such positions (milkweeds, leaves etc.) will be resources. However, a combination of age, size, plant health etc. may substantially decrease the chance of the individual surviving and for this reason we have entered 'unsuitable oviposition site' as a malentity on both larva and female adult envirograms. Such milkweeds are sub-optimal oviposition sites. Notes 11 and 31 cover the extreme cases of milkweed toxicity and non-milkweed oviposition sites.

See n. 14 for effect of presence of immature stages.

18. In Australia there is good general agreement between the distribution of adult *D. plexippus* and the 10°C average isotherm. Areas experiencing an average temperature below 10°C are devoid of the animal. Since 'average' temperature is unlikely to affect a butterfly it is probably some associated factor which is operative (Smithers, 1972).

Urquhart (1960) reports that at temperatures from about 20°C to 32°C eggs take 3 to 4 days to hatch. At lower temperatures the time is extended. At a constant temperature of just over 18°C eggs took 8 to 12 days to hatch.

Zalucki (pers. comm.) reports a developmental zero for Monarch larvae of 11.5°C.

Urquhart (1960) reports that at temperatures of about 32°C to 38°C larvae can mature in about 10 days whereas larvae placed in a refrigerator at just over 7°C took 38 days to mature.

The larvae are usually found on the underside of the leaf, however if the weather is overcast more of them move to the upper surface.

Urquhart (1960) reports that the pupal stage may last between 9 and 15 days and the duration is temperature dependent (see also n. 26).

Adults tend to emerge from the pupal state when the solar radiation and ambient air temperature are high (see n. 26). On emergence the butterfly is immobile, its wings being soft. A few hours of sunlight enables it to remove itself quickly from this precarious situation by completing its post-pupal development.

Urquhart (1960, in N. America) reports that Monarchs cannot move at all at temperatures below 40°F (≃ 4.5°C) and that they have difficulty in flying below 50°F (≃ 10°C). On the latter point, Zalucki (pers. comm., in S.E. Queensland) reports that the Monarch will not fly in air below 15°C but that in such circumstances rapid vibration of the wings can raise the butterfly's temperature to 20°C, allowing it to take off. Zalucki also reports that the butterfly will seek shade in the summer when the ambient temperature rises to 35°C. At lower temperatures he (1981a) found that the butterfly avoids those sections of milkweed patches that are shaded from mid-morning to mid-afternoon, preferring the sunny exposed sections.

There is a range of heat energies that can be considered beneficial, or at least not harmful, to the Monarch - this range will constitute a set of resources. Outside the beneficial range, both above and below, the animal will be increasingly disadvantaged to a point at which it will die - this range will constitute a set of malentities. Where this latter range affects the butterfly's ability to move or fly heat energy will modify both the animal's ability to forage and to escape predators.

Heat energy also modifies 'mates' in various ways - see n. 6.

19. Pliske (1974), in Florida, U.S.A., found that the female can break off a courtship, thus removing that particular male from her environment (males can also terminate a courtship) by:

(i) Aerial evasion, by out-distancing the male.

(ii) Foliage evasion, by flying through the dense foliage, or directly into shrubbery, landing quickly and folidng her wings over her back, and remaining thus 'hidden' until the male has passed out of sight. Foliage thus acts as a modifier of the subject animal, which is in turn modifying the potential mate.

(iii) Struggling and escaping in aerial takedown or on the ground.

(iv) Abdominal evasion, i.e. strong flexing movements of the abdomen to prevent copulation.

Older adult males tend to be more aggressive and persistent in courtship and hence more successful.

In the field Pliske found that only 15% of observed courtship attempts were successful.

20. According to Pliske (1974), in Florida, U.S.A., when several males pursue the same female the initial male breaks off and pursues one of the other males, thus 'other males' will be first-order modifiers.

21. Pliske (1974), in Florida, U.S.A., noted that as part of the mating behaviour the pair alight on the nearest available substrate, usually less than 10 feet above the ground.

    In a later phase of the behaviour the pair remain secluded for 2 to 14 hours, usually in dense shrubbery, while a spermatophore is secreted.

22. Danainae other than *D. plexippus* have been shown to rely to a great extent on chemical stimulants to initiate copulation; dihydropirrolizidine alkaloids are reproduced by the biochemical modification of ingested alkaloids and are emitted from extrusible sex pheromone glands, the hairspencils, located in the tip of the abdomen.

    Pliske states that apparently *D. plexippus* has evolved or is evolving away from the use of such chemical aphrodisiacs. We have, however, tentatively included 'alkaloids' as a modifier of a mate of the subject animal. The plants providing these alkaloids (we do not know the species) would be a second-order modifier.

23. Upon hatching, the first instar larva usually eats its egg. (Orrell, 1970). We have assumed that the egg provides nutriment and is thus a resource. There is at least one observation of a 5-minute old first instar larva eating another unhatched egg. Most often only one egg is laid per leaf so encounters so soon after hatching are not common.

24. The following extract is from Urquhart (1960):

    "Gillette (1888) reported obtaining fifty specimens of a new species of *Pteromalus* from a single Monarch butterfly chrysalis. The specimens were sent to Howard who described the species and gave it the name *archippi*.

Walker (1886) states that of the numerous Monarch butterfly larvae which he had reared, he had not bred an "ichneumon fly or any other parasite". He points out, however, that Riley records a dipterous fly, *Masicera* (Tachina) *archippivora*, Riley, as a parasite of the larvae of the Monarch butterfly.

Scudder (1889) records Riley as stating that an ichneumon fly was reared from the Monarch butterfly "but nothing more is known of it". Eggs sent to Scudder from West Virginia produced several specimens of *Trichogramma intermedium.*

In the course of our rearing experiments a few parasites were obtained and a few others sent to us from our co-operators. The following species of dipterous parasites were examined and identified: *Achaetoneura schizurae* (Town.); *Achaetoneura archippovora* (Will); *Exorista* sp. (In a letter, C.W. Sabrosky states: "some might call this *E. larvarum* (L.) as it is often identified in this country, but there are some differences that make me hesitate to place a species name on it").

No hymenopterous parasites were obtained from the rearing of over two thousand speciments, nor were any sent to us by our co-operators. In August, 1957, however, a number (approximately fifty) of ichneumon flies were found flying about a large rearing cage that contained two hundred larvae. These parasites were quite definitely attempting to gain access to the cage. Specimens were collected and sent to G.S. Walley, who identified them as *Temelucha rectus* (Prov.). Not a single specimen was found inside the cage, and hence it cannot be concluded that this species is a parasite of the larva of the Monarch butterfly. Concerning the genus *Temelucha*. Mr Walley reports as follows: "There are not host records in the literature of *Temelucha rectus*, but the genus *Temelucha*, as far as is known, confines its parasitism ot microlepidoptera, and therefore I suspect the Monarch butterfly would not be a suitable host. All the specimens you sent are males, and these would probably be interested either in searching for females or possibly food material".

From the above information we may conclude that only three species of dipterous parasites are definitely known to attack the larva of the Monarch butterfly. There may be at least one egg parasite and perhaps one ichneumon larva parasite".

25. Monarchs usually seem to avoid large stretches of water. On occasions numbers of dead and partially drowned Monarchs have been seen washed up on the shores of the Great Lakes. (Urquhart, 1960, in the U.S.A.) Thus we classify 'water (lake)' as a malentity.

26. When the stage V larva is fully developed it leaves the host plant in search of a pupation site. Immediately prior to departure enormous quantities of food are eaten. Pupation has already begun when the larva departs and a suitable suspension site for the pupa must be found before pupation has advanced so far that the animal can no longer move. Pupae can be found in a great variety of places: on the underside of logs (those raised at one end); limbs of trees; under leaves, horizontal timbers and fences; eaves and windowsills of buildings - in fact anywhere where the animal is protected.

Some pupae (less than 10%) are found under milkweed leaves but it has been established (Urquhart, 1960) that they have moved from their original host plant and have accidentally encountered another milkweed. Pupae using milkweed as a site may be subject to displacement by later feeding larvae, which are thus a modifier of this kind of resource. An individual is more likely to pupate on a milkweed plant within a patch.

Anything which dislodges a pupa such that it is unable to re-attain a suitable suspension position and thus forms a deformed pupa (and later a deformed butterfly) will act as both a modifier of the resource 'suitable suspension site' and a malentity, in a manner exactly analogous to that described for larvae in n. 10. (cf. pupa envirogram: chains involving kinetic energy (wind), gravitational energy etc.). A special case is covered in n. 29. The piercing of the pupal skin can cause death; the animal is particularly vulnerable during the early semi-exarate stage (i.e. the 12 to 19 hours between larva and fully-hardened pupa). The pupal stage lasts betwen 9 and 15 days, dependent on temperature.

Several 'gold spots' on the pupa may function as light receptors to prevent emergence in adverse overcast conditions; this suggestion by Urquhart is not based on conclusive evidence, however we have tentatively classified light energy (as modified by subject animal) as a resource. The hypothesis gains circumstantial support from the fact that emergence is invariably during daylight, with a unimodal distribution, the mode corresponding to maximum radiation and ambient air temperature - i.e. about noon.

Light energy has been shown on the pupa envirogram as both resource and malentity for reasons analogous to those given for heat energy in n. 18.

27. Emergence from the pupal stage rarely occurs during rain; probably for reasons given in n. 26. If emergence does occur the high humidity will delay the hardening of the wings resulting in increased probability of being predated (see also notes 18, 33).

28. Few predators of adults have been recorded, probably because of the Monarch's cardiac glycosides (see n. 12). Several authors have mentioned birds; Urquhart (1960) names the mouse and shrew, given very particular circumstances: Newly-emerged butterflies which still have soft wings may be attacked if their pupation position is sufficiently close to the substrate. In a case Urquhart recorded only the wings of the butterfly were reachable, and shredded.

Finally Urquhart reports that adult Monarchs have been found caught in the strong web of a yellow garden spider, *Argiope aurantia*. Since it is not clear whether the spider actually ate the Monarch we have classified 'spider web' as a malentity; it seems likely that such accidents will occur elsewhere and with other spider webs.

29. In the U.S.A. during the late autumn and after frosts many Monarchs are found with malformed wings. This occurs because the leaves to which the pupae are attached often fall during this period and emergence takes place on the ground where it is difficult for the wings to harden properly (also the pupa itself may be deformed). Thus 'gravitational energy' (as modified by 'frost') will modify the suspension site resource 'leaves'.

30. Several authors comment on the physiology involved in a female choosing a particular leaf as a suitable oviposition site. Sensory organs in both the tarsi and the ovipositor have been mentioned, however, in neither case is the evidence conclusive. For this reason we have tentatively included 'subject animal' as a modifier of

'milkweeds' as an oviposition site.

31. Occasionally a female may deposit an egg accidentally on the leaf of an adjacent plant that is not a milkweed. When the larva hatches it is unable to feed and dies of starvation.

32. Urquhart (1960), in the U.S.A., reports that occasionally strong winds lasting several days will blow isolated Monarchs well outside their normal range and usually away from the host species milkweeds.

'Kinetic energy (wind)' also modifies 'milkweed' as an oviposition site in another way: when ovipositing, females usually fly from side to side, most often against the wind - this slows their forward speed and allows a more exact survey.

E. REFERENCES

Orrell, J. (1970). The baby is a cannibal. *Wildlife* 7, 44-47.

Pliske, T.E. (1974). Courtship behaviour of the monarch butterfly, *Danaus plexippus* L. *Ann. Entomol. Soc. Am.* 68, 143-151.

Smithers, C.N. (1972). Observations on a breeding population of *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae) at Camden, New South Wales. *Aust. Zool.* 17 (2), 142-148.

Urquahrt, F.A. (1960). *The Monarch Butterfly.* (Univ. Toronto Press).

Zalucki, Myron P. (1981a). Animal Movement and its Population Consequences with a case study of *Danaus plexippus*. Ph.D. thesis: Griffith University.

Zalucki, Myron P. (1981b). Temporal and spatial variation of parasitism in *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae: Danainae). *Aust. ent. Mag.* 8(1), 3-8.

THE TWENTY-FIVE ANIMAL STUDY

(c) *Five higher invertebrates:*

Freshwater snail
Terrestrial snail
Squid
Octopus
Brachiopod

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

VIII. THE WANDERING SNAIL *(Lymnaea peregra)*

by

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ABSTRACT

The precise environment of the Wandering snail *(Lymnaea peregra)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis,* 1982). A diagram developed by H.G. Andrewartha called an 'envirogram' is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger mathematical study, the methodology for which is set out in AES Working Paper No. 9/81.

CONTENTS

A INTRODUCTORY NOTE

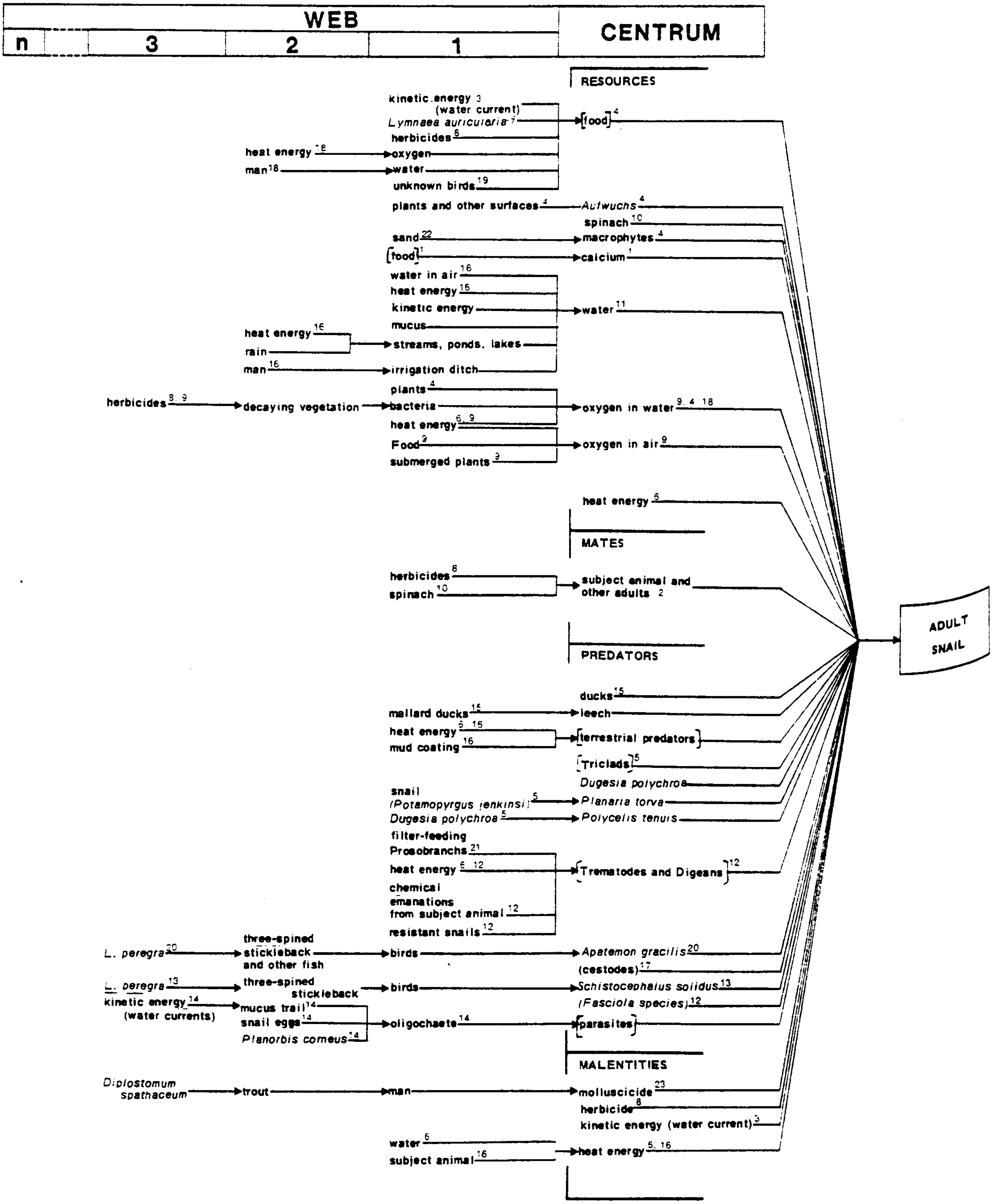
Lymnaea peregra tends to inhabit shallow, fresh or brackish waters, usually within 4m (for exceptions see n. 9) of the surface. Like other pulmonates, it is normally found on 'hard' surfaces, being most densely concentrated on vascular macrophytes (emergent or submerged) though also found on rocks, wood and detritus.

Russell-Hunter (1975) distinguishes five different known life-cycles for *L. peregra* (one biennual twice breeding, two univoltine patterns and two yearly cycles with two generations involved), but does not give environmental factors determining their incidence.

Dussart (1979) observed that in hard and medium water the populations survive a second winter, so that in May three generations are present. However, in soft waters *L peregra* has a simple one-year life cycle with minimal generation overlap. Young snails produced in early spring and summer grow rapidly to approximately 8mm before winter when growth slows, only to be resumed the following spring.

The animal is often called the 'Wandering Snail' (Ellis, 1926). It is found all over Europe. Synonyms for *'Lymnaea peregra'* are *'Limnaea peregra'*, *'Limnaea pereger'*, *Lymnaea pereger'* and *'Radix peregra'*, the latter name being used by Grizimek (1974) for the 'Wandering Snail'.

B. ENVIROGRAM



C. NOTES ON THE ENVIROGRAM

1. The shell of the snail is made from crystalline calcium carbonate in an organic matrix (Machin, 1975). The thickness and mass of shell varies in proportion to the available calcium (water-hardness); thus it seems that the animal spends the same amount of energy in assembling this resource irrespective of environment. While *L. peregra* flourishes in waters with high calcium concentrations, it is still capable of living in extremely soft waters (3mg l^{-1} Ca) (Russell-Hunter, 1975). Dussart (1979) observed that numbers of animals were attracted to 'hard' water where by 'hard' is meant a measure of mineral content including calcium (Ca^{2+}) but also chloride (Cl^-), potassium (K^+), magnesium (Mg^{2+}), phosphate (PO_4^{3-}) and sodium (Na^+). Machin (1975) reports the snail living in the Baltic in 11% Na Cl.

   Young (1975) reared snails on lettuce (with no tracer) in Ca poor and Ca rich waters each containing 45 Ca tracer. In soft water the snails gained 70% of the calcium from food and 30% from the water. In hard water the percentages were, respectively, 46 and 54.

2. *L. peregra*is capable of producing fertile eggs when bred in isolation and cultures have been maintained in the laboratory for many generations using only self-fertilization. However cross-fertilization after copulation is customary. The snail usually lays a cluster of eggs packed in jelly inside a common egg-capsule. Copulation, when in breeding condition, occurs with the first individual encountered, and reciprocal copulation, where the snails alternate roles, has been observed. Breeding chains of three animals have been observed in the laboratory, but not in a natural habitat. Coupling may last from a few minutes to twelve hours, but usually lasts from thirty to ninety minutes. After copulation the first egg-capsules are invariably cross-fertilized while later eggs may be self-fertilized, perhaps when foreign sperm are entirely utilized. Foreign sperm are known to have remained viable in *L. stagnalis* for up to 116 days but no comparable report is available for *L. peregra*. Foreign sperm are generally more effective in fertilization than indigenous sperm; the reason why, probably biochemical, is not known (Duncan, 1975). The mean gross annual egg output for Lymnaea spp is 2,200 per adult (Russell-Hunter, 1975).

2. Continued

Dussart (1979) comments that in 'soft' waters (see n. 1) *L. peregra* often lays its eggs on the shells of its contemporaries, possibly to provide an immediate source of nutrients to the offspring after the post-egglaying deaths of the parent population. The offspring are produced in early spring and early summer.

In other Lymnaea spp. factors significantly affecting oviposition are temperature, oxygen content of water and time since copulation. Temperature and oxygen content are important also for egg development. (Duncan, 1975). Comparable results specifically for *L. peregra* are not available.

3. Jones (1975) comments that in aquatic habitats the snail moves by ciliary locomotion. Because the locomotive force is weak *L. peregra* is excluded from localities with strong water currents. In addition, because the animal moves so slowly - about 17.5 cm/min. - even mild currents may affect its foraging ability.

4. The 'hard' surfaces favoured by *L. peregra* (see Introductory Note) are invariably coated with *Aufwuchs* on which the snail grazes. Russell-Hunter (1975) defines *Aufwuchs* as scum flora of diatoms, blue-green and other single-celled algae, bacteria, fungi, protozoans and other associated microscopic plants and invertebrates in well-lit waters, usually less than 4m deep (for exceptions see n. 9).

Runham (1975) reports that in Canada *L. peregra* is found almost invariably on Canadian Pond Weed, *Elodea canadensis*, yet examination of its crop revealed a complete absence of fragments of the Pond Weed. Instead the crop invariably contained filamentaceous algae and diatoms that were normally epiphytic on the surface of the Pond Weed. Thus the surface provided by the plant modifies the availability of the snail's food resources. Laboratory experiments show that filamentaceous algae are preferred to diatoms and are better assimilated. Runham also reports that *Aegopodium podograria*, the commonest plant species in the snail's normal habitat, was often eaten in the laboratory but rarely under natural conditions.

4. Continued

Skoog (1978) in Iceland reports that the snail's diet is dominated in spring by diatoms. These are eaten throughout the year but by autumn there are increasing numbers of *Rivularia calothrix* and other blue-green algae in the diet. Filamentaceous brown and green algae were also eaten throughout the year. *Pilayella* filaments were eaten in May.

L. peregra can survive in the trophically poorest waters - which also implies low oxygen content hence the snail favours waters with high plant turnover (Russell-Hunter, 1975).

It is known that other *Lymnaea* spp. eat dead animal material when available; their growth, survival and egg production was enhanced by this food. However, this has not been reported for *L. peregra*.

A study of crop contents by Calow (1971) indicated that the snail ingests epiphytic algae rather than macrophytic tissue. Laboratory experiments corroborated this and also indicated that green filamentous algae were assimilated better than the diatomaceous species.

5. Reynoldson and Piearce (1979a, 1979b) report that the following Triclads eat *L. peregra: Dugesia polychroa, D. lugubris* and *Planaria torva*. *Dugesia* spp. are opportunisitc feeders, although their predation of the snail declines during the warmer months. (Presumably some first-order modifier is operating here). *Planaria torva* has a strong preference for the snail *Potamopyrgus jenkinsi* and takes three times as many of these as *L. peregra*. Large prebreeding individuals of *L. peregra* are less susceptible to attack by triclads.

D. polychroa is the most predacious of the Triclads which attack gastropods, while *D. lugubris* and *P. torva* also eat mainly snails.

Triclads longer than 6mm predate snails 4 times as often as those shorter than 6mm.

5. Continued

Polycelis tenuis predates snails 2 to 10 times more often in waters lacking *D. polychroa*; this probably also applies to *P. nigra*.

Polycelis spp. also predate *Asellus* spp.

6. As with other animals in this study, there is a range of heat energies which constitute resources for the snail. Outside the most beneficial range the animal is increasingly disadvantaged. The latter range constitute malentities and will include heat energies corresponding to the temperature which is the LD_{50}. The following graph is from Skoog (1976), working on the north Baltic coast of Sweden.

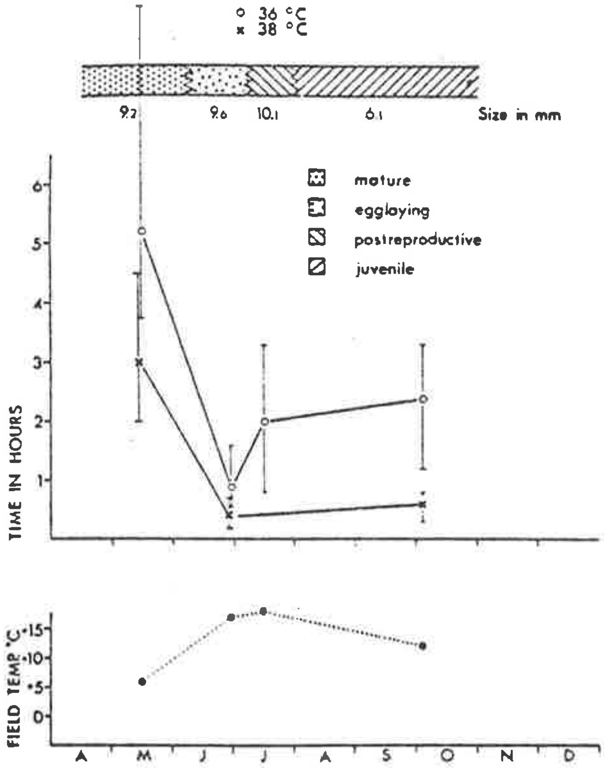


Fig. 3. The survival time in hours of 50% of *Lymnea peregra* exposed to 36 and 38°C at different seasons (centre). Stages of development and shell lengths are given above. Below a record of the habitat temperature at each experiment. The variance is given as the interquartile interval Q_3, Q_1. N = 10 in each point.

6. Continued

Metabolic rate and hence oxygen consumption (see n. 9) is related to temperature (as with other poikilotherms).

Walter (1977) notes that within a year *L. peregra* in Lake Zurich is exposed to temperatures ranging from 5°C to 20°C. Ellis (1926) reports that in Iceland *L. peregra* has been seen living in springs with a temperature of up to 40°C.

Reynoldson and Piearce (1979a) report that in a pond a drought killed most of the young snail spawn when they dehydrated on the rocks after the water level fell. Dehydration is a general hazard when ponds dry up (see n. 16).

7. Knecht and Walter (1977) comment that in Lake Zurich the two snails have almost total dietary overlap, although food is apparently so abundant that competition is not significant.

8. Scorgie (1980) investigated the effects of the aquatic herbicide Cyanatryn on *L. peregra* and its habitat, in this case a drainage ditch. The herbicide killed all vegetation, both emergent and submerged. The population of *L. peregra* was drastically reduced but the mechanism is not clear - whether by destruction of food, by destruction of structural aspects of the habitat, or other. In the laboratory the animal survived but did not flourish when fed only on debris from the bottom of the ditch. Also the relevant concentration of the herbicide was not fatal to *L. peregra* but the snails did produce fewer eggs. For this reason the herbicide is both a malentity and a first-order modifier of mates (see General Introduction).

9. *L. peregra* obtains oxygen in three ways: (a) by rising to the surface and siphoning air into its pulmonary sac; or, when submerged, (b) by cutaneous uptake and (c) by using its pulmonary sac as a 'physical' gill, with or without an air bubble (Russell-Hunter, 1975 and Ghiretti and Ghiretti-Magaldi, 1975). The animal can live indefinitely submerged in well-oxygenated water, with its pulmonary sac full of air and its pneumostone closed. However where oxygen concentration falls below a certain level this is no longer possible and the snail must rise to the surface, either by flotation or by climbing submerged

9. Continued

plants. High dissolved oxygen content and low water temperature enable the snail to endure longer dives. Most pulmonates from temperate regions consume oxygen at rates between 50 and 300 µl/g body wt/h at temperatures of approximately 20°C, presumably depending on activity (Ghiretti and Ghiretti-Magaldi, 1975). (see also n. 6).

One population of *L. peregra* lives completely submerged in Lake Windermere (England), below 9m. Another lives in Loch Lomond below 5.5m (see n. 18). The individuals of both these populations tend to be small and detritus feeders - i.e. feeding on the continual rain of seston from above (Russell-Hunter, 1975).

Bacteria on decaying vegetation (whether or not the decay is facilitated by herbicides) consume oxygen. (However, Scorgie (1980) in the case mentioned in n. 8 comments that oxygen levels were not severely affected). Mason and Bryant (1975) identified the following pectolytic bacteria on the surface of decomposing *Typhia angustifolia* L.: Yellow *Cytophaga*, *Erwinia* sp. and *Pseudomonas* spp. In laboratory experiments *L. peregra* allowed to graze over the litter increased the oxygen uptake of the litter, presumably by stimulating microbial activity.

Starvation leads to a decline in metabolic rate, hence a reduced oxygen consumption.

10. Skoog (1978) reports that in the laboratory *L. peregra* fed on spinach showed poor growth rates but produced a high number of eggs. For the latter reason spinach is both a resource and a first-order modifier of mates (see General Introduction). Spinach is also a resource in the ordinary sense of being a food.

11. Machin (1975) found that in all pulmonates measured more than 80% of the total wet body weight, without the shell, consisted of water. No measurements for *L. peregra* are given. Lymnaea spp. feed more or less continuously on aquatic vegetation and must therefore ingest some water by this means, however the principal mechanism is uptake through the skin.

12. Ewers (1964) records 71 species from 13 families of trematode parasitizing the Lymnaeidae family of molluscs.

Brown (1975) records that a common life cylce for Digeneans is as follows:

(i) A sexual multiplication in first intermediate molluscan host.

(ii) Encystment in a second intermediate host.

(iii) Development to maturity in a definitive vertebrate host.

Sometimes there are three intermediate hosts,the first two being molluscs. Pulmonates are infected by miracidia of trematodes from numerous local vertebrates and in turn emit clouds of cercariae which will infect the next intermediate host. Brown notes that there is very strong evidence ot suggest that miracidia and metacercaria (which encyst) find their host via chemical emanations (see n. 14). Quite substantial distances, up to 9m, may be involved (data from other species of snail). Nevertheless, miracidia may attack incompatible (resistant) snails, causing irreparable damage to themselves. Several reports also suggest that the production of cercariae is reduced or even wholly prevented by the starvation of host snails.

In Russia, Natsvlishvili (1973) reprots the trematode *Cercaria vitrina* infesting *L. peregra.*

Pennycuick (1971) reports the presence of the trematode *Diplostomum gasterostei* in the snail.

Blair (1973) reports a low incidence of trematode infestation from hot springs in Iceland (see n. 6) and suggests that the heat may be excessive for trematode development. He records the following trematodes: *Cotylurus cornutus, Echinoparyphium recurvatum, Apatemon gracilis, Diplostomum* sp., *Hypoderaeum conoideum, Notocotylus attenuatus.*

Fasciola hepatica and *F. gigantica* are known to infest *L. peregra* in the laboratory but this is unlikely in the wild. However

12. Continued

in laboratory experiments Digenetic trematodes have been shown to adapt to new species of host very quickly.

Brown (1975) remarks cryptically that miracidia respond to a variety of stimuli including gravity, temperature, water current and light. Light which elicited the greatest response from miracidia of *Schistosomatium douthitti* (Court.), which develops in Lymnaea spp., was in the blue-green range, i.e. that region of the spectrum which penetrates deepest into clear water. It is not clear to us what responses are elicited, so we have been unable to classify these affective energies.

13. An immature stage of *Schistocephalus solidus,* the plerocercoid, lives in the stickleback body cavity. The stickleback is an intermediate host of the cestode; the definitive host is a fish-eating bird (see also AES Working Paper 12/81 on the environment of the stickleback). (c.f. n. 20). (Pennycuick, 1971).

14. One of the two subspecies of the Oligochaete *Chaetogaster limnaei,* i.e., *C.l. limnaei,* is a commensal of *L. peregra*; it inhabits the outer surfaces of the snail. One snail was found hosting 144 individual worms. The worm is a carnivore which predates parasites attached to the snail and organisms thrown up by ciliary action. The worm is attracted by egg masses and the mucus trail left by the host. The attractants are probably chemical emanations from the host with water currents providing orientation.

The oligochaete worms from *L. peregra* and *Planorbis corneus* cross-infect, but those from other species of snail remain host specific. Host specificity is greater in waters containing a number of host species, and in one pool where 7 species resided the worms could differentiate *L. peregra* from their home pool against those *L. peregra* from other sites (as well as differentiating against other species of snail). (Grzimek, 1974 and Buse, 1974).

15. Reynoldsen and Piearce (1979a) report that the snail population (including *L. peregra*) of a Welsh pond was virtually wiped out by a pair of Mallard Ducks (*Anas platyrynchus* L.). The Triclad, *Polycelis nigra* (see n. 5) was unaffected by the disappearance of snails from their diet, but the population of the leech *Glossiphonia complanata* L. declined markedly.

Benatson (1971) reports the following species of duck as predators of Lymnaea spp. in Lake Myvatn (Iceland): Tufted (*Aythya fuligula*), Barrow's Golden-eye (*Bucephala islandica*), Old Squaw (*Clangula hyemalis*) and Black Scoter (*Melanitta nigra*). Snails formed a greater percentage of the diet for the first two ducks mentioned.

16. Storey (1972) notes that immediately following the drying up of the water *L. peregra* becomes coated in mud. This helps to conceal the animal from would-be predators.

Since *L. peregra* is not uncommonly out of the water, occasionally because a stream (pond etc.) has dried up, the animal is at risk of dehydration. Several cases have been recorded of annual drainage of irrigation systems leaving the snail temporarily without water. The important factors in dehydration are temperature, relative humidity and air movements (Machin, 1975). The snails also lose water from locomotion on land, since they leave a trail of mucus behind them. Storey (1972) observed that adult snails died shortly after the disappearance of the water (by evaporation) although whether by dehydration or accelerated aging is not known. Young and small-sized snails were observed by Storey to survive, although as the dry period was prolonged - in excess of three months, with only occasional showers and dews - the smallest snails succumbed first. Storey considers that the animals capacity to survive is enhanced by its ability to adopt water-conserving body and shell-postures while aestivating; metabolic rate is inferred to be greatly reduced at this time.

17. Valkounova (1973) lists the following cysticercords from the family Hymenolepididae (Cestoda) recovered from *L. peregra*: *Disranotaenia coronula*, *Microsomacanthus compressa*, *M. paracompressa* and *M. paramicrosoma*. "The snails are probably not utilized as intermediate hosts but act as reservoir hosts of these cestode species; the cysticercoids concentrate in the body of the snails without undergoing any further development".

Our environmental classification is tentative; we have put these cestodes in the class of predators since just by their presence they probably reduce the value of the snail's 'H'.

The definitive hosts for these cestodes are domestic and wild ducks; crustaceans are an intermediate host (Valkounova, 1973). However we do not have enough information to know exactly how they should be placed in the snail's environment.

Pennycuick (1971) and other authors record the presence of the cestode *Schistocephalus solidus* in the snail (see n. 13).

18. In work on the completely submered population of *L. peregra* in Loch Lomond it was found that a rise of water level could sometimes create starvation conditions for marginal populations of the snail, presumably because for various reasons the snail is forced to inhabit the new trophically void waters. This effect could occur naturally or via human intervention (dams etc.) (Russell-Hunter, 1975).

Short-term migrations also occur in Loch Lomond where the respiratory needs of the adults, increased by high water temperature in high-level littoral populations, forces them to find water which has greater oxygen content. On occasions this migration will take them to near sterile substrata and may result in temporary starvation. We have classified oxygen as a first-order modifier of all food since, writing x for a particular item of food and w for a particular quantity of oxygen, we have the following section of the definition:

$$\mathrm{w\ Mod}'_{t}\,a =_{\mathrm{Df}} (\ x)[\xi_t \mathrm{wx} \supset \mathrm{xMod}^{\circ}_{t}a) \mathbin{\&} (\sim\xi_t \mathrm{wx} \supset \sim\mathrm{xMod}^{\circ}_{t}a)].$$

The second conjunct is important; it means that when the item of food and a sufficient quantity of oxygen are not 'close' then the

18. Continued

item of food ceases to be in the centrum of the snail because the snail has migrated to another area with sufficient oxygen. Heat energy is a modifier of oxygen and thus a second-order modifier in the environment of *L. peregra*.

19. Russell-Hunter (1975) comments that the distribution of freshwater pulmonates tends to follow bird migration routes and that some snails have been found (alive) on birds in transit.

Presumably the snails climb onto waterbirds. We have classified 'unknown birds' as first-order modifiers of food only although the classification holds good for all other members of the centrum (see General Introduction).

20. Blair (1976) reports that anatomically identical specimens of the trematode *Apatemon gracilis* are found in Iceland and Scotland. *L. peregra* sheds cercariae which infest appropriate fish hosts, including the three-spined stickleback *Gasterosteus aculeatus* (see AES Working Paper 12/81) and other fish from the families Salmonidae, Eleotridae, Cobitidae, Cottidae and Gobiidae. The metacercariae encyst in the fish and do not grow to maturity until the fish is eaten by an appropriate bird host. To complete the life cycle snails will be reinfested by miricidia proceeding from the birds (c.f. n. 17).

21. Nansen *et al* (1976) noticed in experiments to test the host specificity of *Fasciola hepatica* that some Prosobranchs (non-hosts) took up miracidia in an unusual manner. The three 'filter-feeding' Prosobranchs *Bithynia leachii, B. tentaculata* and *Potamopyrgus jenkinsi* sucked miracidia into their gills because of the current set up by their cilia. Prosobranchs which feed in this manner are first-order modifiers of the trematode parasites of *L. peregra*.

22. *L. peregra* does not often eat macrophytes (c.f. Runham, 1975, n. 4) however Russell-Hunter (1975) reports 'a small set of experiments' which suggested that a diet of dicotyledon leaves can be utilized, but only if considerable quantitites of mineral particles are

22. Continued

simultaneously ingested for trituration within the snail's gut. Sibrey (1970) investigated the importance of mineral particles in the diet. Without sand the rate of growth of the animal was adversely affected; the suggestion is made that the presence of sand may allow the utilization of a wider variety of foods than would otherwise be possible. Mineral particles are retained in quantity in the gut when not available in the environment. Storey comments further that a lack of sand in the diet is deleterious and eventually fatal.

Sand is classified as a first-order modifier of the food since without its presence the (potential) food cannot be utilized and thus disappears from the centrum.

23. Crossland (1971) reports the use of the molluscicide Frescon for the control of *L. peregra* in trout reservoirs in England. The snail hosts parasites which damage the trout, including *Diplostomum spathaceum*.

D DETAIL

FOOD

The Following tables are from Skoog (1976):

TABLE 1: Survival and mean growth per snail of juvenile *Lymnea peregra* (initial mean size 2.19, standard error 0.02 mm) after 144 on different diets, n = 24 in each diet, July 1967.

	Diatoms	*Cladophora* with diatoms	Mixed blue-green algae	Pure *Cladophora*
Survival (%)	100	95.8	95.8	95.8
Mean grwoth per snail	0.88	0.70	0.48	0.28
Standard error of mean	0.12	0.07	0.08	0.08

Pattern of significant at the 5% level according to Student-Newman-Kuel's test (Appendix 1A). The diets are ranked with the best diet to the left. Encircled diets are not significantly different.

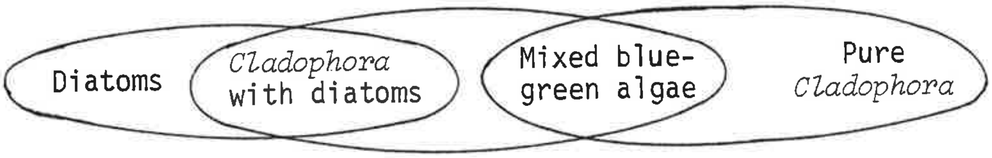
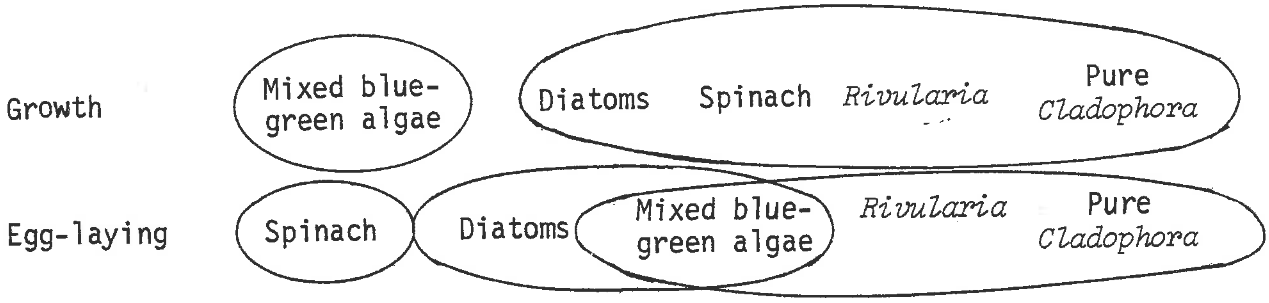


TABLE 2: Survival, mean grwoth per snail per day of survival in µm and mean number of eggs laid per snail per day of survival in adult *Lymnea peregra* (initial mean size 8.9 and standard error of mean 0.1 mm) after 40d on different diets, n = 10 in each diet. July 1968.

	Mixed blue-green algae	Diatoms	Spinach	*Rivularia*	Pure *Cladophora*
Mean number of days of survival per snail	40	33.3	33.2	34.8	38.9
Standard error of mean	6	3.6	2.6	3.1	0.8
Mean growth per snail per day of survival	1.7	5.2	3.0	1.5	1.4
Standard error of mean	2.6	1.9	1.3	0.7	1.1
Mean number of eggs per snail per day of survival	0.9	1.1	2.0	0.5	0.3
Standard error of mean	0.2	0.2	0.3	0.1	0.1

Pattern of significance at the 5% level according to Student-Newman-Keul's test (Appendix 1B). The diets are ranked with the best diet to the left. Encircled diets are not significantly different.



Food items noted by various authors are:

Diatom, *Acnanthes* spp.

Spinach (in laboratory experiment)

Rivularia calothrix and other blue-green algae

Pilayella filaments and other filamentaceous brown and green algae

Cladophora

PREDATORS

Mallard duck, *Anas platyrynchus* L., and other ducks (see n. 15).

Leeches: *Glossiphonia complanata* (L.), *Helobdella stagnalis*.

Acanthocephala: the spiny-headed roundworm *Echinorhynchus clavula*.

Triclads: *Dugesia polychroa*, *D. lugubris*, *Planaria torva*, *Polycelis nigra* (Muller), *P. renuis* (Ijima).

Trematodes: *Cercaria vitrina*, *Cotylurus cornutus*, *Echinoparyphium recurvatum*, *Apatemon gracilis*, *Diplostomum spathaceum*, *D. gasterostei*, *Hypoderaeum conoideum*, *Notocatylus attenuatus*, *Opisthioglyphe megastomus* Baer 1943. In laboratory studies only: *Fasciola hepatica* and *F. gigantica*.

Cestode: *Schistocephalus solidus* and other cestodes from the family Hymenolepididae (see n.17).

E REFERENCES

Bengston, S.A. (1971). Food and feeding of diving ducks breeding at Lake Myvatn, Iceland. *Orvis Fenn* 48(3/4), 77-92.

Blair, David (1973). Observations and experiments on some larval trematodes of freshwater snails and fish from southern Iceland. *J. Helminthol.* 47(4), 409-414.

Blair, D. (1976). Observations on the life-cycle of the strigeoid trematode, *Apatemon (Apatemon) gracilis)* (Rudolph 1819), Szidat 1928. *J. Helminthol.* 50(2), 125-132.

Brown, D.S. (1975). Pulmonate Molluscs as Intermediate Hosts for Digenetic Trematodes. In Fretter and Peake (Eds), Vol. 2, 287-334.

Buse, A. (1974). The relationship of *Chaetogaster limnaei* (Oligochaeta: Naididae) with a variety of Gastropod species. *J. Anim. Ecol.* 43(3), 821-838.

Calow, P. (1970). Studies on the natural diet of *Lymnaea pereger obtusa* (Kobelt) and its possible ecological implications. *Proc. Malacol. Soc. London* 39 (2/3), 203-215.

Crossland, N.O. (1971). A field trial with the molluscicide Frescon for control of *Lymnaea peregra* Muller, snail host of *Diplostomum spathaceum* (Rudolphi). *J. Fish. Biol.* 3(3), 297-302.

Duncan, D.J. (1975). Reproduction. In Fretter and Peake (Eds.), Vol 1, 309-366.

Dussart, G.B.J. (1979). Life cycles and distribution of the aquatic gastropod molluscs *Bithynia tentaculata, Gyraulus albus* and *Lymnaea peregra* in relation to water chemistry. *Hydrobiologia* 67(3), 223-240.

Dussart, G. and R. Kay (1980). Relationships between water chemistry and respiration rate in several populations of *Lymnaea peregra* (Gastropoda: Mollusca). *Hydrobiologia* 69(1/2), 57-65.

Ellis, A.E. (1926). *British Snails.* (Oxford University Press).

Ewers, W.H. (1964). An analysis of the molluscan hosts of the trematodes of birds and mammals and some speculation on host specificity. *Parasitology* 54, 571-578.

Fretter, V. and Peake, J. (Eds.). (1975). *Pulmonates* (Academic Press, Vols 1 and 2).

Ghiretti, F. and A. Ghiretti-Magaldi (1975). Respiration. In Fretter and Peake (Eds.), Vol. 1, 33-52.

Grzimek, B. (ed.) (1974). *Grzimek's Animal Life Encyclopedia,* Vol 1, (van Nostrand Reinhold).

Jones, H.D. (1975). Locomotion. In Fretter and Peake (Eds.), Vol 1, 1-32.

Knecht, A. and J.E. Walter (1977). Comparative investigation of the diets of *Lymnaea auricularia* and *L. peregra* (Gastropoda: Basommatophora) in Lake Zurich. *Schwiez Z. Hydrol.* 39(2), 299-305.

Machin, J. (1975). Water Relationships. In Fretter and Peake (Eds.), Vol 1, 105-164.

Nansen, P., F. Frandsen and N.O. Christensen (1976). A study on snail location by *Fasciola hepatica* using radioisotopically labelled miracidia. *Parasitology* 72(2), 163-171.

Natsvlishvilli, M.G. (1973). [Seasonal dynamics of infestation of mollusks with larvae of trematodes in the vicinity of Tiflis] [in Russian with Georgian and English summaries]. *Soobshch Akad. Nauk. Gruz SSR* 70(3), 725-727.

Pennycuick, L. (1971). Seasonal variations in the parasite infestions in a population of three-spined sticklebacks, *Gasterosteus aculeatus* L. *Parasitology* 63(3), 373-388.

Reynoldsen, T.B. and B. Pierarce (1979a). Feeding on gastropods by lake-dwelling *Polycelis* in the absense and presence of *Dugesia polychroa* (Turbellaria, Tricladida). *Freshwater Biol.* 9, 357-367.

Reynoldson, T.B. and B. Piearce (1979b). Predation on snails by three species of Triclad and its bearing on the distribution of *Planaria torva* in Britain, U.K. *J. Zool.* (London) 189(4), 459-484.

Runham, N.W. (1975). Alimentary Canal. In Fretter and Peake (Eds.), Vol 1, 53-104.

Russell-Hunter, W.D. (1975). Ecology of freshwater pulmonates. In Fretter and Peake (Eds.), Vol 2, 335-384.

Scorgie, H.R.A. (1980). Ecological effects of the aquatic herbicide Cyanatryn on a drainage channel. *J. Appl. Ecol.* 17(1), 207-226.

Skoog, G. (1976). Effects of acclimitization and physiological state on the tolerance to high temperatures and reactions to dessication of *Theodoxus fluviatilis* and *Lymnea peregra*. *Oikos* 27(1), 50-56.

Skoog, G. (1978). Influence of natural food items on growth and egg production in brackish water populations of *Lymnaea peregra* and *Theodoxus fluviatilis* (Mollusca). *Oikos* 31(2), 340-348.

Storey, R. (1970). The importance of mineral particles in the diet of *Lymnaea pereger* (Mueller). *J. Conchol.* 27(3), 191-195.

Storey, R. (1972). Dormancy in *Lymnaea peregra* (Muller) during periods of dryness. *J. Conchol.* 27(5/6), 377-386.

Valkounova, J. (1973). Reservoir parasitism in cestodes of the family Hymenolepididae (Ariola 1899) parasitic in domestic and wild ducks. *Vestn. Cesk. Spol. Zool.* 37(1), 71-75.

Vaucher, C. (1971). [The biological cycle of the trematode *Opisthioglyphe megastomus* Baer, 1943 (Plagiorchidae), a parasite of the aquatic shrew-mouse *Neomys fodiens* (Pennant).] *C R Hebd Seances Acad. Sci. Ser. D. Sci. Nat.* (Paris) 273(20), 1815-1817.

Walter, J.E. (1977). Life cycles of *Lymnaea peregra* in Lake Zurich (Gastropoda: Basommatophora). *Arch. Molluskenkd* 108(4-6), 177-184.

Young, J.O. (1975). A laboratory study using 45Ca tracer, on the source of calcium during growth in two freshwater species of Gastropoda. *Proc. Malacol. Soc. Lond.* 41(5), 439-445.

Zajicek, H. (1970). [The development of *Cotylurus cornutus* (Rud.) (Trematoda: Strigeidae) in the natural conditions of the Lipno locality.] *Vet. Med. (Praha)* 15(11/12), 749-756.

Zajicek, D. (1971). Snails as the second intermediate hosts of the trematode *Plagiorchis muris* Tanabe 1922 (Trematoda: Plagiorchidae). *Ventn. Cesk. Spolecnosti Zool.* 35(1), 75-78.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

IX THE GIANT AFRICAN SNAIL *(Achatina fulica)*

by

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ABSTRACT

The precise environment of the Giant African Snail *(Achatina fulica)* is given, using as a basis for the classification the defining equations of Niven *(Erkenntnis,* 1982*)*. A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in A.E.S. Working Paper No.9.

CONTENTS

A. INTRODUCTORY NOTE.

We have taken almost all the material for this working paper from the excellent book by A R Mead, *The Giant African Snail: a problem in economic malacology* (University of Chicago Press, 1961).

A. fulica is among the largest of the snails. A photograph is given in the book by Mead of an animal with a shell length of 7 7/8ins, and an overall length of nearly a foot. Average shell sizes range from 5-6 ins. down to 3.5-4.5ins. in Micronesia. There is striking variation in shell morphology and colour and evidence that colour in particular is affected by diet.

The snail is thought to live at least 2.5 years in East Africa, its original habitat. One specimen lived 9 years in captivity but spent much of this period in estivation. Mead is of the opinion that an average life span of 5 to 6 years would be a conservative estimate.

The animal has spread through Asia and many Pacific Islands. It has been intercepted alive at American and Australian ports. An introduction to Japan has died out.

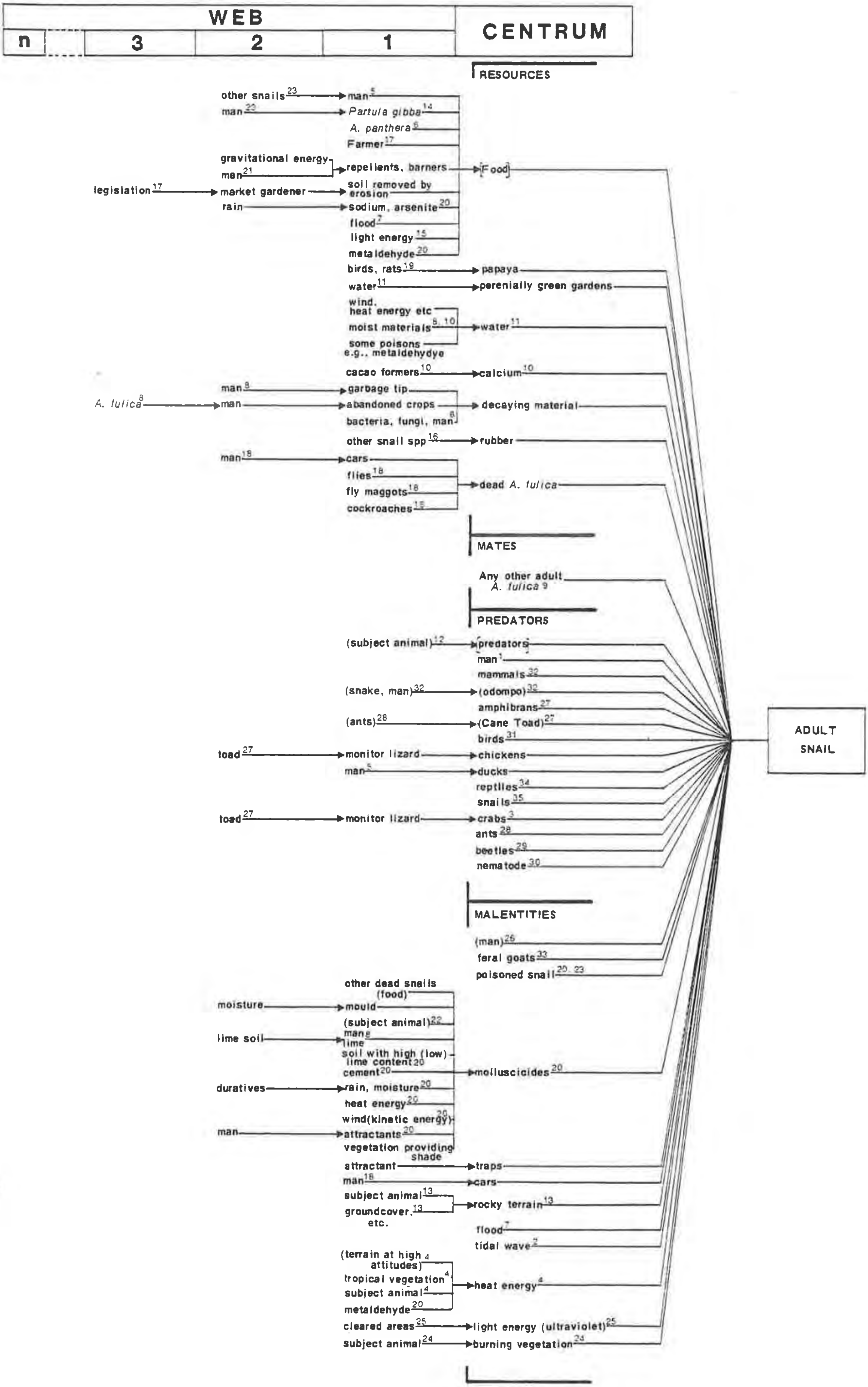
A.fulica estivates; it is not known whether it can undergo hibernation (like, for example, *Helix pomatia*). When estivating, most of the animals are found under only superficial protection, but some work their way into remarkably inaccessible places-under large rocks, in hollow trees, high up in the branches of trees, well under plant debris or man-made litter or even 5 ins underground.

The snail has a very keen olfactory sense. It is able to guage (and presumably smell) the wind and move according to that stimulus and locate attractants and food.

* * * * * * *

The table in n.10 and the list of food in §D are from the book by Mead.

B. ENVIROGRAM FOR ADULT SNAIL



C. NOTES ON THE ENVIROGRAM.

1. The snail has been recommended for medicinal uses in England, about 1900, and until more recently in Japan - certainly up to 1950. The curative substance was said to be orthocalcium phosphate, which was claimed to cure kidney disease and a variety of other ailments.

Man has also used the animal for food, e.g. in Japan and East Africa.

2. On the Bonin Islands a tidal wave on April 2nd 1946 washed over extensive lowland, presumably killing many *A. fulica*, which were very scarce in these areas for the following two years.

3. The hermit crab *Cenobita perlatus* is a significant predator of *A. fulica* on the Bonin Islands and other areas of Micronesia. It consumes the snail and occupies many of its shells. In some limited areas the crab seems to have completely eliminated the snail. The crab is found on land up to 600ft above sea level and 1.5miles inland, although the numbers decrease with increasing height and distance from the sea.

The coconut crab or robber crab *Birgus latro* also eats *A fulica*, particularly on the Auluptagel Islands in the Palau group. In these Islands the coconut trees became virtually extinct following the introduction of various species of coconut beetles; in consequence the crab turned to *A fulica* as an alternative source of food. We have classified coconut trees as a first-order modifier of these crabs since when the trees are present the crabs are no longer predators of the snail.

Another first-order modifier of this predator is man; Micronesians consider the coconut crab a delicacy.

In Kenya a crab tentatively identified as belonging to the genus *Ocypode* has been observed consuming live *A fulica*.

The 'paddy crab' in Ceylon has also been reported as eating the live snails.

4. Although no quantified results are given it is considered that cold weather contributed to the dying out of one introduction of *A fulica* to Formosa. Similarly in India an introduction to the foot of the Himalayas (approx, 6,600 feet) died out after a severe winter. Winter in Japan is

thought to have contributed to an introduction dying out.

At the other end of the scale, *A fulica* dies quickly when exposed to direct sunlight.

Humid, tropical climates offer optimum conditions, with luxuriant growth to provide protection during the day. Nevertheless beach populations in the Bonin and Mariana Island have been able to survive in an environment with frequent barren stretches of sand and vegetation covered in fine salt crystals. The snails' nocturnal habits are a great aid in coping with these areas.

In addition the snails have a strong 'homing' ability, enabling them to find known retreats at the onset of adverse conditions; in experiments up to 70% of the animals were shown to posses this ability.

Experiments have shown that the lethal minimum exposure to 7^{o}C at a R.H. of 40-50% was 4 days for active snails on soil, 4 days for active snails in soil (3in. all round) and 7 days for estivating snails. Of 20 snails exposed to 4.5^{o}C for 24 hours, with R.H. 35-45%, nineteen remained alive after 5 days. Of 10 active snails exposed to -1^{o}C, R.H. 55-65%, for 8 hours all survived 5 days. Only 1 individual of 10 dormant snails exposed to -7^{o}C for 8 hours, R.H. 52-56%, survived 5 days. No attempt was made to simulate the natural microenvironment in these experiments, or to acclimatize the animals.

It is suggested that the greater range of temperature above 5,000ft has limited the animal to the lower altitudes, where the slow acclimatization offered by the onset of winter has a significant effect. Height limits in various countries are: Africa (the original home territory) 1,500ft. Mauritius 2,000, Java 3,300ft, Ceylon 4,000ft.

5. The snail has been introduced by man into many countries for a variety of reasons. A young lady brought them to Hawaii to put in her garden, for aesthetic reasons. Chinese duck farmers bred and transported *A. fulica* in several places, e.g. Hong Kong, Malaysia, Sarawak, in order to feed their ducks and possibly other poultry. Ducks favour young snails and they have been introduced into Ceylon in order to control *A. fulica*. While most introductions have been wilful, unintentional introductions have usually

been connected with the transportation of some sort of plant produce. (However the marked ability of *A. fulica* to secrete itself in recesses and crannies make almost any cargo a potential method of transport.)

6. *Achatina panthera* was introduced in Mauritius and appears to have driven *A. fulica* out of the lowlands, forcing the latter to maintain its population between 1,200 and 2,000ft.

7. On Palau Island in November 1938 a flood washed some snails down into the lowlands - presumably many died, but some survived and established a population there.

8. *A. fulica* has a pronounced appetite for decaying and rotting material, particularly after the age of 4 months, and they frequently congregate around man's garbage tips. Fallen rotting fruit also attract them. As noted in §A the animal has a very keen olfactory sense. It is able to g ge (and presumably smell) the wind and move according to that stimulus and locate attractants and food. Abandoned crops provide a similar situation, this occurred during the war, but may also occur because of climatic conditions or even because of earlier depredations of the snails. (Mead, 1961, who cites instances of this).

The animal eats a tremendous range of food. However it can survive without any food for months. Local populations vary in their eating habits; in some areas a certain food plant will not be eaten at all by the snail whereas in other areas that same plant will be the major food. It is reported as being inordinately fond of watermelon.
Some preferred food items (not in order) are:
(i) Garden flowers and ornamentals (all parts and stages).
(ii) Most vegetables - especially Cruciferae, Cucurbitaceae, Leguminosae
(iii) Cuttings and seedlings, even when the mature plant is not eaten e.g. breadfruit, cassava, teakwood etc. The snails feed almost exclusively on young shoots and succulent leaves.
(iv) Cover crops, especially those that are leguminous.

A. fulica in Guam ate poisoned rat baits (Warfarin) with impunity (thus acting as a first-order modifier in the environment of the rat). The problem was solved by pre-baiting with molluscicide.

Mead describes *A. fulica* as a scavenger *par excellence*; the animal has even been known to eat a dead rat and very wet cardboard. It also relishes the dead bodies of its own species, although cannibalism is unknown, even of eggs of infant snails.

Bacteria and fungi reduce decaying moist matter and are thus first-order modifiers of this type of food. Man's habit of clearing rotting material has the same effect in the environment of the snail, so that, in this sense, man, bacteria and fungi all belong to the same class of first-order modifiers of food.

9. *A. fulica* is hermaphroditic; each individual produces eggs and any adult pair can mate. Self fertilization is unlikely, but has been reported. One copulation can provide sufficient sperm for a number of batches of eggs laid intermittently for many months. Individuals usually become adult at 5-7 months. About 200-300 eggs are laid in each batch, with a maximum of over 500. Very small individuals produce fewer eggs. Under optimum conditions the animal will lay a batch of eggs every few weeks for an apparently indefinite period terminated only by the advent of unfavourable conditions. (Mead calculates that within 5 years one gravid snail could generate 16×10^{15} progeny).

10. A direct correlation exists between the presence of lime in the soil and snail abundance. The animal 'prefers' alkaline soils, in which calcium carbonate remains stable. They are most abundant when the pH is 7.0-8.0; coralline islands of the Pacific tend to be in this range, e.g. Arno Atoll has a pH ranging from 7.2 to 8.7.

Nevertheless *A. fulica* is abundant in the highly acidic soils of the tea-growing areas in Sri Lanka where the pH is approximately 4.5. Here the calcium present is unfavourably 'locked' in silicates and combinations with iron and aluminium, however plants free the calcium and the snail feeds extensively on fallen leaves to gain this essential resource. The calcium content of the leaves is high; ash contains 40%.

Individuals have been observed rasping the shells of dead snails presumably to obtain calcium; also the shells of estivating snails. They commonly rasp their own shells. Snails deprived completely of an external source of calcium can utilize their own shells in this way for a long period of time. All the above will occur most frequently in calcium poor environments.

An abundant supply of calcium carbonate reduces the time the snail takes to reach maturity.

Cacao requires less acid soil (pH 6.0-7.0) than rubber and in Ceylon planters who change crops from rubber to cacao commonly add dolomite lime to the soil. Such plantations support the largest *A. fulica* populations in Ceylon. (see also n. 20).

The animal will eat whitewash off houses and fences (see also n. 20, xiv). It also frequently consumes moist soil, presumably in order to obtain calcium.

The following table is from Mead (1961):

TABLE 4

CHEMICAL ANALYSIS OF SHELLS AND EPIPHRAGMS OF *Achatina fulica* (Ex Ms W.Hes)

	Large Shells	Small Shells	Epiphragms
Water (dried at 105°C)	0.2	0.3	1.4
CO_2	39.6	39.8	36.7
N			0.4
SiO_2	0.1	0.1	0.3
$Fe_2O_3+Al_2O_3$	Traces	0.1	0.2
CaO	54.6	53.7	50.1
MgO	0.3	0.2	0.8
Organic matter	5.0	4.9	9.7

11. *A. fulica* is reported as containing up to 84.7% water, by weight, excluding the shell. The snail eats moist materials (n8,n10) in addition to absorbing water directly through its skin.

The percentage of estivating *A.fulica* in a local population correlates directly with reduced moisture in the environment; even so, the tendency of individuals is to alternate phrases of activity with estivation so that at any time some individuals will be in either phase. A protracted dry spell can produce mass estivation and damage to crops is often reduced during dry periods for this reason. Instead of estivating, some snails may concentrate in the perennially green gardens during these dry spells. Rain after a dry spell can cause the animal to come out of estivation.

It is the well-hidden, estivating individuals that will restock an infested area after the effects of normal, natural or man-made adverse conditions have passed.

12. During mildly adverse conditions, quiescence that does not amount to estivation is often assumed, e.g. in a short dry spell during the rainy season in Ceylon many of the snails were found unmoving on trees 3-9ft from the ground. During this time ground-dwelling predators remained active so this may be the reason why the snails stayed on the trees. In favourable conditions many *A. fulica* forage nocturnally on the ground but return to the trees during the day.

We have tentatively classified the subject animal as a modifier of predators since it is not certain that its quiescent behaviour is a modification in order to escape predation.

13. There is a direct correlation between the incidence of damaged shells and the ruggedness of the terrain. (However *A. fulica* has great facility for repairing even very severely damaged shells). Especially in the Pacific Islands, the habitat is often barren, hard and rocky and the snail often falls, damaging its shell. Groundcover, humus and thick undergrowth in some localities can break a fall thus reducing damage.

14. *A. fulica* seems to be displacing the snail *Partula gibba* in places where the latter is endemic and *A. fulica* has been introduced.

15. *A. fulica* is normally nocturnal. It is active in daylight only when the sky is overcast, or other shade is provided.

16. The slug-like snails *Mariaella dussumieri* and *Parmarion reticulatus* endemic to Micronesia and the land snail *Bradybaena similaris* also attack rubber plants and may be, in this sense, first-order modifiers.

17. Chinese market gardeners in Sarawak are required, in order to minimize damage by *A. fulica*, to keep their plots so clean all the year round that excessive soil erosion results, thus further reducing possible feed for the snails.

Rotation of crops by farmers in infected areas, quick clearing (perhaps by burning - see n.24), followed by planting a crop and then moving to another area all help to prevent the build-up of snail populations.

18. Many *A. fulica* are run over by cars. Since dead members of their own species are favourite food items more snails are run over while feeding on the roads.

Numbers of Sarcophasids, Sciomyzids, Phoroids and other Diptera have been reported as coming from dead *A. fulica*. The blue-bottle flies *Pychnosoma* or *Lucilia dux*, in India, and *Megaselia xanthia*(i.e. Aphiochaeta), in Malaya also the house fly *Musca domestica*, in the Bonin Islands, and other flies all eat dead *A. fulica*, as do cockroaches and maggots. All are thus competitors of live *A. fulica* for this food.

19. The snails climb high into the trees to eat papaya (See §D). Since this fruit (and others) is also eaten by birds, flying foxes and rats we have classified them as first-order modifiers.

20. Because of *A. fulica's* drastic effect on crops many chemical substances have been used by man in attempts to control the snail. (As such man will always be a higher order modifier wherever these substances appear on the envirogram.) The substances utilized fall into four categories:
1) Repellents - used to present access of the snail to crops(sec n.21).
2) Molluscides - substances toxic to the snail which can be sub-classified as:
   (a) Fumigants - usually used to decontaminate transported produce.
      Carbon Disulfide
      Mehtyl Bromide
      Hydrocyanic Acid Gas
      Ethyleme Dibromide (particularly recommended by Mead).

   (b) Contact Poisons - absorbed through the foot (see n.22).
      Sodium Arsenite
      "Bordeaux".

      Copper Sulphate

Metaldehyde ((CH_3CHO)4)
Sodium dinitro - orthocresylate

(c) Stomach Poisons

Calcium Arsenate ($Ca_3(AsO_4)_2$), also a contact poison
Metaldehyde
"Gammaescane" (conflicting reports)

(d) A cross-classification of (b) and (c) are those poisons toxic to only young snails:

"Bordeaux"
"Bordeaux" additionally mixed with white oil emulsion and nicotine sulphate
Chlordane
D.D.T.
Kerosene Emulsion
Pyrethrum
Sodium Chloride

3) Attractants - used to entice snails either to eat stomach poisons, or to crowl over contact poisons, or to enter traps. Snails have a keen olfactory sense and show a marked ability to gauge the wind and move according to that stimulus, thus attractants sited upwind of snails will be most effective.

Bran of wheat, rice and other grains
Fruit pulp
Amyl acetate
Calcium Carbonate
Whitewash
Lime

The last three named attractants will be effectively nullified where soil is naturally calcium rich - e.g. the high coralline content on Guam.

4) Duratives - the effectiveness of many of the above substance is quickly reduced or nullified by rain or moisture diffusion and the following have been used to ensure their effectiveness over time:

Cement (to make brickettes)
Coal tar
engine oil
paraffin oil

Also a variety of barriers, (see also n.23) particularly wood, painted with a mixture of some oil and a molluscicide.

While these prevent rain from nullifying poisons with solid baits moisture will promote the growth of mould which has the same effect.

Many substances will be multiply-classified on the above scheme. Many methods of application have also been tried.

Some of the molluscicides will have additional indirect effects - for example sodium arsenite is also a herbicide and may serve to reduce the number of snails by destroying their food supplies. Sodium Arsenite is one of those chemicals reduced in effectiveness by Yain.

Since *A. fulica* has the habit of eating its own dead (see n.18), toxic concentrations of a molluscicide in one dead snail may kill several in a "chain" reaction.

The following is a treatment in greater depth of <u>one</u> molluscicide - Metaldehyde $(CH_3CHO)_4$: The compound is both a contact and a stomach poison though probably usually the former. It causes water loss in affected snails even under 100% humidity, may cause immobility and also inhibits the feeding response of the snail. Because of the first two effects this chemical accentuates all factors causing water loss and produces a higher % of kills in unshaded areas (combined with the action of the sun on "stunned" individuals). As a corollory a substantial percentage of snails will recover under cloudy, cool and wet conditions. The chemical has only a short effective life - even without diffusing water. Various duratives can increase its durability but sheltering baits from rain has the undesired effect of providing the snails with the shady conditions that will favour their survival.

21. Ashes, or substitutes like sawdust, charcoal, cinders etc are sometimes used as a repellent barrier, which the snail will not cross. Sometimes copper sulphate is added. Another repellent which has neen very successful is coal tar, which is placed in a ring around plants. Because of rapid growth of weeds the coal tar should be replaced every second week. It is mixed with engine oil and placed on barriers to give longer life.

Crude oil has been found to be completely effective as a repellent in Guam where trenches are sprayed with it. A solution of rubber and oil is also used.

Khas khas (*etiveria zizanoides*), an aromatic plant, is reportedly effective in Ceylon.

Salt water sprays can provide an effective and practical barrier only in areas where soil would not be damaged, or where such damage was unimportant.

22. The snail *Theba pisana* has been observed to respond to a molluscicide (ferrous sulphate) by withdrawing into its shell. This behaviour would serve to protect the animal from contact poisons and presumably is also used by *A. fulica*.

23. Barriers have been built of many materials - bamboo, boards, corrugated iron, wire netting and so on. The animals are able to climb over and small snails often go through. Painting the barrier with creosote improves effectiveness. Fences which are built either sloping outwards or with an outward-facing horizontal top are more effective; the snails often drop off. In some instances snails have piled up so high against the fence that others are able to crawl over them and drop onto the far side.

Rattan or coir fibre tied round the trunks of susceptible trees has proved effective as a barrier.

24. Burning over incidentally kills many snails. An animal that is estivating deep under the surface (see n. 11) is likely to survive.

25. By far the majority of snail deaths are due to overexposure to sunlight. Heating and dehydration are obviously important but the ultraviolet light in sunlight may be the main lethal factor according to experiments carried out by Carmichael (in 1928 and 1931, quoted by Mead). Large cleared "buffer" areas act like barriers for this reason.

26. Hand collecting and destroying is the most common method of snail control. In rough terrain or dense vegetation it is not an effective method.

We have classified man tentatively here as a malentity, since it is not obvious that H(man) is increased as a result of these activities. It seems clear from parallel studies being carried out that in order to deal adequately with the environment of man the interpretation of 'H' has to be changed; with a suitable interpretation it seems likely that man in the sense of this note should be classified as a predator.

27. The Indonesian frog *Rana tigrina* is reported to eat the eggs of *A. fulica*. *Bufo marinus*, the Cane Toad, will eat young snails, but not to a significant extent. The indirect effects of *B. marinus* are more likely to be of importance in control of the snail. (see Bailey, 1976 and Tyler, 1976). In the Micronesian Islands, the monitor lizard, which was introduced to control rats, became a pest by consuming eggs and young chickens. Young chickens attack and eat *A. fulica*. Introducing *B. marinus* relieved this situation because the lizards attacked, and were fatally posoned by, the toads. The lizards also eat the coconut crab (*Birgus latro*) which feeds on the giant snail. (see also Working Paper on *Bufo marinus*)

28. *Pheidologeton affinis* and *P.diversus* are known to eat eggs of other snails and have been seen swarming over *A. fulica* eggs. The ant *Solenopsis geminata* Fabr. feeds on the young snails. A number of unknown species of ant have frequently been recorded as swarming over dead and dying *A. fulica* i.e. those affected by the sun. They would be likely to attract the cane toad (*B.marinus*) by their movement. (see Working Paper on *Bufo marinus*.)

29. Larvae of the Indian glow-worm *Lamprophorus tenebrosus* (Walker) (Lampyridae) will, during their development, consume *A. fulica*. However fully grown glow-worms will not attack snails greater than 40mm in size. When the snail is large or the glow-worm well fed the beetle may remove only a small amount of flesh from the withdrawn foot; the snail can consequently regenerate such minor losses. Other beetles of the same family which predate *A. fulica* in Ceylon are a *Diaphanes* sp. and three other unidentified species.

In East Africa larvae of the family Drilidae attack *A. fulica*. Also large black voracious beetles of genus *Tefflus* (Carabidae) in both larval and adult stages consume the snail.

30. An unidentified Rhabditoid nematode is probably, according to Mead "only an incidental symbiont of low incidence and little consequence". Nematode parasites of *A. fulica* have not been studied to any extent.

31. The Jungle Crow in Ceylon (*Centropus chlororhynchus*) attacks and eats the giant snail.

In north-west Madagascar a large native bird called 'famakankora', the snail-breaker (*Anastomus madagascariensis*) feeds on *A. fulica*.

32. Some mamals have a manifest appetite for snails (in general.) The rat is definitely known to eat *A. fulica* on many Pacific Islands. The wild pig is believed to be a predator. There is strong circumstantial evidence in Ceylon that the following animals eat the snail: the mongoose, (*Herpestes mungo*) the giant squirrel (*Sciurus macrurus* Pennant), the bandicoot (*Bandicota malabarica*) and the jackal. In East Africa the civet cats *Bdeogale tenuis* and *B. crassicaudata* eat *A. fulica* and the baboon is reported to do so.

Also in East Africa an endemic wild cat, the odompo, is believed to feed on the giant snails, an important item of food for the local inhabitants, who therefore hunt and kill the odompo. A snake, *Cerastes*, attacks the odompo, and is believed by local people to be the protector of snails.

33. On Agiguan Island (Aguijan, near Guam) a great many feral goats are responsible for killing and injuring *A. fulica* by trampling.

34. In the Belgian Congo the Nile monitor, *Varanus niloticus* (Linne,) feeds principally on *A. fulica*. Reports of predation by the two-bearded monitor *V. salvator* in the Pacific area, also *V. monitor*, are inconclusive.

The pond turtle *Nicoria trijuga thermalis* is known to attack *A. fulica* in Ceylon; because the turtle is aquatic this predation will be minor.

In captivity the small Javanese snake *Pareas c. carinatus* swallows young *A. fulica* whole and pulls the larger snails from their shells in order to eat them.

35. In Africa the following predacious snails attack and eat *A.fulica*: *Gonaxis kibweziensis*, *Edentulina affinus*, *G. vulcani*, *G. quadrilauteraus*, *Gulella wahlbergi* (Krauss) and other *Gulella* species.

The large and voracious molluscan predator *Euglandina rosea* has been imported from Florida to the Philippines and many islands in the Pacific. It took hold immediately and spread rapidly. Another less successful importation is *Oleacina oleacea straminea* (Deshayes) from Cuba.

D. DETAIL

The following list of food resources is from Mead (1961).

Air plant (*Bryophyllum pinnatum*): The common, dense stands of this plant in the uncultivated areas of the Hawaiian Islands are providing an almost unlimited source of preferred food.*

Albizzia: Where unprotected from snails, only 30 per cent survival of *Albizzia falcata* in E. Java(AV): bark of *A. falcata* attacked in Sumatra (He): *A. lebbek* a preferred food plant in Saipan(I).
Amaranthus spp.: A preferred food in Saipan(L); young plants completely destroyed, older ones seriously attacked(W).
Amaryllidaceae: Crinum favored in Malaya(Ja); serious damage to many species(W).
Ampalaya (*Momordica charantia*): Seriously attacked in Philippines(Pg).
Arrowroot (*Canna edulis*): Seriously attacked in Philippines(Pg).
Bananas and plantain (*Musa paradisiaca*): The snails are frequently found on the leaves and trunks; small specimens may work their way deep into the bunches of fruit. Ocasionally young bananas are rasped; when they mature the skin appears very badly scarred and is therefore commercially less valuable, though the fruit itself is unaltered. If the bananas split open on the tree, they will almost invariably be consumed by the achatinas frequenting the treetops. Several native reports indicated that young plantings may be killed by the attacks of the snails. Total damage is small.* Inhabitants of Tinian report no damage(C); young leaves eaten in Saipan(E and T); leaves and stems of "pisang" attacked only slightly in Sumatra(He); unverifiable reports in Ceylon that leaves and apparently blossoms of plantain eaten, therefore fruitless(G); preferred by larger snails in Palau Islands(H and K);

1(A) Anonymous, 1974a; (AV) van Alphen de Veer, 1954; (Be) beeley, 1935; (Be$_1$) 1938; (Be$_2$) 1938; (BJ) Benthem Jutting, 1934, 1952; (Br) Bertrand, 1928; (Br$_1$) 1941; (C) Chamberlin, 1952a; (C and G) Charmoy and Gebert, 1922; (Ca) A. Campbell in litt. Nov, 19, 1951; (Co) Corbett, 1933; (Co$_1$) 1937; (Co$_2$) 1941; (Ct) Cotton, 1940; (D) G S Dunn in litt. Aug. 12, 1949 to Dec. 17, 1953; (Da) Dammerman, 1929; (E and T) Esaki and Takahashi, 1942; (F) Fairweather, 1937; (Fe) Feij, 1940; (G) Green, 1910c; (G$_1$) 1910b; (G$_2$) 1911b; (H) Gutson, 1920; (H and K) Hatai and Kato, 1943; (Ha) Tom Harrisson in litt. Aug. 25, 1952; (He) Heubel, 1937, 1938; (Ho) Holmes. 1954; (Hs) Hes, 1949, 1950; (Ja) Jarrett, 1923; (Jk) Jaski, 1953; (K$_1$) Kondo, 1950c; (K$_2$) 1950a; (K$_3$) 1952; (L) Lange, 1950; (Le) Leefmans, 1933a,b; (L and V)

Leefmans and van der Vecht, 1933a, b; (M) van der Meer Mohr, 1949; (M) 1924; (Ma) Macmillan, 1943; (Mi) Milsum, 1950; (N) R C L Notley in Litt. Dec. 7, 1950; (O) Otanes, 1948; (Pb) Philbrick, 1949; (Pe) Pemberton, 1938; (Pg) Pangga, 1949; (Ph) E Phillis in litt. Jan. 31, 1950; (Pv) Paravicini, 1922; (R) Rappard, 1949; (Ri) Riel, 1933; (Ry) H C Ray in litt. July 22, 1952; (S) South 1926b; (S_1) 1923b; (T) Townes, 1946; (W) van Weel, 1948; (We) Weber, 1954.

a chief food plant in Koror, ripening fruit liable to damage (K_2); fruit, leaves, and new shoots are damaged in Saipan (L); young leaves eaten (Le); attacked in Philippines, peelings eaten (Pg); attacked in Java (Ri); could not verify damage (W).
Beach morning-glory (*Ipomoea pes-caprae*): This very common vine serves not only as one of the main shelter plants for achatina but as a good source of food;* a preferred food plant in Saipan (L).
Beans: Fed upon in Saipan (L); eaten voraciously in Philippine Islands (Pg); *Phaseolus radiatus* seedlings totally destroyed, foliage of older plants skeletonized, but the yam bean (*Pachyrhizus tuberosus*) suffered no damage(W).
Betel pepper (*Piper betle*): Untouched(G); no damage(W).
Bird's-nest-fern (*Asplenium nidus*): A preferred food plant in Saipan(L).
Blimbing (*Averrhoa bilimbi*): Fruit completely stripped in Ceylon(G).
Bougainvillea: Both large and small snails attacked in Riouw Archipelago (L and V).
Breadfruit (*Artocarpus* spp.): The fruit of this tree, whether it be green, overripe, rotting, or dried, is a real favorite of the giant snails. Although the snails have been seen up to about twelve feet in these trees, the fruit which had not fallen was never observed being attacked or showing any signs of attack. Since the native people of many Pacific islands have abandoned the breadfruit for the more easily prepared imported staples, the breadfruit crop in some areas is being allowed to contribute 100 per cent to the maintenance of a larger and still larger snail population which otherwise could not exist. Robert E Burton of the Agricultural Development Station on Ponape reported that all of a number of sprouted breadfruit clippings brought from the Truk Islands in 1948 were killed by having their bark removed by achatinas.* Inhabitants of Tinian report no damage (C); a chief food plant in Koror(K_2); a preferred food plant in Saipan(L).
Cabbage(*Brassica* spp.): This and other Cruciferae are the most preferred food plants in the Philippines(Pg); severe damage in Saipan(L).

Cacao(*Theobroma cacao*): In Ceylon the giant snails were frequently seen congregating in great numbers in the areas where the cacao pods were being harvested; they were observed feeding on the flowers, broken pods, seeds, and seedling plants in nurseries; damage varied from slight to severe;†fed on young shoots and flowers in Indonesia(BJ); young seedlings up to two months of age readily attacked and killed in New Britain (D); no damage (H); direct damage by consuming freshly planted seeds, indirect damage by destruction of cuttings of dadap cover crop in Ceylon (N); killed young plants and injured blossoms of bearing trees, impossible to plant new clearings in Ceylon (S); seriously attacked and damaged(W).

Cactus: Opuntia sp. eaten (BJ); *Opuntia* and *Cereus* suffered damage in Java (L and V); damaged (Pg); attacked in Java(Ri).

Calophyllum inophyllum: A definite preference for the leaves of this plant.*

Canna sp.: Eaten voraciously in the Philippines(Pg).

Carambola (*Averrhoa carambola*): Fruit reported damaged in Ponape.*

Carrots (*Daucus carota*): Severe damage to both the tops and the tuberous roots was reported by the inhabitants of Chichi Jima;* fed upon in Saipan(L).

Cassava (*Manihot esculenta*): Damage is largely restricted to the young plants, reported to be a serious problem in Romalum, Truk Islands;* Tinian inhabitants report no damage (C); badly damaged, young stems heavily peeled off and killed in Java(Fe); leaves and bark damaged in Sumatra(He); a chief food plant in Koror(K_2); attacked in Philippines(Pg); no damage(W).

Chili peppers(*Capsicum* spp.): Untouched(G); the fruit, leaves, and bark of *C. annuum* are attacked in Sumatra(He); stem and leaves of *C. grossum* eaten in Rota but damage not serious(K_3); fed upon in Saipan(L); no damage(W).

Citrus sp.: Near-ripe fallen fruit and foliage of sweet orange(*C. sinensis*) were observed to be eaten on Agiguan;* seedlings seriously attacked in Philippines(Pg).

Coconut (*Cocos nucifera*): No damage observed;*†swarming on fronds but no evidence of injury(G); no damage(H,S).

Coffee (*Coffea* spp.): Slight damage to berries in Malaya (Co); in Sumatra, young leaves attacked only when other food is not present(He); observed to attack in Philippines(Pg).

Corn (*Zea mays*): Only slightest damage to leaves and kernels in Chichi Jima, decaying leaves eaten readily;* inhabitants of Tinian report near distruction of field of very young seedlings, but no appreciable damage to larger plants(C); only slight damage to leaves in Sumatra(He); young seedlings readily eaten in Guam (K_2); fed upon in Saipan(L); seedlings sometimes attacked but no severe damage(W).

Cosmos sp.: Damaged in Philippines (Pg)

Cotton (*Gossypium* sp): In Mauritius "it was responsible for a good deal of damage to cotton seedlings, when the attempt was made to plant cotton, on a large scale, in 1911:(C and G).

Cowpea (*Vigna sinensis*): Cover crop in Ceylon almost completely destroyed (Br); the fruit, leaves, and stems are damaged in Sumatra(He); young plants completely destroyed, older plants skeletonized(W).

Cucumber (*Cucumis sativus*): Very little damage in Koror;* inhabiants of Tinian report serious damage often to entire plant (C); one of favorite foods in Sarawak (Ha); fed upon in Saipan (L); seriously attacked in Philippines (Pg).

Cucurbitaceae: Especially liable to damage(D).

Eggplant (*Solanum melongena*): Plants stripped of bark in Ceylon(G); fed upon in Saipan(L); attacked in Philippines(Pg).

Elephant ear (*Alocasia* sp.): Foliage only sparingly eaten in Ceylon(G); "ape" loaded with snails and eaten(K_1).

Euphorbiaceae: Eaten(BJ); *Euphorbia trigona* eaten in Java(L and V); inflorescences eaten, but no serious damage(W)(*vide* Rubber).

Ferns: Fronds of tree ferns (*Alsophila lunulata*) eaten in Palaus;* young snails especially destructive to garden ferns(G_1).

Flower gardens (general): A wide variety of garden flowers are readily eaten, some of them being quite seriously damaged;* suffering extensively in New Britain if they are not carefully protected(D); the damage killed young *Salvia* plants in Sumatra(Fe); "whole gardens devastated:(JK); do not seem to attack *Salvia*, *Torenia*, or *Coleus* in Ceylon(Ma); serious pest in horticulture(W).

Gourd(*Lagenaria leucantha*): "Upo" seriously attacked in Philippines(Pg).

Grasses: All seem to be nearly completely immune to attack.*†

Gynandropsis speciosa: Complete planting failed in Malaya in spite of controls(S).

Hibiscus spp.: A favorite plant, damage to both flowers and leaves noted;* hedges of this plant were invariably loaded with giant snails; all parts of the plant were subject to attack;†fallen flowers preferred in Palaus (E and T, H and K); damaged in Java(Fe); attacked in Philippines (Pg)(*vide* Okra).

Jak (*Artocarpus heterophyllus*): The fallen fruit is a great favorite; whole areas of bark, even on mature trees(Fig. 5), may be consumed; young seedlings very susceptible to damage;*†"chew up whole seedlings up to three to four feet in height overnight"(Ho).

Leguminosae (general): A number of unidentified species consumed in the field attest to the wide preference for this group;* damage to the cover crop plant *Pueraria thunbergiana* was essentially complete on some estates in Ceylon causing indirect damage to Cacao; the more hardy *Desmodium triflorum* was only slightly attacked; bark of *Gliricidia maculata* and dadap (*Erythrina lithosperma*) subject to extensive attack, even in trees in excess of three inches in diameter; flowers of the dadap are a favorite; large areas in *Pueraria* cover crop in New Britain barren and not reseeding (D); *Centrosema pubescens* damaged in Java (Fe); young dadap trees killed by bark removal in Ceylon (H); in Sumatra, the young leaves and bark of *Deguelia*sp. are damaged, and although under experimental conditions *Cassia multijuga* was not touched, the following were readily eaten: *Cassia mimosoides*, *Crotalaria anagyroides*, *C. striata*, *Indigofera suffruticosa*, *Mimosa invisa*, *Parkia* sp., *Tephrosia candida* and *T. vogelii*(He); indirect damage to tobacco as young plants to tobacco as young plants of cover and green manure crop (*mimosa invisa*) were stripped of their bark in Sumatra (M); particularly destructive to dadap cuttings in cover crop of cacao(N); could not grow leguminous ground cover crops in Ceylon when achatina was at its height(Ph); young dadaps girdled and killed(S).

Lettuce (*Lactuca sativa*): Native people of Tinian indicate no damage(C); severe damage in Saipan(L); plants of all ages completely defoliated, but only seedlings of *L. indica* destroyed(W); food of greatest choice in the laboratory(We).

Leucaena glauca: This exceedingly common introduced species in its characteristic dense stands is clearly a preferred food plant from the Hawaiian Islands (where it is known as "Haole koa") to Chi chi Jima; all parts are avidly consumed, including the water-soaked seeds and the exposed roots; the slender stems are frequently seen bent far over under the weight of snails feeding on the leaflets and tender bark;* occasionally fed upon in Tinian (C); not touched in Sumatra(He); defoliation of young "lamtoro" trees placed in a teakwood stand in Java(R).

Liliaceae: Nearly all lilies seem susceptible to attack;* *Crinum* and other lilies preferred (Da); favored plants(Ja); *Caladium* not attacked(Ma).

Malungay (*Moringa oleifera.*): Observed being attacked in Philippines(PG).

Melons (*Cucumis melo; Citrullus vulgaris*): The fruit and vines of all types are on the preferred list; on Rota, they cause such destruction of watermelon vines that the native people walk several miles to plant their seeds in an achatina-free area; attacks on the young fruit will badly disfigure it, interfere with proper development, and make it worthless for consumption;* inhabitants of Tinian report serious damage often to entire plant(C); severe damage in Saipan(L); rinds consumed(Pg).

Montanoa hibiscifolia: The bark and pithy stems deeply and extensively grooved in Hawaii.*

Morinda(*Morinda citrifolia*): Both the leaves and the mushy, white fruit were among the most preferred items in Koror;* preferred in Saipan(L).

Oil palm (*Elaeis guineensis*): Prefer overripe or underripe fruit in Malaya (Co_1, Co_2); attack mainly fallen fruit but also ripening fruit on branches (F); will attack leaves only if very hungry(He).

Okra (*Hibiscus esculentus*): Plant practically defoliated and fruit injured to such an extent as to make it valueless in Ceylon(G); severe damage in Saipan(L).

Onion (*Allium* spp.): No damage(W).

Orchids: *Phalaenopsis* and *Vanda* damaged in Riouw Archipelago and Java (L and V); *Phalaenopsis* spp. damaged in Philippines(O); attacked in Java(Ri).

Pandanus spp.: No damage observed;* occasionally fed upon(L).

Papaya (*Carica papaya*): A great many times the snails were seen high up in the trees; both fruit and bark are damaged; in Ponape missionaries complained bitterly of attacks on the fruit;* a fallen tree was completely consumed in a week, a near-prostrate tree suffered damage to buds and flowers, snails seldom seen in top of erect trees in Tinian(C); older trees in New Britain are deprived of their bark until they wilt and die, seedlings are eaten away completely(D); ripe fruit damaged in Saipan (E and T); leaves eaten, young stems ringed and killed(Fe); flowers consumed in Ceylon(G); fruit, leaves, and bark of young trees damaged in Sumatra(He); preferred by larger snails in Palaus(H and K); chief food plant in Koror, fruit liable to damage (K_2); preferred food plant in Saipan(L); eaten in Java(L and V); fruit eaten in Philippines(Pg); climb trees and eat ripe fruit(T).

Passion flower (*Passiflora* spp.): One of the commonest plants of choice in the Pacific; fruit, flowers, and leaves eaten; in many areas it is the main if not the sole food item;* greatest preference in Tinian(C); the leaves and ripe fruit are preferred items in Saipan(L); most of the snails' food is the old yellowing leaves and ripe fruit(T).

Peanut (*Arachis hypogaea*): A planter in New Guinea abandoned peanut cultivation largely because the snails made continual appreciable inroads in his fields (D); attacked the leaves, stems, and nuts in Sumatra(He); young plants completely destroyed, older ones seriously defoliated(W).

Pepper vine (*Piper nigrum*): Young pepper vines planted at the base of *Gliricidia* trees in an unthrifty cacao plantation in Ceylon suffered 100 percent kill because the palm frond shields, set up to protect the vines from the sun, provided shelter for great quantities of hungry achatinas; plant killed by eating outer layers of stem; Tinian inhabitants report vines often killed by snails(C); leaves attacked in Sumatra(He).

Pineapple (*Ananas comosus*): No damage observed or reported in the East Caroline Islands, Hawaiian Islands, or Ceylon;* no record of feeding on Pineapple(Pe).

Pipturus albidus: The fallen leaves of the common "mamaki" of the Bonin Islands were observed to be a definite favorite.*

Pumpkin (*Cucurbita pepo*): In Chichi Jima, the pumpkins had to be raised in protected boxes and then transplanted to prevent them from being chewed off as fast as they came up:* inhabitants of Tinian reported serious damage often to entire plant (C): species introduced by Japanese in New Britain entirely eliminated by the snails in some areas (D): leaves skeletonized and stems barked in Ceylon (G); fed upon in Saipan (L).

Ramie (*Boehmeria nivea*): Attacked in Philippines (Pg).

Rice (*Oryza sativa*): No damage (G,H,He,W); no harm except breaking down plants with their weight (S).

Roses (*Rosa* spp.): Do not seem to attack in Ceylon; attacked in Philippines (Pg).

Rubber (*Hevea brasiliensis*): Occasional specimen seen feeding on latex at tapping site; disfiguring or killing damage to young plants in nurseries considerable in some areas; feed on young seedlings and buddings, continued destruction of buds produces distinctive type of fasciation(Be); drink latex and eat sweet cambium layer of bark exposed by tapping thus causing wounds (Be_2); serious economic importance in Malaya (Be_1); feed on young shoots and flowers (BJ); damage to young rubber rather serious in Ceylon (Br_1Ct); G. A. C. Herklots indicates no very considerable losses in rubber industry C_a); young trees severely damaged in Sumatra; bark removed, stems ringed, leaves consumed, growing tips and replacement growth damaged to such an extent that death resulted in some cases; older trees not seriously affected although the snails' consumption of latex (proved by crushing snails and observing the latex in the gut) contaminated the latex, sidetracked its flow, and caused the collecting cups to fall to the ground(Fe); no damage(H); young leaves and bark damaged only when more acceptable food is not present (He); bark stripped off, killing young plants; achatinas seen by the hundreds in Ceylon sucking sap in latex cups(N); "learned to drink rubber latex" (Pb); strip succulent bark from young plants, drink latex(Ph); drink a considerable amount of latex(Pv); impossible to plant new clearings in Ceylon in 1916(S); seriously attacked(W).

Scaevola frutescens: Both leaves and flowers are preferred items*.

Soursop (*Annona muricata*): No apparent damage in Dublon, Truk Islands;* a preferred food plant in Saipan(L).

Squash (*Cucurbita* spp.): Attacked in Philippines(Pg).

Staple crops (General): Left unharmed in Malaya (Be_2); no appreciable damage in Malaya (S_1); damage only a fraction if at all(W).
Sugar cane (*Saccharum officinarum*): Often found congregating in great numbers on the leaves but damage was practically nil;* damage to leaves on Saipan (E and T); damage in Java, especially to the leaf axils where there is much less concentration of silica cells, but of no real economic importance (Hs); a chief food plant in Koror(K_2); no record of damage(Pe).
Sweet patato (*Ipomoea batatas*): The vines provide cover often for phenomenal numbers of snails but damage to leaves and exposed tubers was invariably inappreciable;* not eaten in Tinian according to inhabitants(C); many snails but no damage was noticeable in Ceylon (G); a chief food plant in Koror (K_2); attacked in Philippines(Pg); foliage sometimes attacked but no serious damage(W); foliage a food of choice in the laboratory(We).
Taro (*Colocasia esculenta*): Foliage is not infrequently attacked, though seldom skeletonized; rarely, damage is caused to exposed roots; total damage is surprisingly almost inconsequential even in areas overrun with snails;* a lot of damage in Kabunga, New Guinea (A); feed only on fallen leaves, but according to the inhabitants of Tinian, the rarely exposed tubers are eaten(C); only slightly affected in New Britain as it is particularly hardy andfast growing(D); foliage eaten very sparingly in Ceylon (G); fallen leaves eaten in Palaus (H and K); not affected in Guam (K_1); a chief food plant in Koror(K_2); only occasionally fed upon in Saipan(L).
Tea (*Camellia sinensis*): Every report in Ceylon was negative; young shoots and flowers are eaten(BJ); no damage in Ceylon(H); young leaves attacked only when there is little else to eat(He)/
Teakwood (*Tectona grandis*): Year-old plants damaged in S. Sumatra(AV); up to 90 per cent lethal damage to young plants in Java(R).
Thespesia populnea: A preferred food plant in Saipan(L).
Tobacco (*Nicotiana* sp.): Bark removed from base of plant, stalk weakened so that it blows over easily; leaves of young plants eaten; total damage negligible; will never become a serious pest(M).
Tomato (*Lycopersicon esculentum*): Foliage seriously damaged in Guam immediately following the first big rain of the season;* not attacked in Ceylon(Ma); decaying fruit consumed(Pg); indifferent to plants(W).
Tree nettle (*Laportea crenulata*): Stems and branches completely denuded, killing the trees; practically exterminated in some localities(G).

Vegetables (general): Most varieties were found to be attacked at least to some extent; in some cases serious damage was caused, especially in small plots adjacent to abandoned or uncultivated areas;* suffering extensively in New Britain if they are not carefully protected(D); certain plants defoliated and others denuded in small vegetable patches(G_2); damage to fresh vegetables caused mainly by the smaller specimens(H and K); a pest(H); farmer in Sinajana-Ordot area of Guam reported that it was not possible to raise vegetables as they were to vulnerable to attack by snails(K_1); serious pest in Seychelles(M_1); decided preference for succulent vegetables in Philippines(Pg); a serious pest in Ceylon(Pv); "great depredations" in Calcutta(Ry); in some localities in Malaya the growing of certain vegetables has become almost impracticable(S); particularly destructive(T); seriously attacked(W).

Vegetable sponge (*Luffa* spp.): "Patola" seriously attacked in Philippines (Pg).

Weeds and uncultivated plants: Many species are attacked; some are definitely preferred and others are only occasionally eaten;* Lange(1950) has prepared an impressive list for Saipan and as far as known, it is the only such list extant.

Xanthosoma braziliense: Leaves and stems of "Tahitian spinach" eaten in Hawaii(K_1).

Yam (*Dioscorea alata*): The leaves are an obvious favorite; eaten extensively in Ceylon; no appreciable damage in Tinian(C); young plants eaten down to the ground in Ceylon(G); impossible to plant yams in Rota when snails were abundant(K_3); severe damage in Saipan(L) "ubi" seriously attacked in Philippines(Pg).

Zinnia linearis: Attacked in Philippines(Pg).

E. REFERENCES.

Bailey, P. (1976) Food of the Marine Toad, *Bufo marinus*, and six species of skink in a cacao plantation in New Britain, Papua New Guinea. *Aust. Wildl Res. 3,* 185-188.

Grzimek, Bernhard (Ed.-in-Chief). (1974) *Grzimek's Animal Life Encyclopedia* (van Nostrand Reinhold)

Mead, A.R. (1961) *The Giant African Snail:a problem in economic malacology* (University of Chicago Press).

Tyler, M.J. (1975) The Cane Toad *Bufo marinus*. An historical account and modern assessment. (The Vermin and Noxious Weeds Destruction Board Victoria and the Agriculture Protection Board, Western Australia).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XXI THE PACIFIC COAST SQUID *(loligo opalescens)*

by

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ABSTRACT

The precise environment of the Pacific Coast Squid *(Loligo opalescens)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A. INTRODUCTORY NOTE

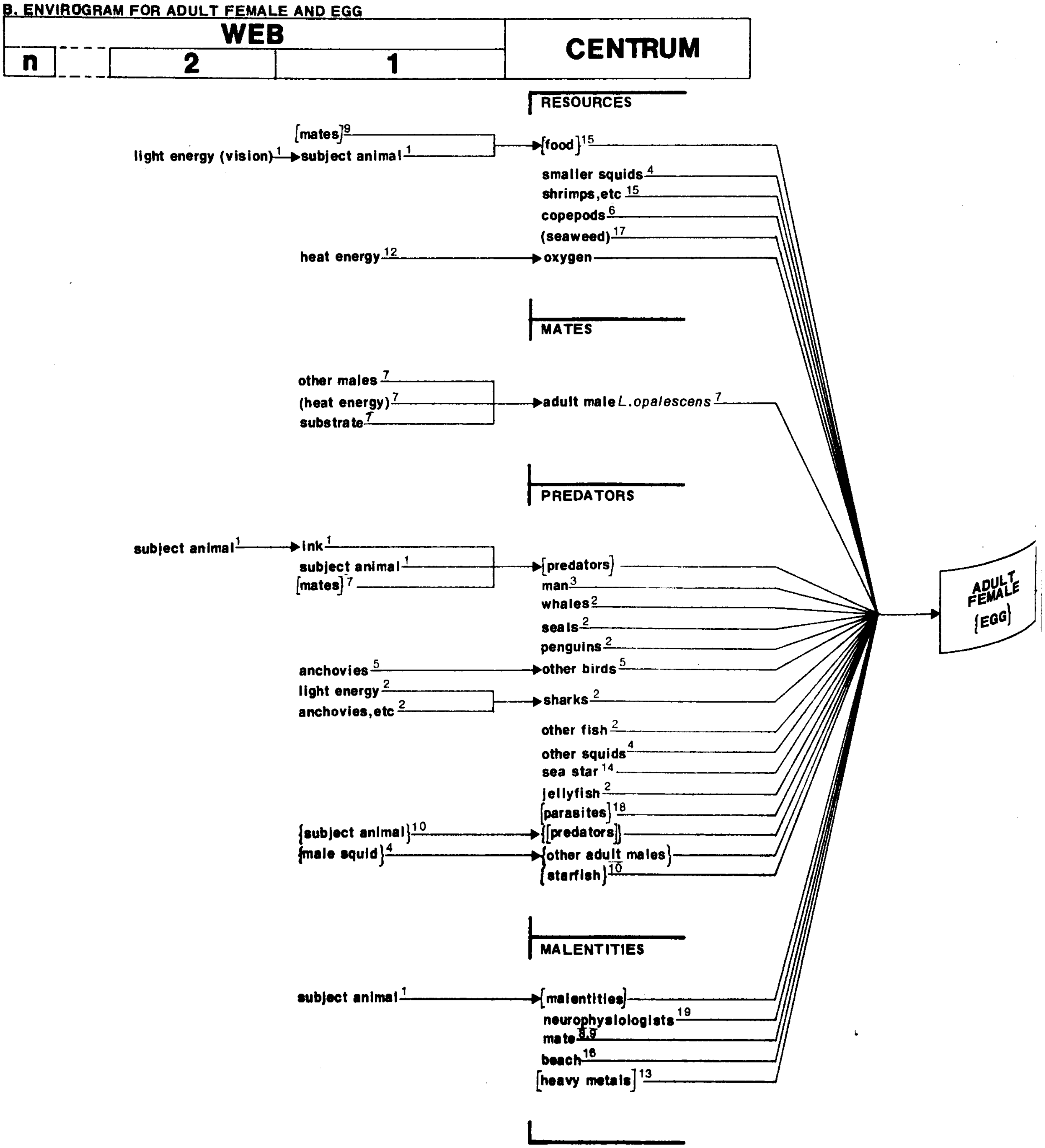
Observations of the Pacific Coast Squid, *Loligo opalescens* have been made mainly off the west coast of North America, or in aquaria.

Squids are the most numerous of the cephalopods. They all have 8 arms and 2 tentacles. The tentacles can be 'shot out' to sieze prey. Like other squids *L. opalescens* possesses poison glands but in this species they are relatively small.

L. opalescens forms schools which are similar in many ways to those of obligate schooling fishes. The schools are marked by parallel orientation of individuals and great cohesiveness. Schools are invariably made up of uniformly-sized individuals. Parallel orientation is weaker in schools of smaller individuals (7cms approx. dorsal-mantle length) than in longer (12cm).

In an experiment with rearing hatchlings from eggs Hanlon *et al* (1979) observed variable growth rates in the young *L. opalescens*, with a range of from 1.1 to 5.6mms in mantle length per month. The maximum mantle length observed in the 79 days of the experiment was 17.3mm. Hurley (1976) reported that newly-hatched individuals had an average mantle length of 2.7mm. He also found highly variable growth rates ranging from 0.5mm to 4.5mm (approx.) mantle length per month.

B. ENVIROGRAM FOR ADULT FEMALE AND EGG



C NOTES ON THE ENVIROGRAM

1. Laboratory experiments indicate that the main sense modality operating in this animal is vision. Squid eyes can each see almost 180°, but they cannot see dead astern, the characteristic swimming direction.

Of all the cephalopods the squid can move fastest. The nervous system of *Loligo* enables it to react almost instantly - for either attack or escape. The speed of conduction of a nerve impulse depends largely on the diameter of the nerve fibre. In the mantle of the squid the longer the fibre, the greater the diameter. The result is that impulses arrive simultaneously at all points of the mantle enabling it to contract as a whole. This accounts for the squid's quick reaction time and great speed. One worker, judging by squids being chased by sea lions, estimated their speed at 5-8 m.p.h. (This seems to be rather low, since *O. vulgaris* is estimated to be able to travel at 8 m.p.h. and we would expect *L. opalescens* to be able to travel faster).

The defensive behaviour is as follows: the animal first turns dark and simultaneously ejects a dark ink towards the predator. Often the ink blob will retain a roughly squid-like shape while the animal itself changes to a lighter colour and escapes. The lighter colour is made possible by the iridophores and leucophores in the epidermis, which enable the animal to assume the colour of its surroundings by reflection of ambient light.

Sometimes hunting is done in the characteristic parallel school formation (see §A), the squids darting and weaving as one unit through a school of fish.

Occasionally the animal has been seen to use the tactic of dropping to the sea floor, matching its colour to that of the surrounding sand, and then propelling itself towards an unsuspecting passing fish.

All squids can regenerate arms which might be broken off or damaged by a predator or malentity.

2. All Antarctic penguins will eat squid, also most of the toothed whales, in particular the 50-ton sperm whale *(Physeter catodon)* and the bottlenosed whale *(Hyperoodon* sp.*)*; 10,000 squid beaks

have been found in the stomach of a bottlenosed whale.

Seals, sealions and sea elephants also attack and eat squid.

Small squid are eaten by jellyfish.

Salmon, the large-billed sword-fish, the dolphin fish *(Coryphaena hippurus)*, tuna and many other fish eat squid.

Tricas (1979) found that the blue shark *Prionace glauca* moved inshore to feed on winter spawning schools of *L. opalescens*. The sharks also feed on the northern anchovy *Engralis mordax*, the pipefish *Syngnathus californiensis*, the jack mackeral *Trachurus symmetricus* and the blacksmith *Chromis punctipinnis*, all of which are thus modifiers of the shark in the environment of the squid. The sharks forage in waters near the surface from near midnight through dawn, thus *L. opalescens* is not attacked during the day; for this reason we have recorded 'light energy' also as a modifier of this predator.

3. Humans (particularly Italians) eat squid (calamari). Fishing for *L. opalescens* off the Californian coast is becoming important economically.

4. The squid will eat other squid with relish. Often larger squid will follow schools of smaller squid, feeding continuously.

5. The following sea-birds are known to eat squid:

albatrosses,
giant petrel *(Macronectes gigantea)*
pacific boobie *(Sulidae)*
King penguin *(Aptenodytes forsteri)* and other penguins
guillemot *(Uria aalge)*
rhinocerous auklet *(Cerorninea monocerata)*, a particularly heavy predator

Many sea-birds prey extensively on the northern anchovy *Engraulis mordax* as well as on *L. opalescens*, so the former appears on the envirogram as a first-order modifier.

6. In an experiment on the rearing of squid hatchlings from eggs by Hanlon *et al* (1979) the young squid were fed on live copepods. Initially there was high mortality among the young squids because of their inability to catch the copepods, until they learnt to approach a copepod from the rear, thus avoiding their antennae.

Hurley (1976) fed young *L. opalescens* on the copepod *Artemia* sp.

7. *L. opalescens* normally breeds from early spring to late summer, though some eggs can be found all the year round. Spermatophores are produced throughout the breeding season; 20-40 may be held at one time.

There is often a migration inshore for the breeding season. There are huge shoals and communal spawning. At these times the animals are oblivious to all else. They do not become alarmed or spray ink and are easy prey.

Normally *L. opalescens* will swim fin forward, but when mating the male reverses and grasps the female round the middle. Often a second male will cut in and sometimes skirmishes break out when the two males grab the same female simultaneously. The successful male will then reture to deeper water with the female. In the absence of a rival, mating is completed quietly on the surface.

During mating, the male flushes brilliant red-brown, first intermittently and continuously. An intruding male can prevent these flushes and delay or terminate the mating. The colour-change is made possible by chromatophores underlying the iridophores and leucophores in the epidermis (see n. 1).

Excited males in a frenzy occasionally deposit spermatophores into the mantle cavity of other males.

Generally squid eggs are laid well below the surface. The females attach the eggs to the substrate. Sometimes males will spray semen over already deposited eggs. Some eggs left in a tidal pool were observed; these failed to hatch, possibly because ultraviolet light killed the embryos. At La Jolla, California, in December 1955, an estimated 220 acres of sea floor was covered with *L. opalescens* eggs. One very large mass began at a depth of 70 feet and continued down a slope past the 114 ft. depth.

Some workers report that *L. opalescens* dies after breeding. Lane (1960) reports the sea bottom littered with dead and dying squid after mating.

8. During a mating frenzy a very vigorous and ardent male may actually kill the female. In this case the male squid is acting like a malentity in the environment of the female, since H (male) is not increased as a result of the encounter (see also n. 9)

9. Both females and males cease feeding during the inshore migration preceding the mating season (see n.7). The females have empty guts during the mating season while the males' guts contain only a few shreds of epidermis apparently ripped from the female when mating (see also n. 8). Thus a male mate is again a malentity and 'mates' are first-order modifiers of food.

10. Squid eggs are distasteful to most marine species. A string of squid eggs fed to an anemone was observed by Lane (1960) to be regurgitated within a few hours, after which they continued to develop normally. However, the starfish *Patira miniata* digested a string of squid eggs - but took 72 hours to do so.

11. According to Lane (1960) the eggs are not cared for by the squid.

However Hurley (1977) observed in an aquarium male *L. opalescens* exhibiting dominance behaviour after mating and oviposition were completed and "standing guard" over egg masses. These males used postural and colour displays (see n. 7) directed towards "challenging" males in order to drive them off. Females, however, were allowed to approach the egg mass.

12. Hurley (1976) found that respiration is temperature dependent; the higher the temperature the higher the oxygen consumption.

13. Martin (1975) analyzed 43 livers from *L. opalescens* for their silver, cadmium, copper, zinc and iron contents. Copper concentrations of up to 15,000 µg/g dry weight were found in conjuction with signficiant correlations between this element and silver, cadmium and zinc. The

latter elements, which are environmental pollutants, are known to affect copper metabolism in terrestrial organisms; whether the correlations occuring in marine organisms represent casual or cause and effect relationships is unknown.

14. Wobber (1973) found that the sea star *Pycnopodia helianthoides* feeds on dead and dying *L. opalescens*, presumably mainly following the mating season (n. 7). The pens (shells) are later extruded from the sea star.

15. The food of squids ranges from plankton to fast powerful fish; the shrimp *Crangon crangon* Linnaeus 1758 is eaten as well as other crustaceans.

16. When hunting fish close inshore, squid have been observed to beach themselves and die. The strandings appear to be accidental, but in attempting to free themselves they invariably fill their funnel and point it seaward, thus driving themselves higher onto the land.

It has been reported that a squid, once stranded, if thrown back into deep water will merely strand itself again.

17. Other species of squid have sometimes been observed to eat seaweed e.g., the Common American Squid bites pieces of eel grass *(Zostera marina)* - however the grass is not digested.

18. Lane (1960) comments that there are many parasites, but gives no details. Nor have we been able to find in the literature an account of the organisms parasitic on *L. opalescens*.

19. The nervous system of the squid has become important in scientific research, (c.f. note 1) and the work done on these animals has given rise to the discipline of neurophysiology.

We have classified 'neurophysiologists' here as malentities, but see the General Introduction to this series of Working Papers (1983 version) for a discussion of the difficult question of incorporating *Homo sapiens* into the environment of other animals.

E REFERENCES

Baltz, D.M. and G.V. Morejohn (1977). Food habits and niche overlap of seabirds wintering on Monterey Bay, California. *Auk* 94(3), 526-543.

Costeau, J.-Y. and P. Diolé (1973). *Octopus and Squid: the soft intelligence.* (Cassell, London).

Hanlon, R.T., R.F. Hixon, W.H. Hulet and W.T. Yang (1979). Rearing experiments on the California Market Squid *Loligo opalescens* Berry 1911. *Veliger* 21(4), 428-431.

Hurley, A.C. (1976). Feeding behaviour, food consumption, growth and respiration of the Squid *Loligo opalescens* raised in the laboratory. *U.S. Natl. Mar. Fish. Serv. Fish. Bull.* 74(1), 176-182.

Hurley, A.C. (1977). Mating behaviour of the Squid *Loligo opalescens. Mar. Behav. Physiol.* 4(3), 195-203.

Hurley, A.C. (1978). School structure of the squid *Loligo opalescens. U.S. Natl. Mar. Fish. Serv. Fish. Bull.* 76(2), 433-442.

Lane, F.W. (1960). *Kingdom of the Octopus.* (Sheridan House, London).

Martin, J.H. (2975). High copper concentrations in squid livers in association with elevated levels of silver, cadmium, and zinc. *Mar. Biol. (Berl).* 30(1), 51-56.

Tricas, T.C. (1979). Relationships of the Blue Shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. *U.S. Natl. Mar. Fish. Serv. Fish Bull.* 77(1), 175-182.

Wells, M.J. (1978). *Octopus: physiology and behaviour of an advanced invertebrate*, (Chapman and Hall, London).

Wobber, D.R. (1973). Aboral extrusion of squid pens by the Sea Star *Pycnopodia helianthoides. Veliger* 16(2), 203-206.

Young, J.Z. (1964). *A Map of the Brain.* (Oxford University Press).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XI THE COMMON OCTOPUS *(Octopus valgaris)*

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ABSTRACT

The precise environment of the Common octopus *(Octopus vulgaris)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

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This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A. INTRODUCTORY NOTE

O. vulgaris lives mainly in tropical and sub-tropical waters. It is especially abundant and well-knwon in the Mediterranean; there are remarks on its occurrence in the works of Aristotle and pottery from the Minoan and Mycenean civilizations is often decorated with stylized and naturalistic representations of octopodes. The animal is rarely found north of the English Channel.

All cephalopods are marine and die quickly in fresh water. They have 2 gills, 2 kidneys and 3 hearts - 2 to pump de-oxygenated blood through the gills and the third to pump oxygenated blood through the body. The blood is blue; the colour is from the copper-containing compound which holds the oxygen.

Eggs are between 1 and 3 mm long. Immediately upon hatching (after 4-5 weeks) the young octopus, now 2-3 mm in length, enters the planktonic stage. This stage lasts a maximum of 3 months, after which the animal will settle out of the planktonic stage at a length of about a centimetre. The growth of newly-settled animals is rapid; on average in 40 days at 25°C in the laboratory they will increase their size by a factor of 10. After 2 years the animal will weigh about 5 kg and apparently usually dies at this weight (see n. 7). However, occasionally individuals weighing 25 kg have been found (Wells, 1978). The largest specimens span 10 feet with bodies 9 ins. across. They are generally found in deeper water than the smaller individuals. The maximum (reliable) depth record for *O. vulgaris* is about a quarter of a mile.

The maximum life span for *O. vulgaris* is unknown.

O. vulgaris is colour-blind.

Among octopodes, the Common Octopus has a particularly virulent poison. The animal captures its prey by seizing it with suckered arms or enveloping the prey in its web.

There is an annual migration inshore in the spring in which the males precede the females.

Octopodes sometimes deliberately leave the water but not for long, nor do they travel great distances. However they have been seen seizing a crab on rocks out of the water. If kept cool they can live up to 48 hours out of water.

The adult *O. vulgaris* swims backwards, but a young animal, up to a week after hatching, will swim backwards or forwards with equal facility. An octopus can also swim by contracting the web-like basal membranes. They characteristically 'glide-crawl' in their usual habitat. An individual with a 2-foot span has been reported as moving at 8 m.p.h. During migration *O. vulgaris* travels quite significant distances at 4 m.p.h. Each expelled jet drives the octopus 6 - 8 ft.

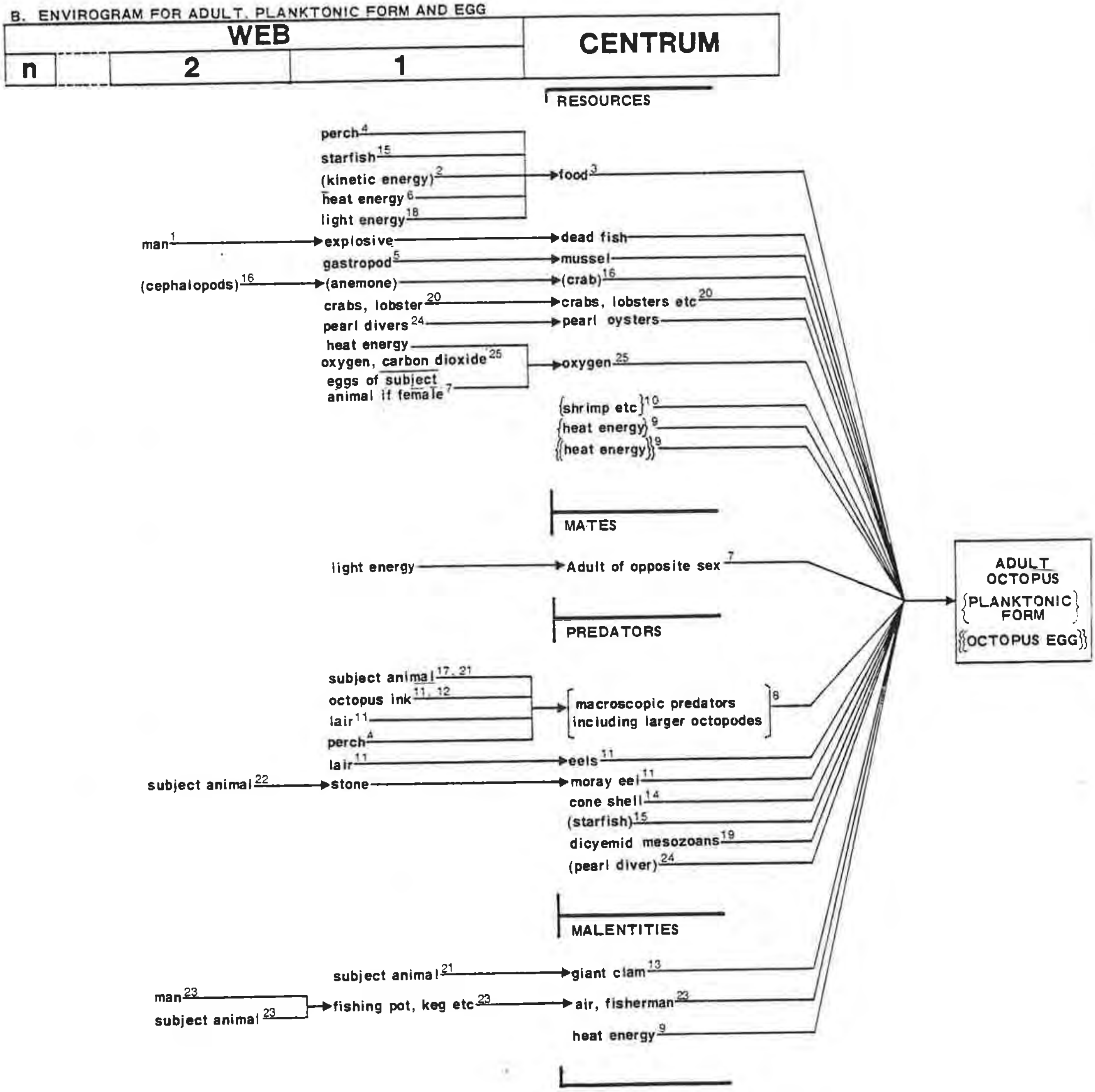
Octopodes have been observed eating themselves, usually arms; such autophagy is a frequent preliminary to death. Detailed reliable observations of this and other forms of cannibalism are not available for *O. vulgaris*, so we have not shown cannibalism on the envirogram.

Parasitism is strongly suspected, but we have not been able to find reports of parasites specifically for *O. vulgaris* (but see n. 26).

Octopodes can squeeze through extremely small holes and spaces. They tend to lurk in crannies (see n. 23).

Several cases have been reported from Japan and the Mediterranean of octopodes being used to retrieve things from the sea floor.

B. ENVIROGRAM FOR ADULT, PLANKTONIC FORM AND EGG



C NOTES ON THE ENVIROGRAM

1. Wells (1978) reports the octopus feeding on fish killed by an explosion at sea. Live fish are probably ignored (see n. 3).

2. The animal nearly always attacks live prey and motionless potential food is usually ignored unless touched (Wells, 1978). Visually detected movement in prey may be an important factor in triggering a response in the animal. Nevertheless, blind octopuses feeding and behaving normally have been reported in aquaria.

3. In the laboratory an octopus will eat crabs (see also notes 16, 21), lobsters, bivalves, gastropods and fish if it can corner them. It will also eat other octopodes if not well-matched in size or preoccupied with mating. Shells and exoskeletons scattered around known lairs indicates that the octopus diet in the wild is similar. However *O. vulgaris* has been observed to ignore live fish in the sea, presumably because they cannot be cornered. Crabs appear to be the favourite food, especially in the Channel Islands.

The adult *O. vulgaris* is probably an opportunistic feeder but is most likely to forage away from its lair between dusk and dawn. It seems likely that at least some of the prey captured in these often quite lengthy excursions may be eaten away from the lair.

In captivity the normal food-gathering method is a visually-directed jet-propelled pounce. Observations of the octopus feeding in the wild are rare and almost always involve an unknown interference effect by the observer. Nevertheless, it is generally assumed that gathering behaviour is similar in the wild.

The octopus will hold the prey, live, in its web, retreat to its lair, then poison the prey by secretations (see § D) from its salivary glands. There is circumstantial evidence that the animal uses some form of external digestion prior to internal digestion.

If there is any disturbance in the vicinity the octopus will raise its head from the lair; sometimes the animal alternately raises and lowers its head suggesting that it may determine distance by parallax.

On seeing prey, the octopus characteristically changes colour to reddish brown. Where several prey are available the animal will go on collecting, for example crabs - even if this results in earlier captures escaping from its web. Finally the octopus will poison all of the crabs before settling down to eat them singly.

In preying upon gastropods the octopus is reported by Wodinsky (1978) and others to bore a hole in the shell, inject toxin, then pull out and consume the affected snail. *O. vulgaris* has a typical molluscan radula and a parrot-like beak of tanned protein. It is widely reported as using the radula to bore holes in shell-fish after which substances from the salivary gland are utilized to kill the shellfish and loosen muscle attachments. However, Wodinsky reports that a brooding female will not bore a hole in a gastropod shell but instead "expend a great amount of energy pulling the living snail out by force - she then scarcely eats the snail". The feeding behaviour of brooding reproducing females undergoes other substantial changes; intake decreases by:

(i) 70% of normal intake per meal,

(ii) 65% of normal number of meals,

amounting to a total decrease of nearly 90%.

According to Hamada (1974) the octopus never bores holes in a molluscan shell. It shows greater appetite for bivalves than snails. "Some gastropods, that have a calcareous operculum or that withdraw too deeply into their shells to be reached by the octopus' mouth, were not eaten, although they were seized by the octopus and carried into the nest." The scars left on the shells clearly indicate that the octopus knew the position most easily accessible for biting.

Any prey which is too large to be bitten by the octopus' beak is never eaten. No nudibranches or echinoderms were eaten.

4. Kayes (1974) reports that around Malta the perch *Serranus scriba* often follows the octopus on its foraging expeditions. The fish is conspicuous where the octopus is not, thus giving away the latter's position to potential prey (which can then seek shelter) and to potential predators.

5. The predatory gastropod *Ocenatra* sp. eats the mussels *Mytilus* spp., also food for *O. vulgaris*. Both the gastropod and the octopus drill through the shells of the mussels with their raduli (Simpson *et al* 1957).

6. In Naples harbour, a natural habitat, the water temperature varies from 25°C in summer (July, August) to 15°C or less in mid-winter. All *O. vulgaris* eat less in winter and some even lose weight. Starvation causes emaciation but not debilitation; the animal will remain alert after losing 40% of its body weight.

Wells (1978) suggests that time for digestion seems to depend only on temperature. Data are far from conclusive, but the suggestion is consistent with information from other poikilotherms. The size of the meal is not important but Wells (1978) remarks that the animal is evidently sensitive to the presence of food in the crop. After feeding there is an increase in the tendency to attack objects seen, which rises to a maximum after about half an hour and then declines progressively. The rise and fall correlates nicely with the weight of the crop over the same period.

7. Although not reflected in the catch it is believed that the sex ratio for *O. vulgaris* is 1:1 (Wells, 1978).

Sperm are packed into spermatophores and are ejected after copulation into the mantle cavity of the female.

There seems to be no specifically sexual display, but it is likely that either subtle visual or chemo-tactile cues are used in recognising the opposite sex.

Females lay eggs in strings and attach them to the roofs of their lairs; if there is no roof as in an aquarium they attach them to the sides. They lay up to 150,000 eggs in strings of many hundreds; this may take a week or more. Average egg size is 1 to 3 mm. The female then broods the eggs for 4 to 6 weeks (at 22° - 23°C). During this time she continually directs jets of water over the eggs. She rarely leaves them, seldom feeds and becomes emaciated (see n. 3). Respiration increases during this period and intruding rubbish and animals (including those normally eaten) are pushed away to arms length.

Shortly after the eggs hatch the female dies. This seems to be universal for octopodes; males grow at the same rate as females and it appears that most males also die by the end of their second year (see exceptions in §A).

Hatanaka (1979) reports that off the north-west coast of Africa males larger than 50 cm in total length carry spermatophores in all seasons. The majority of females larger than 70 cm in total length are mature in the spawning seasons, while those less than 50 cm are usually immature.

8. In the laboratory, when a new octopus is introduced a resident male will immediately flush 'dark' and act aggressively. If the intruder is a male a fight will ensue and the smaller will generally be killed and eaten. If the intruder is a female she will generally submit and copulation (see n. 7) will follow (Wells, 1978). We do not know what occurs when two females are thus thrust together.

9. The development of the eggs takes about 28 days at 22°C. The planktonic stage may last up to three months in the cold waters of the English Channel (i.e. at the northern limit of the range of *O. vulgaris*) but is usually much shorter. Wells (1978) reports Japanese work in which the eggs were raised at 25°C in the laboratory and settled between 33 and 40 days after hatching.

10. During the "planktonic stage" - after hatching but prior to settling on the substrate as adults - the young octopodes feed on plankton. In the laboratory larvae have been raised on live shrimp larvae, *Palaemon serrifer*, fragments of crab meat and finally, as the larvae settle to the bottom, whole small crabs.

11. Large eels, including the Common Moray, *Gymnothorax mordax*, the Giant Moray, *Enchelynassa* spp. and Conger Eels, *Conger* spp., are the most important predators of octopodes.

While both the sight of a Common Moray and its 'smell' will alert an octopus alarm can only be engendered by a combination of both stimuli. The ejection of ink, generally black in octopodes, is the only means of defence. If necessary, several successive ejections can be made - up to six have been observed. Moray eels have poor eyesight and a trace of octopus ink in the water is sufficient to send them into a hunting frenzy. However, high concentrations of ink will paralyse the olfactory sense of the eels; this has been observed in aquaria; whether it occurs even partially, in a natural habitat is unknown. High concentrations of ink in enclosed waters have been fatal to some species of octopus.

Eels will swallow small octopodes whole. Larger octopodes will often fasten their legs around the eel's head but by gymnastic contortions the eel usually succeeds in eating the octopus. Very large octopodes are often eaten arm by arm - the eel grasping and twisting them off successively. During the short pauses while each arm is consumed the octopus may escape (see n. 21).

The lair of the octopus enhances its chance of surviving in two ways. First, the possibility of detection is reduced. Secondly, the lair affords a certain amount of protection and some possibility, therefore, of escape from an attacking eel. Lairs are usually well separated, possibly in order to avoid cannibalism (see §A). The octopus sometimes moves medium-sized rocks into an 'extension' of the lair if the natural terrain does not provide enough protection. However, Bierens De Haan (1929) shows that octopodes will as readily collect transparent as opaque objects to fashion a lair. The octopus also shows no preference between the "hide" given by two parallel sheets of glass and two similarly placed pieces of slat. He concludes that in building a lair the octopus is not seeking to hide itself.

12. In addition to its anaesthetizing uses (see n. 11) octopus ink has other defensive effects. First, the ink can provide a screen behind which the octopus will change colour and dart swiftly away. Secondly, the ink can produce the effect of a decoy; particularly with small octopodes the ink may remain in a concentrated blob, about the size of the animal's body, while it changes colour and escapes.

13. In northern Australia an octopus has been observed with one arm caught in a Giant Clam, probably *Tridacna* sp.. The octopus was later seen swimming away with only seven arms (see n. 21) (Lane, 1960).

14. Lane (1960) records, from northern Australia, a reported encounter in a collecting bucket between a cone shell, *Conus textile*, and *O. vulgaris*. The gastropod, which is poisonous, injects its venom through a radula tooth which is modified to form a hypodermic needle. The octopus put an arm into the shell but withdrew it after 20 seconds, became violently agitated and shed the arm, which was broken off near the body. The octopus died the following night. It was suggested that similar encounters would be frequent in the natural habitat. We classify *Conus textile* as a predator, not a malentity, because it characteristically hunts its prey this way and we see no reason why it should not consume octopus flesh.

15. Many echinoderms have dietary overlap with the octopus, particularly the starfish (Asteroidea) which consume many shellfish.

Lane (1960) reports two unusual cases in which octopodes were paralysed by starfish. In the case in which the brittle star *Ophiocoma echinata* was involved the octopus died. The effect seemed to be well-known to local fishermen.

We have tentatively classified starfish as a predator since the octopus would probably be consumed if it were paralysed after an attack in the wild. However, in its natural habitat it seems likely that an octopus would be able to avoid debilitating contacts.

16. Grzimek (1974) describes the relationship between the pagurid *Eupagurus prideauxi* and the anemone *Adamsia palliata* in which the anemone provides protection for the crab from predation, in particular by fish and octopodes. Ross and von Boletzky (1979) report an association between the pagurid *Dardanus arroser* and the anemone *Calliactis parasitica*; they comment that after a long confinement in an aquarium not containing an octopus the crab "loses its activity towards its symbiotic actinium *C. parasitica*". However in the presence of *O. vulgaris* (and other cephalapods) the activity is restored. Although

visual cues are insufficient, effluent from a tank containing an octopus will revive the activity.

We have used parentheses on the envirogram because in the first case above we are not sure that *O. vulgaris* is one of the predators and in the second case we are unsure of the nature of the 'activity' reported and the precise effects of the anemone.

17. The octopus is able to change its colour to match its surroundings, thus assisting it to escape the attention of predators.

18. Kayes (1974) made hourly inspections, day and night, for eleven days and found that *O. vulgaris* hunts virtually throughout the night with only brief excursions away from its lair during the day,

19. According to Lapan (1975) the dicyemids are very common parasites, known since 1839, in the nephridia of cephalopod mollusks.

20. Crabs are able to shed their claws and sometimes escape this way, thus acting as first-order modifiers of themselves regarded as a resource for the octopus.

Lobsters (*Homarus* spp. Weber 1795) and fiddler crabs (Portunidae) both resist (fight back) attempted octopus predation. This is atypical, most crabs being strangely quiescent.

Crabs which are eaten include *Carcinus* spp. The octopus also eats abalone (*Haliotis* spp.), clam (*Chione* spp.), scallop (*Pecten circularis requisulcatus*) and the little neck clam *(Protothaca jedoensis)*. (see also n. 3).

During the winter of 1899 a plague of *O. vulgaris* occurred in the English Channel and along the French coast. Many fishermen were forced to find other work as oysters, abalone and many varieties of fish became very scarce, undoubtedly due to predation by the octopus. Estimates were that there was an 18% fall in the number of lobsters and a 32% fall in the number of crabs compared to those taken the previous year. 1922 and 1950/51 were also plague years but not to the same extent.

The octopus poison attacks the crab's central nervous system.

21. *O. vulgaris* can apparently shed a limb at will and can suffer severe injuries and mutilation and yet survive. Regeneration of many parts is possible. In one instance, one-third of an arm was broken off and was observed to be fully regenerated and functional, although thinner, after 6 weeks.

22. Lane (1960) reports having seen a film of an individual *O. vulgaris* holding a stone as a shield against the attacks of a Moray eel.

23. The habit of the octopus of lurking in crannies often leads to capture by fishermen using kegs, pots etc., or death from exposure to the air, since the animal tends not to abandon the pot even when it is being raised. The animal itself is a modifier of the fishing pot, since the pot disappears from the animal's environment if the animal changes its behaviour.

As in the case of the pearl diver (see n. 24) a suitable interpretation of 'H(fisherman)' is required here before classifying 'fisherman' as a malentity.

24. Octopuses are often killed by pearl divers because they open pearl oysters.

We have classified pearl divers as appearing two ways in the environment of the octopus:

(a) The diver is a first-order modifier of the resource 'pearl oyster'. The definition may be written semi-formally as:

$$\text{diver Mod}_t^1 \text{ octopus} =_{Df} (\exists \text{ oyster}) \Big| \{\sim\xi_t \text{ diver oyster} \supset \text{oyster Mod}_t^0 \text{ octopus}\} \& \{\xi_t \text{ diver oyster} \supset \sim \text{oyster Mod}_t^0 \text{ octopus}\} \Big|$$

(b) Tentatively, the pearl diver is either a malentity or a predator of the octopus. It may be argued that many pearl divers do in fact eat the animal after killing it in the course of their duties. In this case it would seem natural to classify the human as a predator, since 'H(pearl diver)' can be given an interpretation essentially the same as the usual interpretation for the 'H' of some (non-human) animal. However, if the octopus is killed only because it is interfering with the diver's livelihood, and it is not eaten, the situation is more difficult. The matter is discussed in the second (updated) version of the General Introduction.

25. Experiments on oxygen uptake at 15°C showed that the ventilation rate is increased by both lack of oxygen or by excess carbon dioxide. It is 51 times per min. at 2.5 kg O_2 pressure and 12/min. at 8 kg O_2 pressure.

Oxygen consumption increases with temperature.

D. DETAIL

O. vulgaris poison contains many pharmacologically active substances including:

Dopamine, tyramine, octopamine, 5-HT, histamine, acetylcholine and taurine.

'Cephalotoxin' appears to be a glycoprotein.

E. REFERENCES

Bierens de Haan, J.A. (1929). *Animal Psychology for Biologists.* (London University Press).

Grzimek, Bernhard (Ed.) (1974). *Grzimek's Animal Life Encyclopedia.* 3. (van Nostrand Reinhold).

Hamada, S. (1974). Feeding behaviour of *Octopus vulgaris* Cuvier on mollusks. *Venus Jpn. J. Malacol.* 33(3), 138-143.

Hatanaka, H. (1979). Spawning seasons of common octopus *(Octopus vulgaris)* off the northwest coast of Africa. *Bull Jpn. Soc. Sci. Fish* 45(7), 805-810.

Hyman, L.H. (1940). *The Invertebrates.* Vol. 1. *Protozoa through Ctenophora.* (McGraw-Hill).

Kayes, R.J. (1974). The daily activity pattern of *Octopus vulgaris* in a natural habitat. *Marine Behaviour and Physiology* 2, 337-343.

Lane, F.W. (1960). *Kingdom of the octopus.* (Sheridan House, New York).

Lapan, Elliot A. (1975). Studies on the chemistry of the octopus renal system and an observation on the symbiotic relationship of the dicyemid mesozoa. *Comp. Biochem. Physiol. a Comp. Physiol.*, 52(4), 651-657.

Laubier-Bonichon, A. and K. Mangold (1975). Sexual maturation in male *Octopus vulgaris* (Cephalopoda: Octopoda) in relation to photo-sexual reflex. (In French). *Mar. Biol. (Berl.)*, 29(1), 45-52.

Messenger, J.B. (1974). Reflecting elements in cephalopod skin and their importance for camouflage. *J. Zool. Proc. Zool. Soc. Lond.* 174(3), 387-395.

Messenger, J.B. (1977). Evidence that *Octopus* is colour blind. *J. Exp. Biol.* 70, 49-55.

Packard, A. (1961). Sucker display of *Octopus*. *Nature* 190, 736.

Ross, D.M. and S. von Boletzky (1979). The association between the pagurid *Dardanus arrosor* and the actinian *Calliactis parasitica*: Recovery of activity in inactive *D. arrosor* in the presence of cephalopods. *Mar. Behav. Physiol.* 6(3), 175-184.

Simpson, G.C., C.S. Pittendrich and L.H. Tiffany (1957). *Life: An Introduction to Biology* (Routledge & Kegan Paul).

Wells, M.J. (1978). *Octopus: physiology and behaviour of an advanced invertebrate.* (Chapman and Hall, London).

Wodinsky, J. (1978). Feeding behaviour of broody female *Octopus vulgaris*. *Anim. Behav.* 26(2), 803-813.

Young, J.Z. (1964). *A Map of the Brain.* (Oxford University Press).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

XXVI THE BRACHIOPOD *(Lingula anatina)*

by

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This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

ABSTRACT

The precise environment of the brachiopod *(Lingula anatina)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

CONTENTS

A. INTRODUCTORY NOTE

Lingula is the most widely known of the brachiopods. This sessile marine organism is "a textbook example of evolutionary stability. - - - The first known brachiopods are found in some of the earliest Lower Cambrian strata, and some are alive today. This represents a time-span of nearly six hundred million years". (Rudwick, 1970). Romer (1968) remarks (of brachiopods): "Shells so similar in pattern to those of the lviing forms as often to be included in the same genus have been identified in the later Palaeozoic - - -. *Lingula* is, like the nautilus, very much of a living fossil." Nevertheless, Hyman (1959) remarks cautiously that "no existing species of *Lingula* dates back to Ordovician, (although the genus dates back that far)."

The animal is a lophophore-bearing filter feeder. A lophophore is a horse-shoe shaped sheet of tissue, considerably folded. The individual is enclosed within a two-valved shell. It is supported by a flexible stalk called a pedicle or peduncle, which is attached to a rock beneath or is firmly anchored in the mud (see n. 9). The shell valves are connected by ligaments, and strong muscles can clamp the two valves firmly together. The contraction of the various muscles within the pedicle serves to raise, lower or rotate the rest of the brachiopod. The lophophore bears rows of small parallel tentacles, each vested with actively beating cilia. *Lingula*, unlike some other brachiopods, has an anus. The pedicle can be shed and regenerated (see n. 7).

Like most brachiopods *Lingula* is dioecious.

The larva is free-swimming. Swimming is accomplished by the cilia, limited to the tentacles of the lophophore. As the larva grows the pedicle elongates but remains coiled up in the posterior part of the mantle cavity until bottom life begins.

The larva develops directly into adult *Lingula* without any very definite process of metamorphosis.

The shell of the adult may reach a length of 5mm in one year after the larval stage. Maximum shell length may be over 50 mm. A larva has been found measuring 1.6 mm in length; most are smaller.

Typically, *Lingula* is found in intertidal zones. It is widely distributed:

(i) Indian and Pacific Oceans: coasts of Karachi, Korea, Java, Viti, Moluccas, Samoan Islands, Hawaii, North and North-East Australia, China, Japan, Ecuador, California.

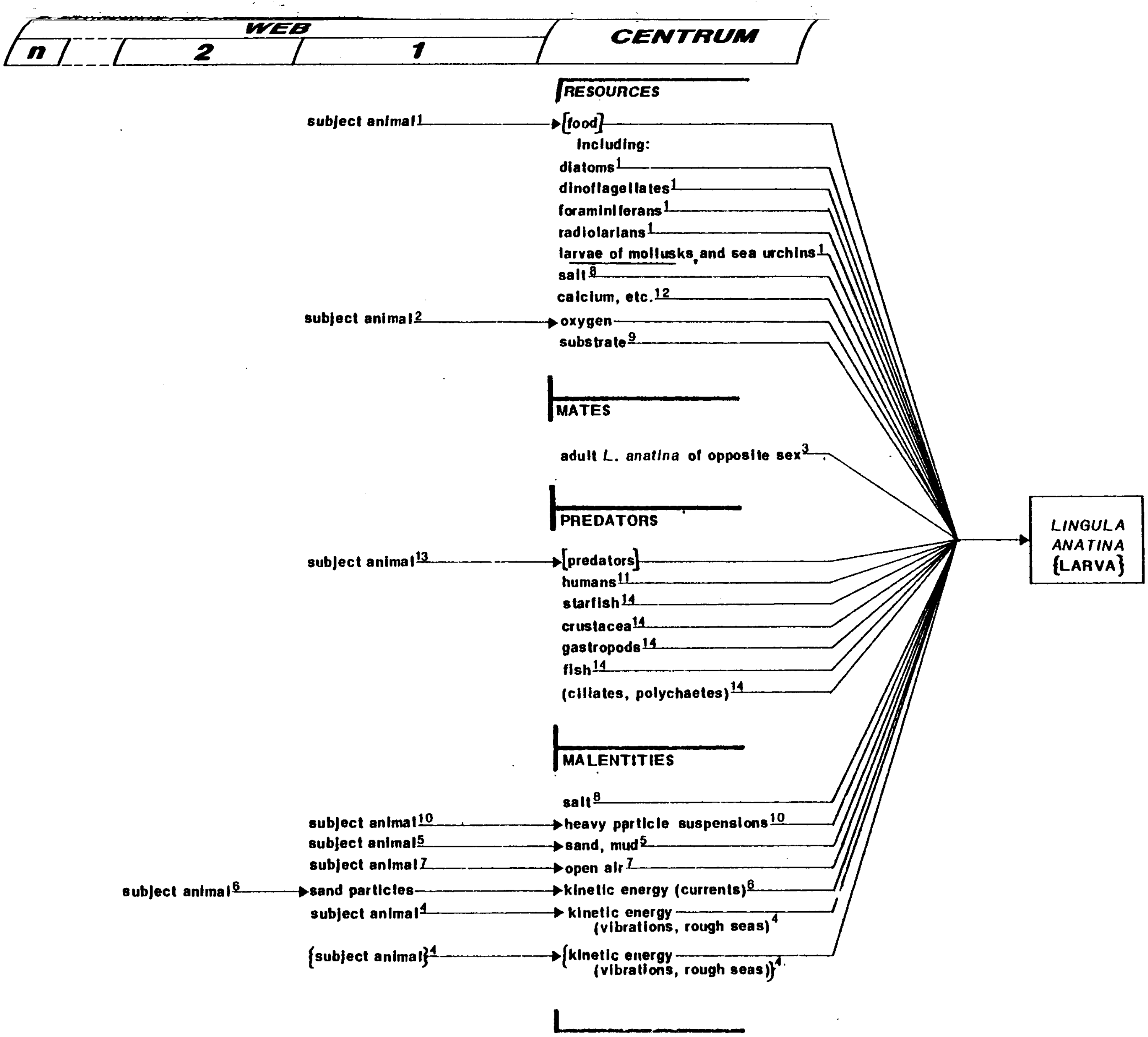
(ii) Atlantic Ocean: Florida, North Carolina, Gulf of Guinea, North and South Africa.

These localities cover a belt of latitude ranging between approximately 40°N and 30°S. Larvae have been collected in the Red Sea and 200 miles distant from the coast of Sri Lanka. The adult animal is gregarious and characteristically lives in shoals on banks or mud-flats exposed at low tide. It has however been found in deeper water e.g. Craig (1952) mentions a report by Hatai (1939) of finding *L. anatina* at an estimated depth of 50 fathoms near Seto in Japan.

Chuang (1961) reports that longevity is still uncertain, but may be as much as 12 years. The free-swimming existence of the larva probably lasts about a month (Craig, 1952).

Lingula unguis is synonymous with *L. anatina*. In this Working Paper, following the work of Hammond and Kenchington (1978) it is assumed that *L. bancrofti, L. exhusta, L. hians* and *L. murphiana* are all the same species as *L. anatina*.

On the envirogram objects in the environment of the larva are indicated by '{---}'.


WEB
n
2
1
CENTRUM
RESOURCES
subject animal[1]
[food]
including:
diatoms[1]
dinoflagellates[1]
foraminiferans[1]
radiolarians[1]
larvae of mollusks, and sea urchins[1]
salt[8]
calcium, etc.[12]
subject animal[2]
oxygen
substrate[9]
MATES
adult L. anatina of opposite sex[3]
PREDATORS
subject animal[13]
[predators]
humans[11]
starfish[14]
crustacea[14]
gastropods[14]
fish[14]
(ciliates, polychaetes)[14]
MALENTITIES
salt[8]
subject animal[10]
heavy particle suspensions[10]
subject animal[5]
sand, mud[5]
subject animal[7]
open air[7]
subject animal[6]
sand particles
kinetic energy (currents)[6]
subject animal[4]
kinetic energy (vibrations, rough seas)[4]
{subject animal}[4]
{kinetic energy (vibrations, rough seas)}[4]
LINGULA ANATINA {LARVA}

C. NOTES ON THE ENVIROGRAM

1. There seem to be no detailed lists of the food normally eaten by *Lingula anatina*. There is general agreement among a number of authors that the following organisms are consumed: diatoms, dinoflagellates, foraminiferans, radiolarians and the larvae of mollusks and sea urchins.

Chuang (1956) reports on detailed laboratory study of the ciliary feeding mechanism of the animal, using coloured particles which were observed under a microscope. Small quantities of fine particles are accepted; larger quantities of finely divided matter and coarse particles are rejected. The animal may simultaneously, by using different groups of cilli, accept suitable and reject unsuitable particles.

Rudwick (1970) states that there is some evidence that the rate of filtration is geared to the concentration of food particles in the water. There are no special sorting mechanisms; all particles which are small enough to be in suspension, whether food or not, are accepted.

Westbroek *et al* (1980) remark that the mantle cilia of the main inhalant chambers always transport particles away from the inhalant opening towards the food-gathering surface of the lophophore. They infer, therefore, that the mantle assists the lophophore in the transport and gathering of food. There is general agreement that the mantle surface is active in the removal of (pseudo-) faeces. Particle sorting appears to be mainly confined to the lophophore. Only particles below a critical size appear to be allowed into the lophophoral food grooves.

The following graphic description is from Grzimek (1974):
A mucous string, constantly moving towards the mouth, collects food particles "like a conveyer belt". "The food-laden mucous strand is conducted into the mouth". "The mucous flow is amazingly rapid: in *Lingula* a particle travelled 1.4 cm, from the tip of the arm to the mouth, in only 75 seconds".

See also n. 10.

2. A water current is set up by the subject animal which provides it with oxygen (as well as food). Thus the animal acts as a first-order modifier of the resource 'oxygen', as well as the class '[food]'.

Manwell (1960) showed that the hemerythrin pigments in the blood of *Lingula* may bind oxygen at normal oxygen tensions for subsequent use during periods of low oxygen availability. The animal is thus acting as a first-order modifier of 'oxygen' in two quite different ways.

3. According to Hyman (1959) the sexes cannot be distinguished externally unless the colour of the ripe gonads shows through the shell; the ovaries are often orange or red; the testes are pale.

Fertilization takes place in the seawater outside the shells. Some workers have thought that the expulsion of gametes is more likely to occur when the subject animal is close to another adult of opposite sex, however this is not borne out by the laboratory observations of Chuang (1959).

Grzimek (1974) writes as follows: "According to many reports, eggs are discharged during the summer months. Several species reproduce twice a year. A tiny brachiopod with a diameter of 0.35mm will hatch from a *Lingula* egg after six days. This tiny creature possesses wax-paperlike valves which protect the transparent and delicate body. Six tentacles protrude from the valve gap like a funnel."

Kenchington and Hammond (1968) report that the breeding season off the North Queensland coast extends from November to April.

Chuang (1959) observed planktonic larvae of *Lingula* in almost every month of the year, suggesting continuous breeding off Singapore Island. Chuang also watched the spawning of female *L. anatina* in the laboratory; the smallest specimen that spawned had a ventral-valve length of 22.6mm and the largest 46.0mm. The presence of ripe ova in many specimens exceeding 50mm in length seems to indicate that the spawning power is retained in old age. All the ova of an individual are not exuded at once. Spawning occurs in a series of bursts separated by rest intervals. The first burst is the most intensive and continues over 1 to 23 days. Other bursts of lower intensity follow at irregular intervals over a period of 2 to 3 months. Time of spawning in the laboratory is not related to phases of the moon or rhythm of the tides. It occurs both day and night. Ova are squirted out of the central exhalent setal tube. In 24 hours a female may produce anything from 6 to about 3000 ova. A newly-formed ovum is spherical with a diameter of about 1.5µ. Females in the laboratory continue to spawn even in complete isolation from males.

4. Both larvae and adults close their valves at the slightest disturbance.

A pair of statocysts permits the larva to perceive vibrations as well as changes in its normally vertical body position. The larva sinks to greater depths during even moderately rough seas.

Ramamoorthi *et al* (1973) report thousands of *L. anatina* washed ashore for a mile in stretch in the intertidal area after storms on November 23 and December 6, 1972. Most of the animals were fresh and healthy. Bottom samples collected from different depths contained only dead *Lingula*. They suggest low salinity and cyclonic storms as reasons for the mass mortality.

5. The walls of the burrow are soaked and fastened with mucous secreted by the animal, presumably in order to stop inward collapse of the narrow tube (see also n. 9).

Sand and mud can cause injury to *Lingula*. In particular, in severe cyclonic storms the animal may be covered by sand or mud and die (see n. 4).

6. The basal part of the animal's pedicle is enlarged and is very sticky, so that sand particles adhere to it. The added weight helps to anchor the animal to the substrate,

thus preventing it from being swept away by currents. Sand particles thus modify the action of the water currents which act as malentities; the sand particles in turn appear in the environment (in this sense) and they are modified by the subject animal itself.

7. The pedicle is able to contract, stretch or coil spirally. If *Lingula* is exposed (by a storm or the receding tide) the wormlike motions of the pedicle quickly move the animal back to a safe place.

Hammen and Lum (1977) report that when unable to burrow after dislocation *Lingula* frequently discards the entire pedicle, and after 6 days begins to regenerate a new one; the maximum rate of new growth is 0.5mm/day.

The animal is able to extrude about half of its shell-length above the surface of the substrate. When alarmed it retreats into its burrow, sometimes as much as 15cm below the surface.

8. Emig (1981) reports that in extremely diluted salinities, less than 15%, *Lingula* emerging from sediment dies after several days. In high salinities, more than 40%, the animal dies in its burrow.

Hammen and Lum (1977) have observed *Lingula reevii* transferred abruptly from seawater of 35% salinity to water of 26.5, 17.8 and 5.1% salinity. Those in the two higher salinities survived 10 days; those subjected to 5.1% died after 3.5 hours. Weight increased no more than 4% in any of the three conditions while the animals were alive. Comparable results for *L. anatina* are unknown.

See also n. 4.

9. Adult *L. anatina* burrows tubes up to 35cm into the sand and mud of the intertidal zone. Burrows are usually but not always vertical; they may sometimes be oblique or almost horizontal.

Kenchington and Hammond (1978) found that *L. anatina* in North Queensland occupies a wide range of substrate types; it is found in sands containing from 35% fine particles (less than 0.10mm) to 65% coarse particles (greater than 2.00mm). Nevertheless, they report for one local population a significant inverse relationship between median particle diameter and the density of the population. In this particular local population the animal appeared to prefer sediments with mean particle diameter below about 0.2mm (i.e. fine sand).

In their interesting survey of the burrowing emthods of marine animals Trueman and Ansell (1969) write as follows:

> "The best known genus of those inhabiting soft substrata, is the inarticulate *Lingula*. Lingulids are more active than other brachiopods and live in vertical burrows in sandy or muddy shores (Francois, 1981; Morse, 1902). Chuang (1956) regards the mucus-lined burrow as made up of two regions of approximately equal length, an upper wide part for the shell and a lower narrower region for the pedicle. When disturbed the shell is withdrawn into the burrow by the contraction of the pedicle: he reported that a pedicle of 16cm can contract to 6cm or expand to 30cm pushing the shell above the surface of the sand when the animal is feeding. In *Lingula* the long and flexible pedicle emerges from between the beaks of the valves but is attached only to the ventral valve (Hyman, 1959). It encloses a coelomic lumen continuous with the main body coelom and associated lining peritoneum. The wall is leathery in appearance, but glandular and apparently somewhat adhesive distally, and with a thick cuticle of concentric layers together with a thick longitudinal muscle layer. The burrowing process of the lingulid *Glottidia* has been described by Morse (1902) who removed the animal from its burrow and observed the pedicle being thrown into a succession of worm-like convolutions. It burrows by shovelling with the dorsal valve using up and down movements or by the vermiform movements of the pedicle. The

> burrow was widened by lateral movements of the valves.
>
> The adhesive properties of the distal part of the pedicle indicate that this may act as a terminal anchor for movement into the burrow and the presence of a coelomic cavity continuous from the body to the pedicle suggests that fluid pressures may operate in extension of the pedicle or the attainment of terminal anchorage in a manner similar to the haemocoele in the foot of a bivalve. The presence in the pedicle of a fluid-filled cavity, longitudinal muscle, and a thick cuticle indicates an organ functioning somewhat similarly to *Ascaris* (Harris and Crofton, 1957), for both lack circular muscle fibres and the longitudinal muscles may be antagonized by the elasticity of the cuticle. However, a personal communication from Professor Purchon, who has observed living *Lingula*, suggests that there may be only weak longitudinal muscles, and that in the strictest sense *Lingula* cannot burrow. Dr S H Chuang (pers. comm.) also considers that adult *Lingula* can not actively burrow, but states that the pedicle of small post larvae is very active, pulsating with the inrush of body fluid, and that at this stage burrowing into sand is possible. Further experimental observations are clearly required into the behaviour and functional anatomy of this very interesting genus".

Substrate varies from fetid mud to clean sand, according to Craig (1952) who also remarks that fossil *Lingula* occurs in many different fossil communities.

Newall (1970) in a study of fossil *Lingula* infers that it is possible that larvae of the Silurian form happened by chance upon - and used - previously bored burrows in the hard substrates. Newall writes: "Sometimes these borings were in live coral, where *Lingula* lived symbiotically with the coral. It is suggested that the presence of *Lingula* irritated the coral and caused some distortion of its structure; thus the upper part of some borings were formed by the coral growing upwards around the inhabiting *Lingula*". However workers with modern *Lingula*, although obviously not altogether satisfied that the burrowing mechanism is understood, have not made this suggestion.

10. Westbroek *et al* (1980) quote Rudwick (1964) as reporting that the mantle margins of the animal are sensitive to a variety of stimuli and may cause the shell to snap shut in response to the approach of heavy particulate suspensions. Rudwick (1970) writes "... if ... the water becomes highly turbid, a rejection mechanism comes into operation, and prevents the lophophore from becoming clogged up. The lip closes off the food groove and prevents any more particles from reaching the mouth, and the lateral cilia stop beating".

The animal is not able to cope well with a habitat in which mud or silt is being actively deposited. It has to keep its valves free from sediment by frequent snapping of the shell; but there are limits to the efficacy of this mechanism, especially for small and young individuals.

11. According to Hyman (1959) *Lingula* is (or was) so common in certain Japanese localities as to be gatherable by the basketful and used as food, either whole, or just the pedicle. Hyman quotes Barfield (1918) to the effect that the pedicles are also eaten off Queensland.

12. Rudwick (1970) reports that in *Lingula* 42% of the shell material is organic, being composed of true chitin and protein in roughly equal amounts. The inorganic material is mostly calcium phosphate, with small amounts of other inorganic salts.

According to Hyman (1959) in 4 species of phosphatic inarticulates the organic content of the valves ranges from 25 to 40% and of the inorganic constituents 75 to 92% consists of calcium phosphate, highest in *Lingula*.

13. In *Lingula* shells the organic material forms alternating layers with inorganic material, largely calcium phosphate. Such shells are never penetrated except by the finest cytoplasmic threads (Rudwick, 1970). Thus the subject animal renders itself almost immune to attack by many potential predators, acting therefore

as a first-order modifier in its own environment.

The animal's ability to clamp its two valves firmly together also serves as a protection against predators.

14. There seem to be no lists of predators specifically of *Lingula*, however, of brachiopods in general Rudwick (1970) records as predators starfish, crustacea, gastropods (particularly those that bore through shells) and fish which devour the smaller brachiopods. Ciliates and polychaete worms are predators of newly-settled larvae. According to Rudwick few parasites have been recorded in living brachiopods; only a trematode and a sporozoan have been found in present-day inarticulates.

E. REFERENCES

Chuang, S.H. (1956). The ciliary feeding mechanisms of *Lingula unguis* (L.) (Brachiopoda). *Proc. zool. Soc. Lond.* 127, 167-189.

Chuang, S.H. (1959). The breeding season of the brachiopod *Lingula unguis* (L.). *Biol. Bull. Woods Hole* 117: 202-207.

Chuang, S.H. (1961). Growth of the postlarval shell in *Lingula unguis* (L.). (Brachiopoda). Proc. zool. Soc. Lond. 137, 299-310.

Craig, G.Y. (1952). A comparative study of the ecology and palaeoecology of *Lingula*. Trans. Edinb. geol. Soc. 15, 110-120.

Emig, Christian C. (1977). (In French with English summary). *Lingula murphiana* Reeve (Brachiopoda) collected in Madagascar. *Bull. Mus. Natl. Hist. Nat. Zool.* 309, 401-410.

Emig, Christian C. (1977). (In German). *Lingula anatina* Lamarck, found during the 26th *Meteor* expedition (1972) (Brachiopoda). *Senckenb Biol.* 58 (1/2), 101-104.

Emig, Christian C. (1981). (In French). Observations on the ecology of *Lingula reevi* (Brachiopoda: Inarticulata). *J. Exp. Mar. Biol. Ecol.* 52(1), 47-62.

Grzimek, Bernhard (Ed.-in-Chief) (1974). *Grzimek's Animal Life Encyclopedia* Vol. 3 (Van Nostrand Reinhold).

Hammen, C.S. and S.C. Lum (1977). Salinity tolerance and pedicle regeneration of *Lingula*. *J. Paleont.* 51, 548-551.

Hammond, L.S. and R.A. Kenchington (1978). The biometric case for revision of the genus *Lingula* (Brachiopoda: Inarticulata) from Queensland, Australia. *J. Zool. (Lond.)* 184(1), 53-62.

Hyman, L.H. (1959). *The invertebrates: smaller coelomate groups.* Vol. 5. (McGraw Hill, New York).

Jawed, M. and M.A. Khan (1974). Zonation in the macrofauna inhabiting the mud flats of Baba Island with special reference to *Lingula murphiana* King. *J. Sc(Karachi)* 3(1/2), 78-83.

Kenchington, R.A. and L.S. Hammond (1978). Population structure, growth and distribution of *Lingula anatina* (Brachiopoda) in Queensland, Australia. *J. Zool. (Lond)*. 184(1), 63-82.

Manwell, C. (1960). Oxygen equilibrium of the brachiopod *Lingula* hemerythrin. *Science*, N.Y. 132, 550-551.

Newall, G. (1970). A symbiotic relationship between *Lingula* and the coral *Heliolites* in the Silurian. *Geol. J. Special Issue* No. 3, 335-344.

Ramamoorthi, K., K. Venkataramanujan and B. Srikrishnadhas (1973). Mass mortality of *Lingula anatina* (Lam.) (Brachiopoda) in Porto Novo waters, S. India. *Current Sci.* 42(8), 285-286.

Romer, Alfred S. (1968). *The Procession of Life.* (Weidenfeld and Nicholson; London).

Rudwick, M.J.S. (1970). *Living and Fossil Brachiopods.* (Hutchinson University Library, London).

Trueman, E.R. and A.W. Ansell (1969). The mechanisms of burrowing into soft substrate by marine animals. *Oceanogr. mar. Biol.* 7, 315-366.

Westbroek, P., J. Yanagida and Y. Isa (1980). Functional morphology of brachiopod and coral skeletal structures supporting ciliated epithelia. *Paleobiology* 6(3), 313-330.

THE TWENTY-FIVE ANIMAL STUDY

(d) *Nine vertebrates:*

Fish
Frog
Toad
Fulmar
Penguin
Wallaby
Dolphin
Gorilla
Chimpanzee

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

IV. THE THREE-SPINED STICKEBACK (*Gasterosteus aculeatus*)

by

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ABSTRACT

The precise environment of the three-spined stickleback (*Gasterosteus aculeatus* leiurus is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

CONTENTS

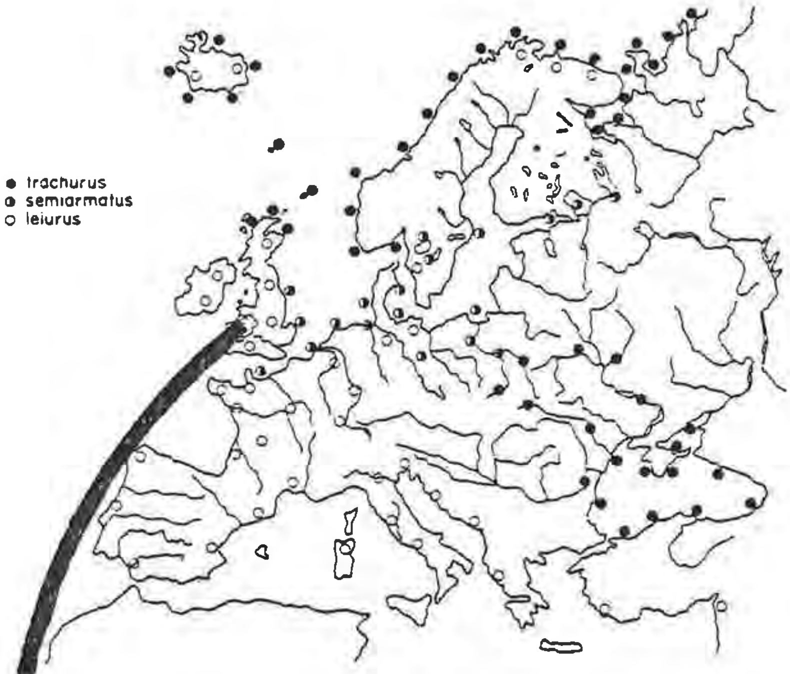


Fig. 11. European distribution of *Gasterosteus aculeatus.*

(From Wooton, 1976, and the British Ordnance Survey)

A INTRODUCTORY NOTE

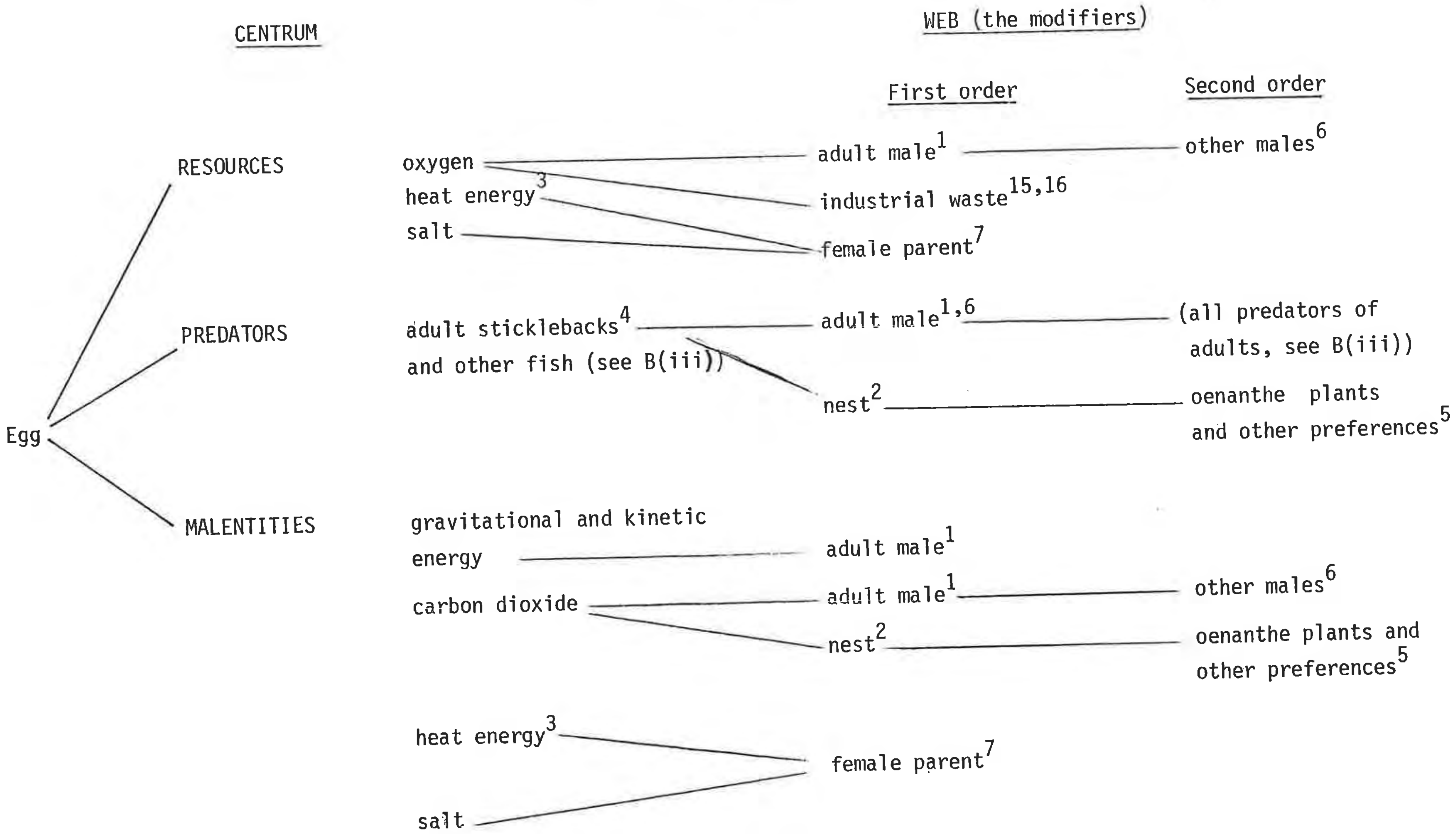
1. In the envirograms we have utilized field studies on *Gasterosteus aculeatus* leiurus undertaken mainly in the Birket River, Wirral Peninsula, north-west England. In addition, we used the results from numerous laboratory studies and some information from other field studies which we felt were applicable. We follow Wooton (1976) in accepting 'leiurus' as describing a morphological form "used in a purely descriptive sense --- not intended to have any formal taxonomic significance and so --- not italicised" (Wooton 1976, Preface). We have made extensive use of Wooton's excellent book on the stickleback in this study. Since our hypothetical animals live in the Birket River certain important aspects of the environment of the stickleback in other habitats do not appear in the envirograms e.g. the Pacific Salmon is a competitor for food in the United States and the U.S.S.R. Average life span, maximum life span, and age at maturation vary widely depending on geographical location. In the Birket River the maximum length of life is almost four years and most fish breed for the first time in their second summer. In many populations all or most of the adults die after breeding; it is not certain that this applies to the Birket River populations.

2. Three envirograms are given: one for an egg, the other two for female and male adults. Not enough information is yet available to justify drawing up a separate envirogram for juveniles. Wherever 'egg', 'adult female', or 'adult male' appears in an envirogram, the entire relevant envirogram may be added; we have emphasized this point in the egg envirogram, by adding "all predators of adults" as a second-order modifier.

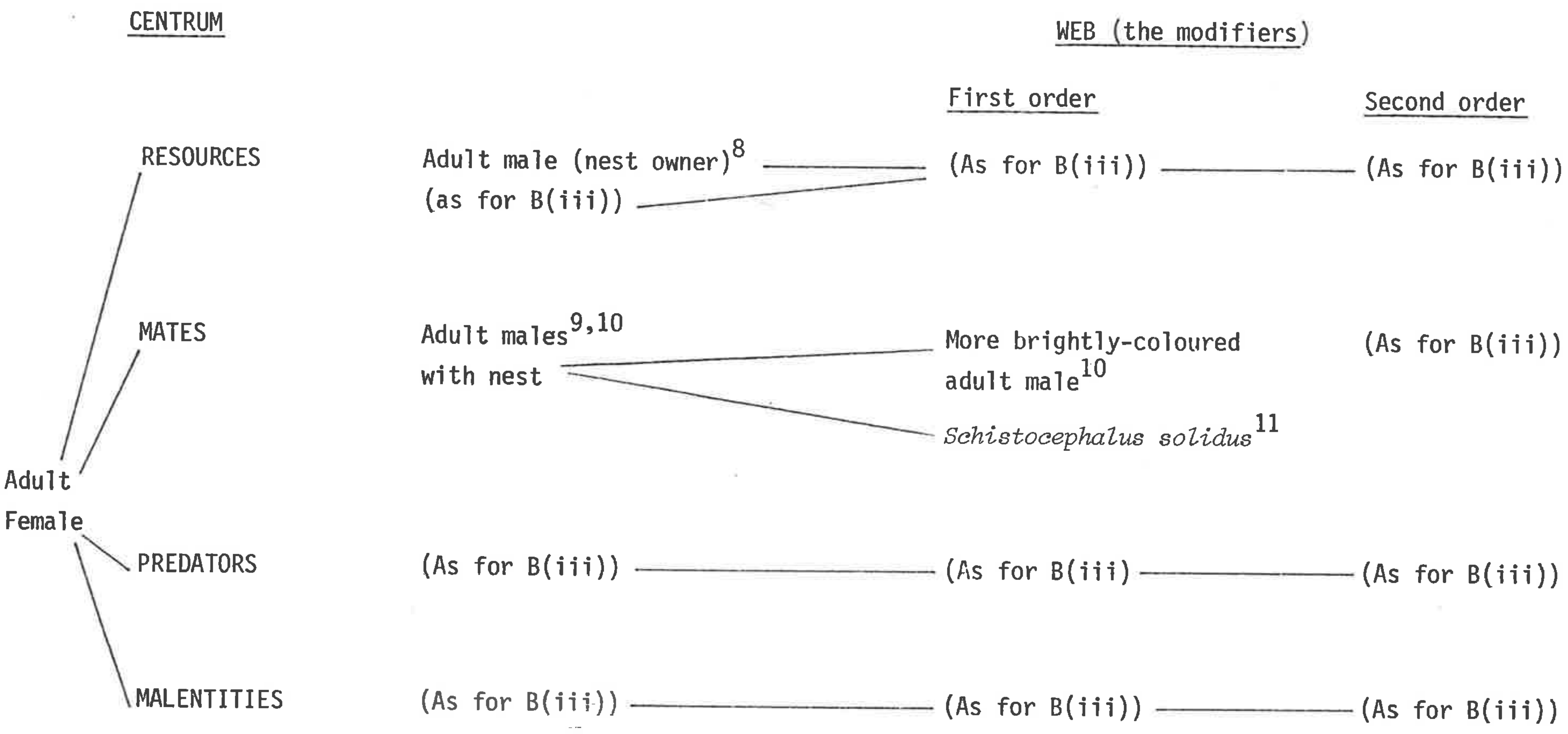
3. The maps and graphic are from Wooton (1976) and the British Ordnance Survey.

4. The methodology used in the construction of the envirogram is explained in detail in the general introduction to the series (AES Working Paper 9/81). The defining equations for the environment of an animal are also given in the general introduction, together with some indications as to the place of the present study within the development of a mathematical theory of ecology.

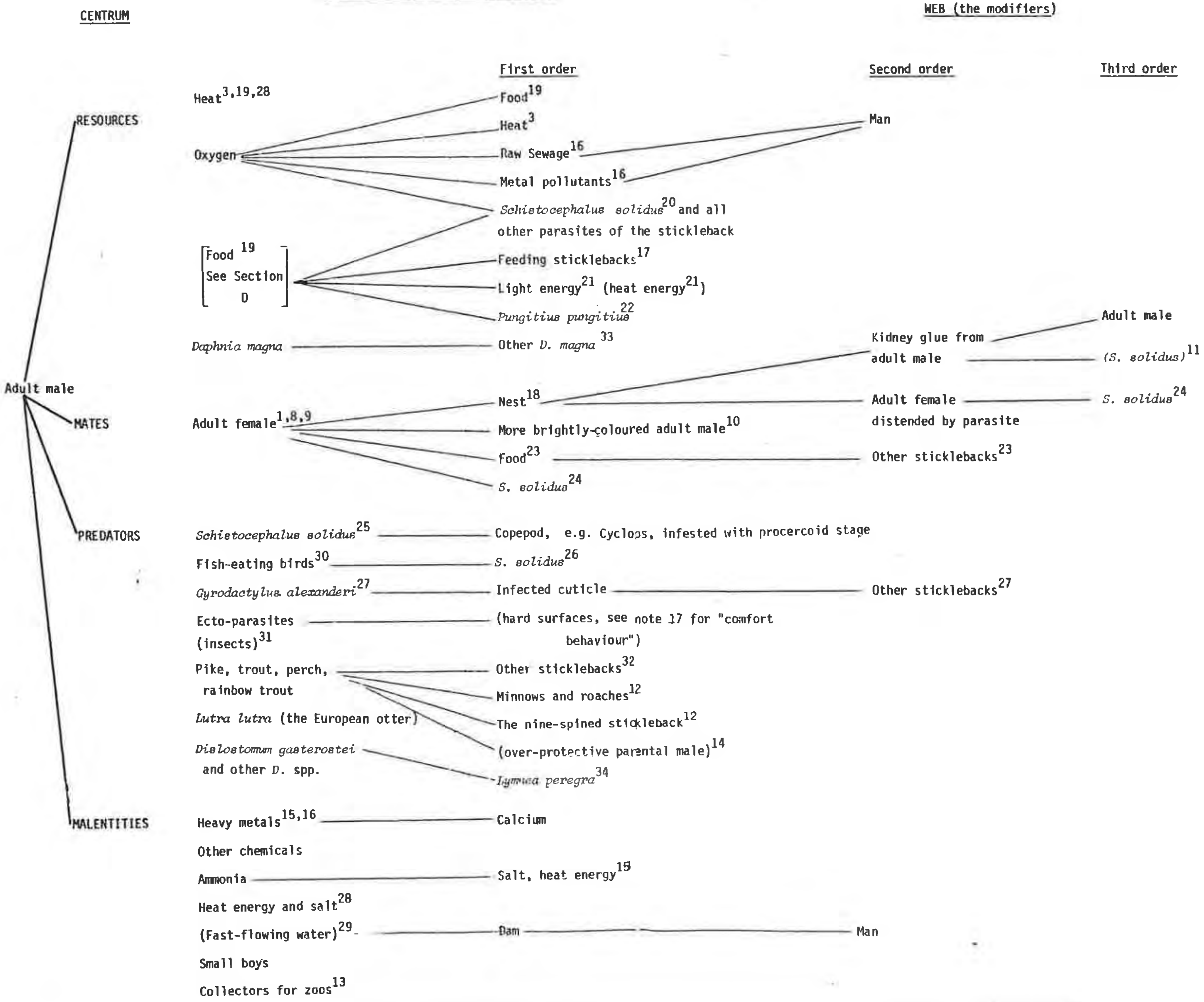
B(i) ENVIROGRAM FOR EGG



B(ii) ENVIROGRAM FOR ADULT FEMALE



B(iii) ENVIROGRAM FOR ADULT MALE



C NOTES ON THE ENVIROGRAMS

1. The adult male guards the nest. Any eggs which lie outside or fall out of the nest are picked up by the male (in his mouth) and replaced. After the female has laid her eggs the male usually chases her out of his territory (this takes only a few seconds). He then fertilizes the eggs and flattens the mound, thus expediting aeration and creating space for future clutches. Prior to his next courtship he spends the bulk of his time fanning; this "drives a current of water over the eggs and through the nest, removing de-oxygenated water and introducing oxygen." In the absence of adequate ventilation the eggs become mouldy and die (this happens to some eggs in every clutch). They are then picked out by the male and eaten. An increase in carbon dioxide or a decrease in oxygen will prompt an increase in fanning; this reaction becomes less marked for older eggs (they hatch after about eight days). The male parent also chases off predators, e.g. raiding males. Eggs are eaten if they are not fertilized within thirty minutes, although fertilization is still possible for three hours. All eggs, fertilized or not, may be eaten by an adult stickleback including the male guarding the nest (not necessarily the parent, see notes 4,8).

   In a theoretical study Rohwer (1978) has suggested a solution to the apparent discrepancy between the number of stickleback eggs in the stomachs of adult male sticklebacks and the number we would expect given the relatively few opportunities for predation (see note 4). Very briefly, his suggestion is that the male, constrained by his parental and territorial behaviour, supplements his meagre diet by moderate "filial cannibalism" of the early clutches, thus ensuring an improved overall survival rate.

2. An egg has no chance of survival outside a nest. But the nest also attracts raiding males. So the nest acts as a modifier in both senses.

3. Hatching time depends on temperature. The following table is from Wooton (1976).

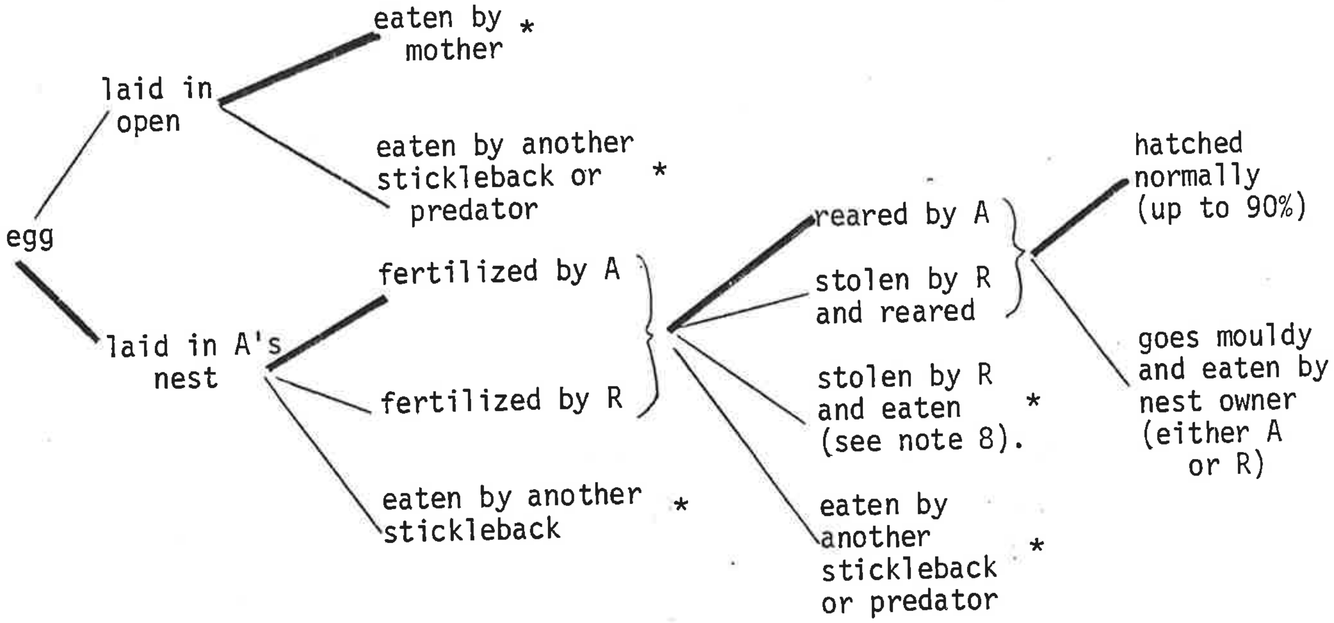
Temperature (°C)	Hatching time (days)
8	40
12	18-20
18	8 (the most common hatching time)
25	6

Abnormal embryos (most commonly triploid, with 63 chromosomes) were produced when eggs were subjects to either very high (33°C) or very low (0°C) temperatures for between an hour and a half and three hours. Thus stickleback eggs (like their parents) can survive in a broad range of temperature; the corresponding quantities of heat energy constitute a resource, while those outside this range constitute a malentity.

Salt interacts with heat in several aspects of the stickleback's environment, see notes 7, 15, and 28.

Heat also interacts with oxygen consumption in that a stickleback will consume more oxygen at a higher water temperature.

4. The following diagram shows the possible fates which may overtake a stickleback egg. An '*' is used for the death of the egg. 'A' stands for the male who guards the original nest and 'R' for a raiding male. A heavy line indicates a more probable path. The majority of eggs which are eaten by adult sticklebacks are unfertilized.



5. Sticklebacks will nest almost anywhere if the following preferred conditions are not available:

   (i) oenanthe plants;
   (ii) mud substrate;
   (iii) still water;
   (iv) water discoloured by organic material;
   (v) subdued light;
   (vi) shallow water.

6. Although the temporal pattern of fanning behaviour remains the same the presence of other nearby males acts to reduce the total time spent in fanning. Shorter bouts of fanning coincide with territorial defence. The reduction in bout length retards the rate of egg development, and thus lengthens the parental phase for the adult male.

7. Leiurus eggs survive better in fresh water or at low salinity. Their optimum salinity and temperature corresponds to that of the mother.

8. Unfertilised eggs may be fertilized by a raiding male. If this occurs then the eggs may be reared either by the nest-owner or the raiding male (see note 4). In either event the nest-owner has acted as a resource, not as a mate.

9. During the breeding season (April, May for the Birket River) an adult female will produce a minimum of two clutches. In absolutely ideal conditions she may produce a maximum of twenty clutches. Food supply is the most important determiner of both the number of clutches and clutch size. Given adequate food supply a larger female will produce more eggs/spawning than a smaller female.

	Female size (gms)	Eggs/spawning
(Min mature size)	0.4	20 - 30
(Very large female)	3.0+	300 - 400

After a spawning the female will return to the school (contrast with male territorial behaviour) and feed voraciously, up to 33% of wet body weight - contrasted with the normal 4-5%/day, while another clutch matures; she is unlikely to return to the same male when this occurs, if only because he is likely to be well into his parental phase by that time (see note 10).

10. Other things being equal, a female will be attracted by a more brightly-coloured male, a male with appropriate courtship behaviour, or nest position (see note 7 on temperature and salinity). After a spawning the male will flatten and arrange the eggs (see note 1) and then spend approximately twenty minutes lengthening and repairing his nest. Thus after an hour he will again be ready to court. Over the next few days he will accept a maximum of seven clutches and then assume his parental role (fanning etc., see notes 1 and 6). He continues in this role until a few days after hatching (see note 3 for temperature/hatching time) and then will be ready to build another nest - up to five in captivity.

11. *S. solidus* is an endoparasite; an immature stage, the plerocercoid, lives in the stickleback body cavity. The stickleback is an intermediate host; the definitive host is a fish-eating bird. A result of infection is that the male stickleback is unable to complete his nest, possibly because he lacks kidney glue. (See also notes 20, 24, 25 for other effects of parasitism by *S. solidus*).

12. Because sticklebacks can lock their dorsal and ventral spines in the erect position their predators frequently have difficulty in swallowing them. Studies in North America have shown that in stickleback communiti which have a large number of potential fish predators the sticklebacks have longer spines. Experimental evidence shows that predatory fish prefer, in descending order: non-spined fish (like the minnow, roach, rudd etc.); the low-spined nine-spined stickleback (*Pungitius pungitius*); the three-spined stickleback.

13. Collectors for zoos are classified here as malentities because of the initial shock to the animal. Cases of captive sticklebacks living a relatively long time have been recorded; thus it could be argued that some collectors act as first-order modifiers of resources and predators. Under ideal laboratory conditions at 20°C and plentiful food the animal can reach sexual maturity in four months, with a length of 45mm. This takes about a year in the natural state in the Birket River.

14. This note refers to larvae. The time spent by the male in guarding fry varies greatly, from four to fourteen days. For example he will return straying fry to the nest (as with the eggs). Orphaned young will be wary of predators. By contrast if the parental male is 'over-protective' the young will be less wary until they experience an attempted predation.

In general, experienced fish at all ages are more wary of predators.

15. The following table is from Wooton (1976).

Metallic substance	Concentration (ppm)	Stickleback survival time (hours)
Copper nitrate	0.02	192
Copper sulphate	0.03	160
Lead nitrate	0.10	336
Zinc sulphate	0.03	204

The toxicity of all four substances was reduced when calcium salts were added to the water.

Heavy metals were also tested. Zinc, lead, copper and mercury are in ascending order of toxicity. The stickleback is able to detect heavy metals and take avoiding action (if possible). In contrast to the order of toxicity of the metals, sticklebacks can detect copper at a lower concentration and then zinc, mercury and lead in that order.

Cyanides, sulphides, chloroform and ammonia are also toxic. The animal is more resistant to ammonia at higher salinities and lower temperatures. It is able to detect and avoid (if possible) higher concentrations of ammonia.

Sticklebacks avoid water with Ph greater than 11.4 or less than 5.6.

16. Raw sewage reduces the oxygen content of water. The minimum oxygen concentration at which sticklebacks can survive is about 0.25 parts per million.

Metal pollutants cause an increased rate of gill ventilation, which persists for a time, then stops completely. Oxygen consumption increases initially but declines long before ventilation starts to decline. The gills become coated with a layer of coagulated mucus which possibly prevents oxygen diffusion and hence leads to asphyxiation. There is also some structural damage; if the animal is removed from the toxic solution the gill filaments will recover or regenerate within nine days.

17. Outside the breeding season sticklebacks are normally found in schools. The longer the animals have been without food the greater is the dispersal of the school. Feeding behaviour by one individual will soon attract a large group (school). "Comfort" behaviour - rubbing the body, particularly the opercular region, against hard surfaces, may uncover food; it may also dislodge ectoparasites.

18. A male without a nest is unlikely to attract a female. For preferred nesting conditions see note 5.

19. Under ideal laboratory conditions: at 20°C and with plentiful food the animal can reach sexual maturity in four months, i.e. a length of 45 mm. This takes about a year in the natural state in the Birket River.

As the stickleback grows it has a wider range of potential prey; in the Birket River the young fish eat Cladoceran, Copepod and Chironomid larvae; older fish eat the higher crustaceans, caddis fly larvae and Chironomid pupae as well (see Section D). Food also interacts with oxygen consumption in that an increased rate of food intake results in higher oxygen intake.

20. Infested fish have higher oxygen consumption because of the energy demands of the parasites; similarly for food (see also notes 11, 24, 25 and 26).

21. Sticklebacks feed only during the day or in artificial light. Vision is the dominant sense of the animal; its colour vision and form/shape distinction are both very good. The fact that it feeds only during the day retards its rate of growth, compared to growth under ideal conditions (note 19). There is a slight decrease in the total food consumption during the winter, probably due to the shorter days and hence less feeding time, possibly also due to a slower passage of food through the digestive canal due to the lower temperatures.

22. *Pungitius pungitius* the nine-spined stickleback competes for the same food; it has the same diet in the same proportions. During the breeding season however *P. pungitius* prefers to be amongst weed, possibly for protection from predators, whereas the three-spined stickleback prefers open areas. This reduces the competition for food.

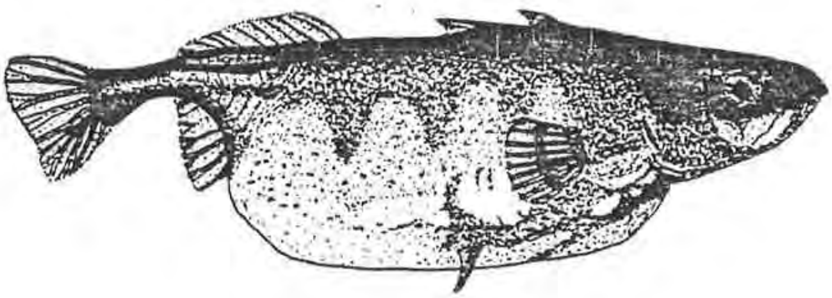


Fig. 25. Distortion of body shape of *Gasterosteus aculeatus* by *Schistocephalus solidus*

(From Wooton (1976))

23. A low food supply inhibits ovarian maturation, also the eggs will fewer and smaller; there will be less clutches. Crowding has the same effect, possibly via reduction of food.

24. Severe infection will distend the body, purely because of the bulk of the parasites. An affected female is likely to be unresponsive to courtship; even if she is, she will break up the nest in attempting to spawn. The demands of the parasite also affect egg maturation (see also note 23). (See also notes, 11, 20, and 26).

25. Many dead sticklebacks in Priddy Pool (near Cambridge) contained very high intensities of *S. solidus* (see notes 11, 20, 24 and 26).

26. High infestations of *S. solidus* (and *D. gasterostei*, see note 34 and other parasites) severely limit the growth of the stickleback (weight more than length) because of the energy demands on food resources. It is suggested that this gives advantage to the parasite because the fish becomes easier prey for the definitive host, nearly always a bird. Severely infested sticklebacks (see note 24 and graphic) also tend to swim higher in the water, i.e. closer to the surface.

27. *G. alexanderi* lives on the stickleback's skin and breeds prolifically and may kill it. The fish can shed a mucoid layer "cuticle" which may carry away some of the parasites, thus helping to prevent lethal buildups. Parasites shed in this manner can live for two days and may re-infest other sticklebacks.

28. The following table is from Wooton (1976).

Salinity	Acclimatized Temperature (°C)	Upper Lethal Temperature (°C)
3.0%	10	21.6
1.2%	10	28.0
1.2%	20	28.0

Acclimatized salinity had no effect in contrast to acclimatized temperature. A stickleback's tolerance of salinity is postively correlated with the number of lateral plates. Leiurus cannot survive in salt water below 4°C. All sub-species have a lower salinity tolerance during the breeding season. Thus during the breeding season 3.5% salinity (sea water) will be lethal but at other times a leiurus will survive in 4.5% salinity. Sticklebacks are most tolerant of high temperatures when in a salinity of 1.2% (approximately isotonic with stickleback blood).

29. Strictly, kinetic energy.

30. In the Birket River area, at least the following are predators: two terns, a heron and the black-headed gull. In addition these birds are definitive hosts of many stickleback parasites and would thus appear as modifiers in a complete envirogram.

31. Large predatory aquatic insects eat stickleback larvae when they rise to the surface to fill their air-bladders.

32. Sticklebacks pack together when threatened by predators. Some evidence suggests that this will reduce the intensity of predation. In addition, of a given number of sticklebacks, a predator is more likely to choose a more brightly-coloured fish. For unknown reasons the number of lateral plates determines the probability that a particular stickleback will be attacked by a predatory fish.

33. Sticklebacks prefer single *Daphnia magna* as targets in preference to dense swarms. This is true in all cases though hungry fish will choose the swarm more often.

34. Metacercariae of *D. gasterostei* live in the pigmented layer of the retina. The fish are infested by cercariae which penetrate the skin. These are released from infested water snails (e.g. *Lymnaea peregra*). A low incidence of snails will maintain a significant infestation in a stickleback population. The definitive host for this parasite is a fish-eating bird. It is suggested that the parasite gains advantage by making the stickleback easier prey as for *S. solidus* (see note 26). It is also possible that sticklebacks eat *Lymnaea peregra*.

D DETAIL

Food

Coleopteran larvae
Zygotperan larvae
Cladocerans (*Daphnia, Bosmina,* ---)
Mosculium (fresh water lammelibranch)
Palaemonetes (decapod crustacean)
Chironomids(larvae and pupae)
Copepods (both nauplii and copepodid stages)
Higher crustaceans
Caddis fly larvae
Harpacticus uniremis
Zooplankton
Tubifex worms are fed to stickleback in aquaria.
Gammarus
Ephemeroptera
Sialis
Trichoptera
Hemiptera
Corixid *(Vermicorixa nigrolineata)*
Cyclops
Stickleback eggs
Algae and higher plants

The following table is from Wooton (1976).

TABLE IV

Seasonal variations in the diet of the three-spined stickleback *(Gasterosteus aculeatus)* from the Birket River in England. Figures give the percentage composition of the food.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
CRUSTACEA												
Cladocera	0.7	5.3	11.3	6.0	20.5	33.4	39.2	3.5	1.6	9.2	0.8	0.2
Copepoda	11.6	20.1	27.8	23.4	14.0	10.5	27.9	38.2	11.9	25.0	6.5	15.0
Ostracoda	0.6	0.6	3.5	0.9	3.4	2.4	0.8	10.5	6.7	4.1	4.2	5.0
Asellus	7.4	6.2	-	13.0	6.3	7.8	6.7	11.4	19.6	12.7	15.2	19.0
INSECTA												
Chironomid larvae	18.8	11.5	17.1	20.0	14.5	23.7	15.6	23.4	21.8	8.7	18.7	15.9
Chironomid pupae	0.6	0.7	14.5	18.5	15.7	2.5	1.3	1.9	0.5	3.7	0.3	0.5
Trichoptera larvae	0.7	1.5	14.2	1.8	-	0.9	-	-	0.2	-	-	-
Other diptera	9.7	2.4	1.2	0.3	5.8	-	1.5	-	2.0	0.7	0.3	3.7
Terrestrial insects	1.6	0.2	1.7	2.0	4.4	0.1	-	-	3.7	1.8	9.7	5.7

TABLE IV CONTINUED

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Mollusca	15.7	2.3	1.3	0.8	0.7	3.0	0.9	0.3	2.3	9.1	23.8	12.3
Oligochaeta	13.3	39.6	3.9	1.2	0.9	-	-	-	1.0	5.1	2.5	16.9
Fish eggs and larvae	-	-	-	8.1	3.5	1.7	-	-	-	-	-	-
PLANT												
Algae	0.1	0.1	0.1	-	0.7	7.6	2.9	9.4	22.4	6.2	0.8	0.1
Higher plants	2.4	3.8	1.2	1.9	2.1	0.4	0.3	-	0.4	2.0	9.9	1.7
Unidentified	13.1	1.8	-	0.6	1.1	-	-	-	3.8	4.2	5.7	3.2

Predators

Heron *(Ardea cinerea)*

Black-headed gull *(Larus ridibundus)*

Terns *(Sterna paradisia* and *S. hirundo)*

European otter *(Lutra lutra)*. An occasional predator only.

Dragon-fly nymphs (predate larvae)

Dytiscus (predate larvae)

Pike *(Esox lucius)*

Trout *(Salmo trutta)*

Rainbow trout *(S. gairdneri)*

Perch *(Perca fluviatilis)*

We have included only three parasites in the envirogram; more specific information regarding other hosts etc. is available for many of those mentioned below from Wooton (1976) from which we have extracted the following tables.

TABLE V

Parasites recorded from *Gasterosteus aculeatus* for U.K.

Protozoa

1. SPOROZOA

Sphaerospora elegans Thelohan, 1892. Endoparasite in the kidney tubules and urinary bladder.

Glugea anomala (Moniez, 1887). Endoparasite in connective tissue.

Dermocystidium gasterostei Elkan, 1962. Endoparasite in skin.

Henneguya sp.

2. CILIATA

T. domerguei (Wallengren, 1897). Ectoparasite on gills and skin.

T. reticulata Hirschmann and Partsch, 1955 (= *T. megamicronucleata)*. Ectoparasite on skin.

T. tenuidens Faure-Fremiet, 1943. Ecotparasite.

Ichthyophthirius multifiliis Fouquet, 1876. Endoparasite of skin. Commonly known as "white-spot" or "ich".

Platyhelminthes

1. MONOGENEA (All ectoparasites)

Gyrodactylus arcuatus Bykhovskii, 1933. Gills and fins.

G. rarus Wegener, 1909. On fins.

G. elegans Nordmann, 1832. On gills and fins.

G. pungitii (Malmberg, 1956).

2. DIGENEA

Diplostomum spathaceum (Rudolphi, 1819). Endoparasite in lens capsule of the eye. Stickleback is intermediate host, definitive host is a bird.

D. gasterostei Williams. 1966. Endoparasite in pigmented layer of eye. Stickleback is an intermediate host, definitive host is a bird.

Bunodera luciopercae (Muller, 1776). Endoparasite in intestine.

Crepidostomum sp.

Phyllodistomum folium (Olfers, 1816). Endoparasite in the urinary bladder.

Tylodelphys clavata (Nordmann, 1832) (= *Diplostomum clavatum*). Endo-parasite in the humour of the eye. Stickleback is an intermediate host.

3. CESTODA

B. claviceps (Goeze, 1782). Endoparasite in intestine.

Diphyllobothrium dendriticum (Nitzsch, 1824). Endoparasite in body cavity and viscera as a plerocercoid. Stickleback is an intermediate host, definitive host is a gull or tern.

D. norvegicum Vik, 1957. Endoparasite, encysted plerocercoid in stomach, intestine and liver. Stickleback is an intermediate host which must be eaten by a second intermediate host, a trout or char. Definitive hosts include birds, men and cats.

Schistocephalus solidus (Muller, 1776). Endoparasite, plerocercoids in body cavity. Stickleback is an intermediate host, definitive host is a bird.

P. filicollis (Rudolphi, 1802). Endoparasite in intestine.

Eubothrium crassum (Bloch, 1779). Endoparasite in intestine.

Aschelminthes

1. NEMATODA

Raphidascaris cristata (Linstow, 1872). Endoparasite. Stickleback is an intermediate host.

2. ACANTHOCEPHALA

Neoechinorhynchus rutili (Muller, 1780). Endoparasite in the intestine.

Pseudoechinorhynchus clavula = (?) *Acanthocephalus clavula* = *Echinorhynchus clavula* (Dujardin, 1845). Endoparasite in intestine.

Pomphorhynchus laevis (Müller, 1776). Endoparasite in the intestine.

Arthropoda

1. CRUSTACEA

(i) Copepoda

Thersitina gasterostei (Pagenstechner, 1861). Ectoparasite, on the internal surface of the operculum.

L. cyprinacea L. 1758. Ectoparasite on skin.

(ii) Branchiura

Argulus foliaceus (L. 1758). Ectoparasite on skin and gills.

Molusca

Unionidae gen. sp. Ectoparasite of gills, larvae (glochidiae of fresh water mussels).

TABLE VI

Incidence and intensity of parasitic infestation of *Gasterosteus aculeatus* in a Yorkshire pool (Chappell, 1969a).

Parasite	Sept	Nov	Jan	Mar	May/ June	Aug
(i) Percentage of fish infested (Incidence of infestation)						
Trichodina sp	100	100	100	100	100	100
Gyrodactylus rarus	93	79	99	100	82	0.8
Phyllodistomum folium	34	49	48	48	45	55
Diplostomum gasterostei	97	99	97	88	95	41
D. spathaceum	97	98	97	95	92	98
Proteocephalus filicollis	40	41	35	28	41	12
adults	18	20	16	15	23	5
plerocercoids	26	26	28	22	29	6
Schistocephalus solidus	1	31	15	18	55	16
Neoechinorynchus rutili	7	11	22	13	4	7
Number of fish in sample	100	100	91	99	91	120
(ii) Mean number of worms per infested fish (intensity of infestation)						
Gyrodactylus rarus	6.7	6.1	11.5	23.5	6.2	2.0
Phyllodistomum folium	1.8	1.8	1.9	1.9	2.1	3.1
Diplostomum gasterostei	4.5	4.9	3.8	3.3	4.7	5.6
D. spathaceum	5.9	4.7	4.9	4.5	4.0	12.6
Proteocephalus filicollis	1.5	1.5	2.4	2.4	4.5	1.3
adults	1.4	1.3	1.6	1.8	4.2	1.3
plerocercoids	1.3	1.4	1.8	1.7	3.0	1.1
Schistocephalus solidus	1.0	1.4	1.2	1.1	1.6	1.1
Neoechinorynchus rutili	1.6	1.1	1.4	1.9	1.5	1.0

E REFERENCES

Adalsteinsson, H. (1979). Size and food of Arctic Char and Stickleback in Lake Myvtan (Iceland). *Oikos* 32, 228-231.

Blair, D. (1976). Observations on the life cycle of the strigeoid trematode, *Apatemom* (Apatemom) *gracilis* (Rudolphi-1819) Szidat 1928. *J. Helminthol* 50 (2), 125-132.

Dartnall, H.J.G. and M. Walkey (1979). Parasites of marine sticklebacks (Loch Etnee, Scotland). *J. Fish. Biol.* 14, 471-474.

Garside, E.T., D.G. Heinze and S.E. Barbour (1977). Thermal preference in relation to salinity in the three-spined stickleback, *Gasterosteus aculeatus* leiurus with an interpretation of its significance. *Can. J. Zool.* 55(3), 590-594.

Lester, R.J.G. and H.W. Huizinga (1977). *Diplostomum adamsi* description, life cycle and pathogenesis in the retina of *Perca flavescens*. *Can. J. Zool.* 55, 64-73.

Kynard, B.E. (1978). Breeding behaviour of a lacustrine population of three-spined sticklebacks *(Gasterosteus aculeatus* L.*)*. *Behaviour* 67 (3/4), 178-207.

Kynard, B.E. (1979). Nest habitat preference of low plate number morphs in three-spined sticklebacks *(Gasterosteus aculeatus)* (Washington, U.S.A.) *Copeia* 0(3), 525-528.

Milinski, M. (1977). Experiments on the selection by predators against spatial oddity of their prey. *Z. Tierpsychol.* 43(3), 311-325.

Peeke, H.V.S., M.H. Seigler and N. Blenkinsop (1979). Retention and recovery of habituated territorial aggressive behaviour in the three-spined stickleback *(Gasterosteus aculeatus)*: the roles of time and nest reconstruction. *Behaviour* 69, 171-182.

Rohwer, Sievert (1978). Parent cannibalism and egg raiding as a courtship strategy. *Amer. Natur.* 112, 429-440.

Roed, K.H. (1979). The temperature preference of the three-spined stickleback collected at different seasons. *Sarsia* 64, 137-142.

Wooton, R.J. (1976). *The biology of sticklebacks.* (Academic Press).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS
X THE LEOPARD FROG *(Rana pipiens)*

by

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ABSTRACT

The precise environment of the leopard frog *(Rana pipiens)* is given, using as a basis for the classification the defining equations of Niven *(Erkenntnis, 1982)*. A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in A.E.S. Working Paper No. 9.

CONTENTS

A INTRODUCTORY NOTE

The habitats in which *R.pipiens* may be found are described in detail by Whitaker (1961); they range from dense vegetation in which the frog cannot be seen from above, which Whitaker describes as 'good', to habitats with little or no vegetation, described as 'poor'. The following tables are from Whitaker (1961):

TABLE 2 - Habitats of *Rana pipiens* and *R. clamitans* (1959)

		Rana pipiens		*Rana clamitans*	
Habitat	Trap-nights	No.	No./100 trap-nights	No.	No./100 trap-nights
Swamp	3900	8	0.21	15	0.38
Marsh and pond edge	2550	53	2.08	16	0.63
Open field	8700	43	0.49	2	0.02
Brushy field	3450	8	0.23	0	0.00
Woods	3300	11	0.33	4	0.12
Recently cut fields	2100	4	0.19	0	0.00
Totals	24000	127		37	

TABLE 3 - Relationship of *R.pipiens* and *R. clamitans* to cover (1959)

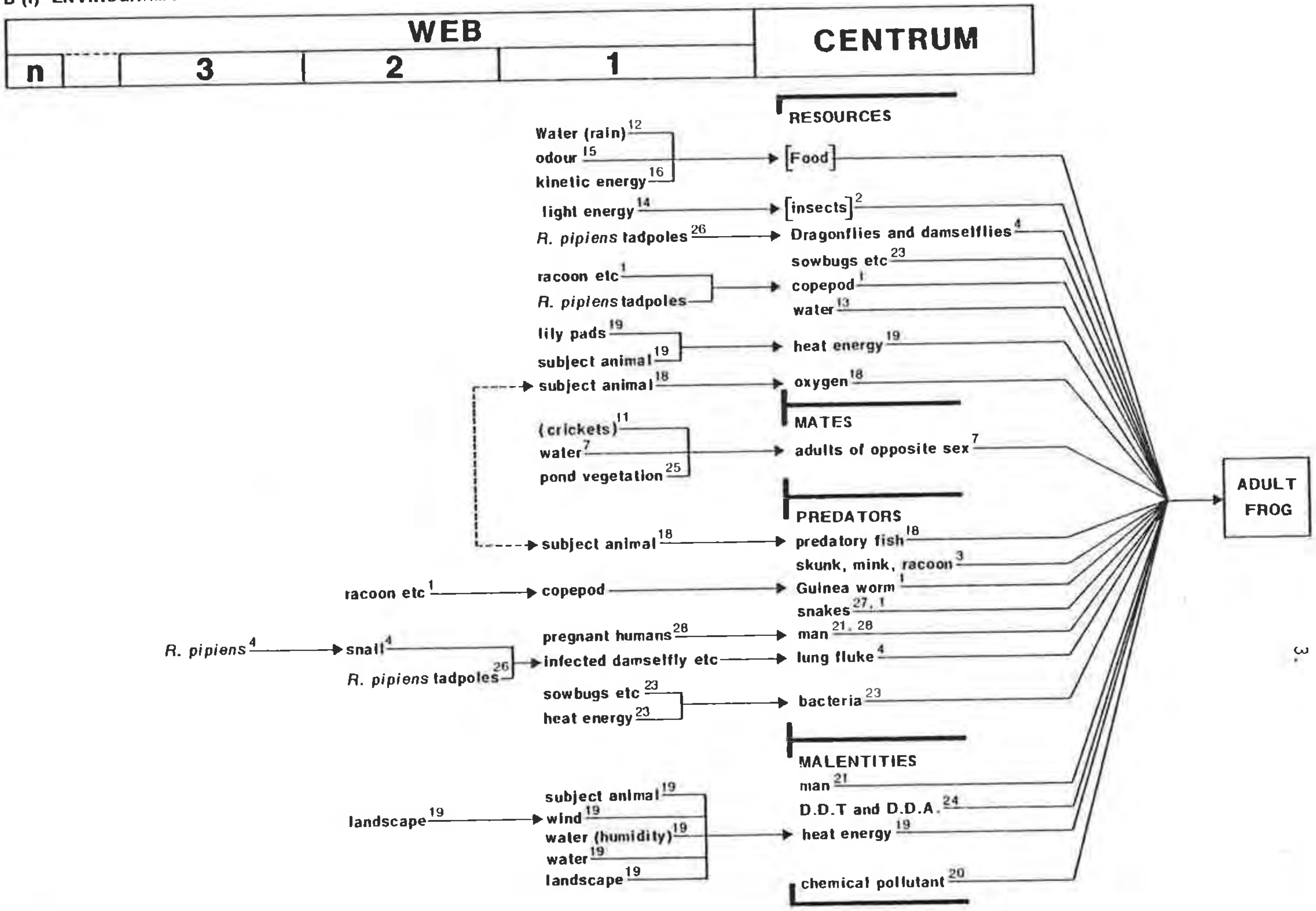
		Rana pipiens		*Rana clamitans*	
Cover	Trap-nights	No.	No./100 trap nights	No.	No./100 trap-nights
Good	4350	60	1.38	16	0.37
Fair	10500	53	0.50	12	0.11
Poor	9150	14	0.15	9	0.10
Totals	24000	127		37	

Under natural conditions eggs hatch in 13-20 days and transformation from tadpole to adult occurs after 60-80 days of larval life. The size at metamorphosis can be from 18 to 31mm in length. Adult males are from 52-82mm long, adult females from 54 to 93mm. In the Ithaca (New York State) area a few individuals reach adult size by the end of the season (October) in which they metamorphose; metamorphosis usually occurs from June through August. Hibernation usually starts in October. Maximum size is probably reached 2 full seasons after metamorphosis. One individual lived a record 5 years 11 months in captivity; the natural life span is not known (Ryan, 1953).

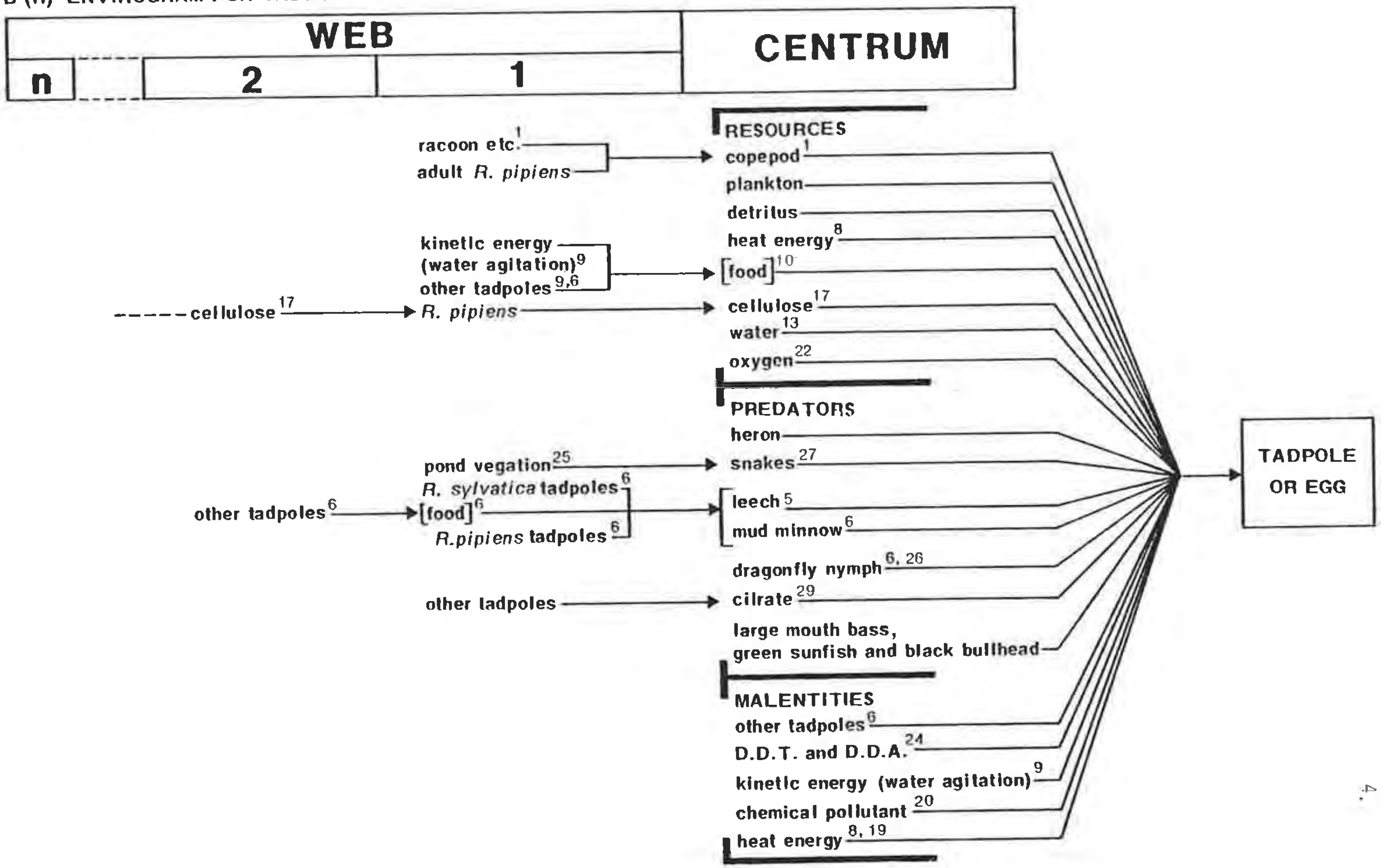
Smith-Gill and Gill (1978) report that the average size of eggs is 1.7mm in diameter. This will supply the larvae with a considerable amount of food thus reducing the amount they need to ingest before metamorphosing. Size or age of parent determines in considerable part the egg size (Adolph, 1931).

Brown (1973) considers mounting evidence that there are several distinct species in a '*Rana pipiens* complex' . In this Working Paper we have concentrated on work done in the N-E United States, in the hope that the frogs referred to all belong to the same species. Brown notes that the division of species distribution occurs somewhere in the Arizona/Texas region. Platz (1976) distinguishes 4 named species, with little hybridization among them.

B (I) ENVIROGRAM FOR ADULTS



B (II) ENVIROGRAM FOR TADPOLES AND EGGS



C. NOTES ON THE ENVIROGRAM

1. Eggs of the Gumea worm (*Dracunculus insignis*) are shed from its verterbrate hosts racoon (*Procyon lotor (L.)*), mink (*Mustela vison*), garter snake (*Thamnophis sirtalis*) and water snake (*Natrix sipidon*) and hatch in the copepod *Cyclops viridis*. The copepod is ingested by both tadpoles and frogs, and also by racoons. The worms develop in the frog; they remain dormant in the tadpole until metamorphosis; in the racoon they infect the lower limbs, encyst, calcify and continue their life cycle. The major source of infection for the racoon is via ingestion of frogs. Thus *R.pipiens* serves as a second intermediate host.

2. *R.pipiens* readily eats many insects. In the laboratory Cawthorn and Anderson (1976) observed the frog eating the common field cricket *Acheta pennsylvanicus* and Farrer and Frye (1979) fed the frog with *A. domesticus.* In many laboratory studies the animal will eat mealworms and other larvae of the Tenebrionidae beetles. In other laboratory studies the frog has been force-fed with aquatic oligochaetes (see n. 4). It has also been given flies *(Protophormia terraenovae)*, sawbugs *(Armadillidium* sp) and wax moth larvae (*Galleria mellonella*). Frogs rarely display lack of interest in eating flies or sawbugs but are often not too keen on crickets and wax moth larvae.

   Linzey (1967), in reporting a field study, writes "... the Coleoptera seem to act as a cushion, being always available and forming a substantial part of the diet, but giving way at intervals to other forms which become unusually abundant for short periods. As these forms disappear, the frogs tend to again focus upon the beetles.....".

3. Hamilton (1936) observes that skunks eat *R.pipiens* but all reptiles and amphibians combined constitute only 1.14% of the skunk's diet.

Sealander (1943) reports from an examination of the contents of stomachs and intestines that *R.pipiens* was eaten, to an extent of 8% of the mink's diet by volume and 11% by weight. Schoonover and Marshall (1951) found *R.pipiens* remains in racoon (*Procyon lotor hirtus*) scats, to a slight extent (.2% by volume and 2% by occurrence).

4. *R.pipiens* is the definitive host of the lung fluke *Haematoloechus coloradensis*. Secondary intermediate hosts of the fluke are the nymphs of dragonflies and damselflies (*Anax, Libellvia, Tramea* and *Enallagma;* order Odonata). The sporocysts and xiphidiacercariae of the fluke develop in the snail *Physa virgata*. In the laboratory infected snails shed cercariae 35 days after infection. Cercariae penetrate and encyst in the odonate nymphs which are then eaten by the frog. In the frog the metacercariae encyst and migrate into the lungs where they mature (Dronen 1975).

5. The small leech *Batrachobdella picta* was seen by De Benedictis (1974) eating *R.pipiens* tadpoles and was probably the most important predator in the pond. A leech is too small to kill a large tadpole.

6. De Benedictis (1974) presents strong circumstantial evidence for the mud minnow *Umbra limi* being a fairly important predator of tadpoles. It accounted for many of the tadpole losses in his experiment.

The effect of food was to alter the variance of size at metamorphosis rather than the average size, but the influence was complex (cf n 10). Under some circumstances, additional food allows more animals to achieve the same length before metamorphosis, reducing the variance in size; in other cases it seemed to allow smaller animals to metamorphose, increasing the variance. The presence of *R.sylvatica* tadpoles reduces the variance in size at metamorphosis even more. The density of tadpoles affected variance in size as follows: where high variance could be expected it lowered it. We have classified 'food' as a first-order modifier here since the mud minnow, like the leech (n.5) is able to predate small tadpoles only.

By measuring biomass De Benedictis determined that *R.sylvatica* grows at the expense of *R.pipiens* at high densities of tadpoles, but at a low density (similar to the usual in the wild) the reverse is the case.

R.pipiens metamorphosed sooner as the density decreased. Also the addition of food resulted in the larval period being shortened by 6 days. *R.pipiens* had a longer larval period when *R.sylvaticus* tadpoles were present. De Benedictus adduces some evidence that late metamorphosis and small size increases mortality in the frogs.

De Benedictus' claim that the main result of mixing *R.pipiens* and *R.sylvaticus* is increased survivorship of *R.pipiens* is supported by Smith-Gill and Gill (1978), who also found that landscape (whether hilly or not) affects the competition.

We have classified 'other tadpoles' as malentities since Smith-Gill and Gill (1978) and others (Gromko, 1973; Adolph, 1931) remark that crowding of tadpoles inhibits growth and that the effect is not because of lack of food or substances produced by tadpoles (e.g. faeces foul the water).

7. Dickow (1978) notes that when clasped by males unreceptive female frogs emit a release call; this call is inhibited in receptive females. Water pressure due to hormonal action is the mechanism. Salthe and Mecham (1974) suspect an interesting relationship between water and amphibian reproduction. They write "water is obligatory for reproduction, and moisture is often the most important trigger of reproductive behaviour...."

8. Adolph (1931) found that the optimal temperature for the growth of tadpoles was 19°C (in laboratory studies). He collected data about growth of tadpoles in the wild which suggested that temperature was the primary influence on the growth rate. At lower temperatures initial growth was slowed.

Moore (1942) reported that *R.pipiens* breeds and spawns in early April when water temperatures reach 12°C. Eggs can tolerate temperatures ranging between 6°C and 28°C. 6°C is the lowest temperature at which 50% of eggs develop into normal tadpoles. Normal development will rarely take place below 2.5°C. Thus 60°N. is approximately the northern limit of *R.pipiens*.

9. Adolph (1931) conducted experiments in which he found that water agitation inhibited growth in tadpoles. We have classified this as a malentity, although it is not altogether clear that the expectation of life (and hence 'H') is reduced. Crowding and water agitation decrease food ingestion of tadpoles and that is how growth is retarded; it is not that food is less available in crowded conditions, rather that those conditions modify the tadpoles' behaviour so that they become idle instead of feeding. Crowding also acts so as to increase the variance in size among tadpoles (c.f. n 6).

10. Tadpoles subjected to complete inanition are either retarded or accelerated in metamorphosis depending on the developmental stage at which food is withdrawn. The turning-point occurs during the early development of the hind limbs. Animals fed an adequate diet upto the critical stage of development and then starved metamorphose at a greater rate than animals fed a normal diet. Tadpoles which are starved before the critical stage remain in metamorphic stasis for many days (it can be as long as 80 days) after comparable normally-fed animals metamorphose. The animals do not feed after metamorphosis reaches the stage in which the forelimbs are developed (d'Angelo, 1939).

11. Rittschof (1978) reports that *R.pipiens* fed on crickets (*Achaeta domestica*) had larger ovaries and oviducts than those fed on other diets. The effect on mates is not clear to us, but we have tentatively classified 'crickets' as first-order modifiers.

12. Whitaker (1961) reports that *R.pipiens* is more active on rainy nights than on dry ones. We have recorded water (rain) as a first-order modifier of food; it is likely, however, that rain is a first-order modifier in this sense of all elements of the centrum.

13. Young frogs do not move far from water. Whitaker (1961) compared *R.pipiens* with *R.clamitans* and gives the following table:

TABLE 4 - Distance to water of trapped *Rana pipiens* and *R.clamitans*.

		Rana pipiens		*Rana clamitans*	
Dist. to water	Trap-nights	No.	No./100 Trap-nights	No.	No./100 Trap-nights
0-20 yards	10050	90	0.90	33	0.33
21-40	2850	9	0.32	-	-
41-60	2700	12	0.44	-	-
61-80	900	1	0.11	-	-
81-160	21000	-	-	-	-
	18600	112		33	

The growth rate of tadpoles depends not on the volume of water but on that volume through which the tadpoles can move umimpeded (John and Fenster, 1975).

Dumas (1964) reports that *R.pipiens* has much greater powers of dispersal than *R.pretiosa*. Marked adult *R.pipiens* after the breeding season were often found 100 yards from the nearest open water. Three marked animals were found 1.5 miles upstream after 2 summer periods. In observations and experiments in the field Dumas observed that *R.pipiens* populations tended to overwhelm *R.pretiosa* populations, suggesting that *R.pretiosa* presents only minimal competition for *R.pipiens*.

14. Robertson (1978) notes that the ratio 'No. hours light/No. hours darkness' affects the frog's activity. When there are more than 12 hours of darkness, there is no pattern of activity but at 9½ - 12 hours darkness there are maxima of activity for two hours around sunrise and during the three hours before midnight.

We have shown 'light energy' in parentheses on the envirogram since the same patterns of activity are known to occur for the insect prey of the frog and it is not clear whether the frog's patterns are induced by the variation in light or the variation in the amount of available food.

15. Odours alone can attract *R.pipiens* to prey and can trigger a strike (with its tongue). Olfactory cues are usually, however, only a supplement to visual cues (n. 16, Shinn and Dale, 1978).

We refer to 'odour' as an object since we assume that definite physical particles affect the olfactory sense of the frog.

16. Shinn and Dole (1978) note that movement of prey causes the strike response in the frog and that visual cues are more important than olfactory ones in eliciting response to prey.

The frog is not always an efficient predator: Fife (1973) reports that *R.pipiens* does not always orient itself with respect to its prey and frequently strikes at prey located 45° or more from the frontal midline without prior orientation (c.f. Working Paper on *Bufo marinus*).

17. In experiments on the mixing of *R.pipiens* tadpoles with *R.sylvatica* Gromko et al (1973) report "... it seems possible that feces comprise a normal food source for tadpoles and are eaten as part of the normal diet....". Cellulose taken in by tadpoles is available only after it has been through the entire digestive tract and passed out as faeces. Some of the cellulose taken into the digestive tract for the second time will be again passed out as faeces, still with some nutritional content.

18. *R. pipiens* hibernates in ice-covered ponds during the winter. Emery, Berst and Kodiara (1972) observed that the frogs excavate a pit in the mud at the botoom of the pond, which is slightly larger than themselves. From tiem to time they move slightly and the action flushes the pit, renewing the oxygen supply and removing silt from the sides of the body to allow easier epidermal breathing. While this behaviour allows the frogs to avoid the threat of anoxia it also exposes them to the threat of predation as the pond fish forage by preying on objects which make small movements. The predatory fish are the rainbow trout, *Salmo gairdneri*, the brook trout *Salvelinus fontinalis* and the lake char *S. namaycush*.

Thus precisely the same object at time t - the subject animal - modifies two objects in different classes of the centrum, a resource and a predator.

19. From observations of their behaviour, the frogs are strongly heliothermic, basking on lily ponds or the edge of ponds and lakes. It is also apparent that the frogs use evaporative cooling to prevent overheating (Thorson 1955, Brattstrom 1960).

On cool nights the animal is often found at the bottom of small depressions about ponds, where the air flow is reduced, thus reducing the loss of body heat. On nights when the ponds are warmer than the air the frogs are usually found in the water rather than on land.

Brattstrom (1963) reports that body temperatures of a sample of 25 Leopard Frogs in the S-E United States (note this may be a different species of *Rana*, see §A) in August-September 1954, ranged from 22°C to 27°C, with a mean of 24.1°C. For a sample of 19 frogs from Cass County in August 1955, the figures were 18°C to 29°C, mean 24.6°C. For a sample of 7 from Ramsey County, Minnesota, they were 17.8°C to 27.7°C, mean 24.1. The low figure occurred when the ambient temperature was 2.5°C. Two individuals sitting in the sun at the edge of a lake near Rapid City, South Dakota, on August 8, 1955, had temperatures of 33.5°C and 32.0°C. Two frogs in the sun near a pond in Veracruz, Mexico, August 18 1958 had temperatures of 34°C and 34.7°C. At this time the frogs concerned were all classified as *R.pipiens*; the observed range of body temperature is from 17.8°C to 34.7°C.

Dumas (1964) reports that *R.pipiens* dies after 2½ hours in an RH of 65% at 25°C. A sample of 183 active adults had cloacal temperatures ranging from 15°C to 32°C. *R.pipiens* tadpoles were found in ponds with water temperatures from 14°C to 30°C. The tadpoles develop normally in the laboratory at 10°C. Under field conditions at high altitudes where waters are cooler the time necessary for metamorphosis at 10°C is so long that freezing weather often kills all young frogs before they are ready for hibernation. This would probably prevent *R.pipiens* from inhabiting the colder waters of high mountains.

Brattstrom (1963) found two *R.pipiens* (complex) on August 25 1954 at 11.45 in a near-lethal situation in Eastland County, Texas. The temperature in the dry soil was 45^{O}C; the air outside the first hole where a frog was found was 38.5^{O}C. Wet soil and the air inside the hole had temperatures of 28^{O}C and 29^{O}C and the frog's body temperature was 27^{O}C. The animal had retreated to the shady part of the hole, avoiding the sun's range.

Smith-Gill and Berven (1979) report that (in Vermont) below 13^{O}C most *R.pipiens* involved in an experiment failed to complete metamorphosis.

Audilet and Gray (1973) noticed that fall *R.pipiens* embryos and tadpoles grow faster at 10^{O}C and 20^{O}C than do spring embryos and tadpoles.

The hibernating termperature is about 3^{O}C.

20. A chemical pollutant dispersed during Air Force operations, an amine N-phenyl-α-napthylamine, was found in Vermont to be toxic to *R.pipiens* larvae and embryo, as well as adults. Low concentrations of the pollutant arrested growth and resulted in abnormalites and sometimes death. Concentrations of more than 5mg/litre resulted in death in all frogs which were poisoned. (Greenhouse, 1976).

21. Grzimek (1974) writes "The greatest enemy of anurans today is man". *R.pipiens* is edible, however we have classified 'man' in the environment of the frog also as a malentity (see General Introduction for discussion of 'man' in the centrum of an animal's environment). Like *Bufo marinus* in Australia, *R.pipiens* is widely used (in the United tates) for laboratory and teaching work.

22. When the dissolved oxygen content of the water drops below a critical level in the vicinity of 3 parts per million of dissolved O_2, *R.pipiens* tadpoles come to the surface to gulp air. The number of times that they do this has a negative linear relationship with oxygen content when it is below 3ppm. An oxygen content greater than 3ppm seems to be adequate for premetamorphosing *R.pipiens*. However, metamorphosing tadpoles gasping for air come to the surface at a rate bearing a negative linear relationship with O_2 content when the water contains less than 8ppm O_2 (Wassersug and Seibert, 1975).

23. Sowbugs (*Oniscus*), green bottle flies (*Phoenecia sericata*) and southern field crickets (*Acheta domestica*), which are eaten by *R.pipiens*, are sources of a number of species of bactereria. Low temperatures - about 3°C which is similar to the frogs' hibernating temperature - were found to reduce the amount of bacterial infection in both frogs and prey. (van der Waaij, 1974).

The bacterium *Aeromonas hydrophila* causes septicemia in the frog, the most common cause of death in the laboratory.

A list of bacteria is given in §D

24. Both D.D.T. and D.D.A. at high concentrations have large effects upon the frogs nervous system (Hille, 1968). The concentrations used in Hille's experiments are much in excess of those the animal is likely to encounter in its native habitat. Both D.D.T. and D.D.A. were found by Punzo et al (1979) in Iowa in *R.pipiens* in both eggs and tadpoles.

25. In a study of *R.pipiens* and *R.pretiosa* Dumas (1964) notes that while general vegetation type appears to have no effect on the distribution of either species of *Rana* both species appear to shun, as breeding sites, ponds which lack vegetation. Aquatic plants furnish not only feed for developing tadpoles, but also cover and refuge from predators, particularly snakes of the genus *Thamnophis*.

26. DeBenedictus (1974) presents strong circumstantial evidence that the dragonfly nymph *Anax junius* is a predator of *R.pipiens* tadpoles. He also observed *A.junius* preying upon tadpoles in the laboratory.

27. The garter snake and the water snake both eat the frog in the laboratory but it is not certain that they eat it in the wild although there is strong circumstantial evidence that they do. The situation with respect to the red-sided garter snake is similar (Lichtenfels and Lavres, 1976). DeBenedictus (1974) also observed garter and water snakes in the locality of the pond that he studies and thought it likely that they were both predators of the tadpoles.

28. *R.pipiens* can be used for a human pregnancy test. We classify 'man' as a predator here, with the understanding that some suitable interpretation of 'H' must be made (c.f. A.E.S. Working Paper on the Cane Toad, *Bufo marinus* and see General Introduction).

29. John and Ferster (1975) reported some work by Dourbagher in 1969 to the effect that crowding among tadpoles reduced the physiological resistance of the animals to infestations of the ciliate *Opalina*.

D. DETAIL

Resources

The following is quoted from Knowlton (1944):

> "Since 1931, 92 specimens of *Rana pipiens* Schreber have been collected in various localities in Utah, and 6 additional specimens from Fish Haven, Preston and Riverdale in southern Idaho. An examination of the stomach contents of the 97 specimens revealed that they had recently eaten: 91 *Orthopters* (in 58 of the stomachs), 4 nymphal and 82 adult short-horned grasshoppers, 3 long-horned grasshoppers, and 2 field crickets; 1 may-fly naiad; 8 Odonata, 5 naiads and 3 mature damsel flies; 1 stone-fly adult; 43 Hemipters included the injurious *Lygus elisus, L. Hesperus,* the false chinch bugs, 6 pentatomid bugs, besides 16 water striders, 1 backswimmer and 5 shore bugs (*Saldidae*); 13 Homoptera included 7 adult and 1 nymphal leafhopper; 1 of 5 aphids present was a pea aphid and another an English grain aphid. The Coleoptera (124) included such injurious forms as 13 adult click-beetles, 1 leaf beetle and 2 scarabaeids; one of 4 weevils was an alfalfa weevil; while beneficial or non-injurious forms included 37 ground beetles, 10 ladybird beetles one a *Hippodamia convergens* and two 13-spotted ladybirds), 3 silphids, 1 dermestid, 2 hydrophilids and 12 adult and 15 larval dytiscids. Three adult Trichoptera were found; 42 Lepidoptera, 2 of which were adults; the rest being larvae, of which 6 were sugar-beet webworms, at least 10 cutworms and 1 zebra caterpillar; 53 Diptera included 1 housefly, 2 blowflies, 14 adult mosquitoes, approximately 500 mosquito eggs in one stomach, 3 midges, 2 Dolichopodidae and 1 deer fly *Chrysops discalis;* 28 Hymenoptera included 7 ants, 1 vespid, 4 sphecid and 1 chrysidid wasp, 1 honey bee, 1 halictid bee and 1 ichneumonid-fly. Seventy-four spiders were recognised in 41 of the stomachs;

there were 3 sow-bugs; and 30 snails in 16 stomachs. Five stomachs contained plant material, probably ingested while capturing animal prey. In addition, 6 stomachs held recently shed frog skin. One full-grown frog collected inthe field west of Logan, Utah, September 11, 1934, had a small frog of the same species in its stomach.

The following tables are from Linzey (1967):

TABLE 1 - COMPARISON OF FEEDING HABITS OF MATURE AND IMMATURE *Rana p. pipiens* (April-October, 1962)

	Mature (50-80mm.)		Immature (20-35mm.)	
Food	% Freq.	% Vol.	% Freq.	% Vol.
Insect larvae	51.9	18.2	43.3	10.9
Vegetable matter	73.2	15.3	58.3	11.8
Unidentified animal matter	51.4	10.2	45.7	9.5
Arachnida	33.3	4.0	23.6	3.6
Miscellaneous	2.2	3.5	-	-
Snails	9.8	1.1	5.5	0.8
Slugs	5.0	0.7	0.8	0.2
Annelida	2.7	0.8	-	-
Leech	0.5	0.2	0.8	0.5
Diplopoda	2.0	0.2	-	-
Chilopoda	0.5	0.1	-	-
Sowbugs	0.5	0.1	-	-
Acarina	0.5	0.1	0.8	trace
COLEOPTERA		(22.6)		(29.3)
Conculionidae	40.0	5.7	15.0	1.9
Carabidae	24.0	4.3	44.9	13.2
Colydiidae	0.5	2.4	1.5	0.2
Byrrhidæ	0.5	1.4	-	-
Elateridae	6.0	1.4	-	-
Staphylinidae	8.2	1.4	16.5	3.5
Coccinellidae	5.0	0.6	11.0	3.0
Lampyridae	1.1	0.5	-	-

	Mature (50-80mm.)		Immature (20-35mm.)	
Food	% Freq.	% Vol.	% Freq.	% Vol.
Hydrophilidae	2.7	0.4	0.8	0.7
Chrysomelidae	2.2	0.4	5.5	1.5
Dytiscidae	2.2	0.4	0.8	trace
Heteroceridae	1.1	0.2	-	-
Gyrinidae	0.5	0.2	0.8	0.1
Haliplidae	0.5	0.2	1.6	0.3
Cantharidae	0.5	0.1	-	-
Cerambycidae	0.5	0.1	-	-
Scarabeidae	1.1	trace	1.5	0.7
Lathrididae	-	-	0.8	0.1
Biphyllidae	-	-	0.8	0.1
Erotylidae	-	-	0.8	trace
Unidentified Coleoptera	20.8	2.9	22.0	4.0
ODONATA		(5.9)		
Coenagrionidae	12.5	4.8	-	-
Libellulidae	1.1	0.8	-	-
Unidentified Odonata	1.6	0.3	-	-
HYMENOPTERA		(5.7)		(8.4)
Apidae	6.0	2.6	1.6	0.2
Apis melifera	6.0	2.6	0.8	0.2
Formicidae	15.3	0.9	14.2	2.9
Sphecidae	0.5	0.5	1.5	0.3
Megachilidae	0.5	0.2	-	-
Braconidae	1.1	0.1	3.9	0.8
Ichneumonidae	1.1	0.1	2.4	0.2
Halictidae	0.5	0.1	-	-
Platygasteridae	1.1	trace	2.4	0.1
Diapriidae	0.5	trace	0.8	0.1
Pompilidae	0.5	trace	-	-
Andrenidae	-	-	0.8	0.4
Cynipidae	-	-	3.2	0.3
Pelecinidae	-	-	1.5	0.2
Chalcidoidea	-	-	1.5	0.7
Unidentified Hymenoptera	6.0	1.2	16.5	2.2

Food	Mature (50-80mm.) % Freq.	Mature (50-80mm.) % Vol.	Immature (20-35mm.) % Freq.	Immature (20-35mm.) % Vol.
DIPTERA		(3.5)		(3.6)
Muscidae	5.0	0.6	0.8	0.2
Sepsidae	0.5	0.5	-	-
Mycetophilidae	2.7	0.2	-	-
Tipulidae	1.1	0.2	0.8	0.3
Otitidae	0.5	0.2	0.8	0.1
Empidae	1.1	0.1	-	-
Ceratopogonidae	0.5	0.1	-	-
Tachinidae	0.5	0.1	-	-
Strationyidae	1.1	trace	-	-
Chloropidae	0.5	trace	1.5	0.2
Drosophilidae	0.5	trace	-	-
Calliphoridae	-	-	0.8	0.4
Pipunculidae	-	-	2.4	0.2
Lonchopteridae	-	-	0.8	0.2
Phoridae	-	-	1.5	0.1
Dolichopidae	-	-	0.8	trace
Proctotrupoidea	-	-	0.8	trace
Unidentified Diptera	0.1	1.5	10.2	1.9
ORTHOPTERA	8.2	2.5	7.0	6.0
HOMOPTERA		(2.1)		(8.1)
Cicadellidae	15.8	1.1	23.6	4.8
Cercopidae	12.6	0.7	16.5	2.6
Aphidae	5.0	0.2	3.9	0.7
Membracidae	0.5	0.1	-	-
HEMIPTERA		(1.9)		(6.0)
Pentatomidae	2.2	0.5	0.8	0.1
Lygaeidae	6.0	0.4	9.4	1.3
Hydrometridae	2.2	0.2	1.5	0.3
Miridae	3.2	0.2	2.4	0.2
Notonectidae	1.1	0.2	-	-
Gerridae	0.5	0.2	-	-

Food	Mature (50-80mm.)		Immature 20-35mm.)	
	% Freq.	% Vol.	% Freq.	% Vol.
HEMIPTERA (Cont.)				
Nabidae	-	-	1.5	0.8
Corixidae	-	-	0.8	trace
Unidentified Hemiptera	5.0	0.2	15.7	3.3
LEPIDOPTERA		(0.6)		(0.3)
Noctuidae	0.5	0.2	-	-
Unidentified Lepidoptera	2.2	0.4	0.8	0.3
COLLEMBOLA		(0.6)		
Entomobryidae	0.5	0.5	-	-
Smynthuridue	1.1	trace	-	-
Unidentified Collembola	1.1	trace	-	-
EPHEMEROPTERA		(0.2)		
Ephemeridae	0.5	0.2	-	-
THYSANOPTERA	0.5	trace	-	-
		99.9		99.7

TABLE 2 - MONTHLY FREQUENCY OF MAJOR FOOD ITEMS OF 463 FROGS (20-80mm.) BETWEEN APRIL 28 - OCTOBER 18, 1962.

Food	Apr n = 17.	May n = 78	Jun n = 64	Jul n = 94	Aug n = 88	Sep n = 94	Oct n = 27
Larvae	.06	.45	.64	.52	.33	.47	.37
Vegetation	.12	.63	.67	.67	.59	.74	.89
Arachnid	-	.41	.34	.22	.24	.19	.22
Snails	-	.09	.08	.15	.01	.11	.15
Coleoptera	.12	.81	.53	.68	.86	.59	.89
Odonata	-	.05	.36	.05	-	.01	-
Hymenoptera	-	.32	.28	.48	.40	.39	.37
Diptera	-	.35	.13	.21	.16	.18	.15
Orthoptera	-	.05	-	.06	.10	.20	.26
Homoptera	.06	.41	.23	.43	.32	.36	.33
Hemiptera	.06	.17	.16	.17	.31	.19	.19
Lepidoptera	-	.03	.02	.02	-	.06	-
Empty	.79	.01	.02	.01	-	.02	-

The following table is from Whitaker (1961):

TABLE 1 - STOMACH CONTENTS OF 95 YOUNG *Rana pipiens* from Ithaca, N.Y.

Food	% Freq.	% Vol.	Food	% Freq.	% Vol.
Insect larvae, mostly Lepidoptera	38.9	15.4	Muscoidea	8.4	3.0
			Syrphidae	1.0	0.8
Unidentified animal matter	28.4	10.0	Colicidae	1.0	0.2
			Mycetophilidae	1.0	trace
Vegetable matter	37.8	8.9	Unidentified Diptera	6.3	0.7
Snails	28.4	8.8	HEMIPTERA		(5.8)
Oniscidae (sowbugs)	18.9	4.0	Cicadellidae	25.2	3.6
Araneae (spiders)	12.6	3.3	Pentatomidae	2.1	0.4
Limacidae (slugs)	7.3	3.0	Nabidae	1.0	0.3
Chilopoda	1.0	0.7	Membracidae	1.0	0.3
COLEOPTERA		(12.6)	Neididae	1.0	0.1
Curculionidae	18.9	3.4	Miridae	3.1	0.1
Carabidae	7.3	2.5	Aphididae	3.1	0.1
Staphylinidae	8.4	2.2	Reduviidae	2.1	0.1
Chrysomelidae	3.3	1.0	Cercopidae	1.0	0.1
Cantheridae	1.0	0.4	Unidentified Hemiptera	6.3	0.9
Silphidae	1.0	0.3			
Coccinelidae	1.0	0.2	HEMENOPTERA		(5.8)
Elateridae	1.0	0.1	Formicidae	28.4	4.0
Unidentified Coleoptera	11.5	2.6	Vespidae	1.0	0.4
			Tenthredinidae	2.1	0.4
ORTHOPTERA		(10.7)	Ichneumonidae	4.2	0.2
Acrididae	11.5	6.9	Unidentified Hymenoptera	7.3	0.8
Tettigonidae	6.3	2.7			
Gryllidae	2.1	0.9	Lepidoptera (adult)	6.3	3.8
Raphidophoridae	1.0	0.1	Odonata	1.0	0.4
DIPTERA		(6.5)			
Tipulidae	2.1	1.8			99.9

PREDATORS

The following are occasional predators:

Racoon (*Procyon lotor (L)*), mink (*Mustela vison*), skunk (*Mephitis mephitis*).

Snakes of the genus *Thamnophis* are important predators in some habitats (Dumas 1964).

Predators of tadpoles are: Great Blue Heron (*Ardea herodias*), largemouth bass (*Micropterus salmoides*), Green sunfish (*Lepomis eganellus*) Black bullhead (*Letalurus melas*).

The following parasites have been found in *R.pipiens*:

Gram-negative aerobic bacteria: *Escherichia coli, Klebsiella pneumonia, Enterobacter liquifaciens, Proteus morganii, Pseudomonas aeruginosa, Spirometra mansonoides* "A" and "B", and *S. mansoni*, causing a small loss of weight. *Lernaea cyprinacea*, causing tissue damage.
Two species of *Lankesterella* infacting the blood.
The Platyhelminthe *Cephalogonimus brevicirrus.*
The Digenean *Halipegus occidualis.*
Levine and Nye (1977), in 137 *R.pipiens* complex found :

	No. of frogs
Trypanosoma pipientis	2
Tocoplasms ranae	1
Isospora lieberhuehni	1
Haemogregarina magna	44
Lankesterella minima	3
Leptotheca ohlmacheri	3
microfilariae of *Foleyella* sp.	6

The lung flukes *Haema toloechus breviplexus* and *H. coloradensis* in *R.pipiens* were studied by Dronen (1977).

The trematode *Glypthelmins facioi.*

Nematotoeetoides ranae

Five species of cestode were recovered from *R.pipiens* by Ulmer and James (1976).

The larval nematode *Eustrongylides* sp.

E. REFERENCES

Adolph, E.F. (1931). The size of the body and the size of the environment in the growth of tadpoles.
Biological Bulletin 61, 350 - 375.

Arhem, P. and B. Frankenhaeuser (1974) D.D.T. and related substances: effects on permeability properties of myelinated xenopus nerve: potential clamp analysis.
Acta Physiologica Scandinavia 91(4), 502 - 511.

Audilet, D.O. and I. Gray (1973). Temperature influences in developing tadpoles: I. Influence of temperature on the enzymatic activity of glucose-6-phosphate dehydrogenase.
Cryobiology 10(4), 308 - 314.

Brackett, S. (1938). Description and life history of the nematode *Dracunculus insignis* N. sp. with a redescription of the genus.
J. parasitol. 24, 353 - 361.

Brattstrom, B.H. (1960). The role of evaporative cooling as a thermoregulatory device in tropical amphibians.
Yr. Bk. Am. Philos. Soc. 1959, 225 - 226.

Brattstron, B.H. (1963). A preliminary review of the thermal requirements of amphibians.
Ecology 44(2), 238 - 255.

Casterlin, M.E. and W.W. Reynolds. (1977). Behavioural fever in Anuran amphibian larvae.
Life Sciences 20(4), 593 - 596.

Cawthorn, R.J. and R.C. Anderson (1976). Development of *Physaloptera maxillaris* ( ) in skunk *(Mephitis mephitis)* and the role paratenic and other hosts in the its life cycle.
Can. J. Zool. 54(3), 313 - 323.

Charon, N.W. (1975). Antileptospiral activity in lower-verterbrate sera.
Infection and Immunity 12(6), 1386 - 1391.

Crichton, V.F.J. and M. Beverley-Burton (1977). Observations on the seasonal prelevance, pathology and transmission of *Dracunculus insignis* in the racoon *(Procyon lotor* (L)) in Ontario. *J. Wildlife Diseases.* 13(3), 273-280.

Christiansen, J. and D. Penney (1973). Anaerobic glycolysis and lactic acid accumulation in cold submerged *R. pipiens. J. Comp. Physiol.* 87(3), 237-245.

D'Angelo, S.A., A.S. Gordon and M.A. Charrippe (1939). The role of the thyroid and pituitary glands in the anomalous effect of inanition on amphibian metamorphosis. *J. Exp. Zool.* 87, 259-275.

DeBenedictis, P.A. (1974). Interspecific competition between tadpoles of *Rana pipiens* and *R. Sylvatica:* an experimental field study. *Ecol. Monographs* 44(2), 129-151.

Diakow, C. (1978). Hormonal basis for breeding bevaviour in female frogs: vasotocin inhibits the release call of *Rana pipiens. Science* 199(4336), 1456-1457.

Dronen, N.O. (1975). The life cycle of *Haematoloechue coloradensis* Cart 1915 (...) with emphasis on host susceptibility to infection. *J. of Parasitol.* 61(4), 657-660.

Dronen, N.O. Jr. (1977). Studies on the population structures of two species of *Haematoloechus* 1899 ( ) in Ranid Frogs in New Mexico. *Proc. Helminthological Soc. Wash.* 44(1), 68-72.

Dumas, P.C. (1964). Species pain allopatry in the genera *Rana* and *Phrynosoma. Ecology* 45, 178-180.

Dunlap, D.G. and K.C. Kruse (1976). Frogs of the *Rana pipiens* complex in the Northern and Central Plains States. *Southwestern Naturalist* 20(4), 559-571.

Emery, A.R., A.H. Berst and K. Kodiara (1972). Under-ice observations of wintering sites of Leopard Frogs. *Copeia.* 1972(1), 123 - 126.

Farrar, E.S. and B.E. Frye (1979). Factors affecting normal carbohydrate levels in *Rana pipiens.* *Gen. Comp. Endocrinol.* 39(3), 358 - 371.

Fife, K.V. (1973). The visual fields of the frog and toad: a comparative study. *Behavioural Biology.* 9(6), 707 - 718.

Frost, J.S. and J.T. Bagnara (1976). A new species of Leopard Frog *(Rana pipiens* complex) from Northwestern Mexico. Copeia 1976 (2), 332 - 338.

Gibbs, E.L. (1973). *Rana pipiens:* Health and disease - how little we know. *Amer. Zool.* 13, 93 - 96.

Gibbons, J.W. and D.H. Bennett (1974). Determination of Anuran terrestrial activity patterns by a drift fence method. *Copeia.* 1974 (1), 236 - 243.

Greenhouse, G. (1976). The evaluation of toxic effects of chemicals in fresh water by using frog embryos and larvae. *Environmental Pollution.* 11(4), 303 - 315.

Gromko, M.H., F.S. Mason and S.J. Smith-Gill (1973). Analysis of the crowding effect in *Rana pipiens* tadpoles. *J. of Experimental Zoology.* 186(1), 63 - 72.

Grzimek, Bernhard (Ed.-in-Chief) (1974). *Grzimek's Animal Life Encyclopedia Vol. 5.* (van Nostrand Reinhold).

Hamilton, W.J. (1936) Seasonal food of skunks in New York. *J. Mammalogy.* 17, 240 - 246.

Heller, G. (1974). The fine structure of *Lankesterella* sp. sporozites parasitic in the frog *Rana pipiens*. *Scientiarum Hungaricae.* 24(1/2), 151 - 157.

Hille, B. (1968). Pharmacological modifications of the sodium channels of frog nerve. *J. Gen. Physiology.* 31, 199 - 219.

John, K.R. and D. Fenster (1975). The effects of partitions on the growth rates of crowded *Rana pipiens* tadpoles. *Amer. Midland Naturalist.* 93(1), 158 - 167.

Knowlton, G.F. (1944). Some insect food of *Rana pipiens*. *Copeia.* 1944(2), 119.

Kruse, K.C. and M.G. Francis (1977). A predation deterrent in larvae of the bullfrog *Rana catesberanna*. *Trans. Amer. Fish Soc.* 106(3), 248 - 252.

Lehman, G.C. (1978). The effect of four arthroped diets on the body and organ weights of the Leopard Frog, *Rana pipiens*, during vitellogenesis. *Growth.* 42(4), 505 - 518.

Levine, N.D. (1977). Toxonomy of *Toxoplasma*. *J. Protozoology.* 24(1), 36 - 41.

Levine, N.D. and R.R. Nye (1977). A survey of blood and other tissue parasites of Leopard Frogs in the United States. *J. Wildlife Diseases.* 13(1), 17 - 23.

Lichtenfels, J.R. and B. Lavies (1976). Mortality in Red-sided garter snakes *Thamnophis sirtalis parietalis* due to larval nematode, *Eustrongylides sp.* *Lab. Animal Science.* 26(3), 465 - 467.

Linzey, D.W. (1967). Food of the Leopard Frogs, *Rana pipiens*, in central N.Y.
Herpetologica. 23, 11 - 17.

Mace, T.F. and R.C. Anderson (1975). Development of the Giant Kidney Worm, *Dioctophyma renale* (Goeze, 1782) (...)
Can. J. Zool. 53(11), 1552 - 1568.

Moore, J.A. (1942). The role of termperature in speciation of frogs.
Biological Symposia. 6, 189 - 213.

Nollen, P.N. and J.L. Pyne (1979). Observations of spermatogenesis and inseminative behaviour of *Megalodiseus temperatus* adults in frogs.
Parasitology. 65(1), 35 - 37.

Pace, A.E. (1974). Systematic and biological studies of the Leopard Frogs (*Rana pipiens* complex) of the United States.
Misc. Publ. of Museum Zool, Uni. Mich. 148, 1 - 140.

Peifer, R.W. (1979). Great Blue Heron *(Ardea herodias)* foraging for small mammals.
Wilson Bulletin. 91(4), 630 - 631.

Phares, C.K. and K.C. Corkum (1974). Effects of spirometrid pleroceroids on several species of lower verterbrates.
Comp. Biochem. and Physiol. a Comp. Physiol. 49(3), 525 - 531.

Platz, J.E. (1976). Biochemical and morphological variation of Leopard Frogs in Arizona.
Copeia. 1976(4), 660 - 672.

Punzo, F., J. Loveglia, D. Lohr and P.A. Dahm (1979). Organochlorine insecticide residues in amphibians and reptiles from Iowa and lizards from the southwestern U.S.A.
Bull. Environmental Contamination and Toxicology. 21(6), 842 - 848.

Ralph, C.L. (1978). Non-optic phototaxis of two species of Ranid Frogs *(Amphibia, Anura, Ranidae)*. *J. Herpetology.* 12(2), 197 - 202.

Robertson, D.R. (1978). The light-dark cycle and a nonlinear analysis of lunar perturbations and barometric pressure associated with the annual locomotor activity of the frog, *Rana pipiens*. *Biological Bulletin.* 154(2), 302 - 321.

Ryan, R.A. (1953). Growth rates of some Ranids under natural conditions.

Copeia. 1953(2), 73 - 80.

Salthe, S.N. and J.S. Mecham (1974). In *Physiology of the Amphibia*, vol. 2, B. Lofts ed. (Academic Press, N.Y.)

Schoonover, L.J. and W.H. Marshall (1951). Food habits of the racoon *(Procyon lotor hirtus)* in North-Central Minnesota. *J. Mammalogy.* 32, 422 - 428.

Sealander, J.A. (1943). Winter food habits of mink in Michigan. *J. Wildlife Management.* 7, 411 - 417.

Shields, R.J. and W.M. Tidd (1974). Site selection on hosts by 8 copepodids of *Lernaea cyprinacae* L. (Copepoda) *Crustaceana* (Leiden) 27(3), 225 - 230.

Shinn, E.A. and J.W. Dole (1978). Evidence for a role for olfactory cues in the feeding response of Leopard Frogs, *Rana pipiens*. *Herpetologica.* 34(2) 167 - 172.

Smith, A.K. (1977). Attraction of bullfrogs (Amphibia, Anura, Ranidae) to distress calls of immature frogs. *J. Herpetology.* 11(2), 234 - 235.

Smith-Gill, S.J. and K.A. Berven (1979). Predicting amphibian metamorphosis. *Amer. Nat.* 113(4), 563 - 585.

Smith-Gill, S.S. and D.E. Gill (1978). Curvilinearities in the competition equations: on experiment with Ranid tadpoles. *Amer. Naturalist.* 112 (985), 557 - 570.

Sternthal, D.E. (1974). Olfactory and visual cues in the feeding behaviour of the Leopard Frog *(Rana pipiens).* *Zeit. f. Tierpsychologie.* 34(3), 239 - 246.

Sullivan, J.J. (1976). The trematode genus *Glypthelmins* Stafford 1905 (...) with a redescription of *G. facioi* from Costa Rican Frogs. *Proc. Helminthological Soc. Wash.* 43(2) 116 - 125.

Thorston, T.B. (1955). The relationship of water economy to terrestrialism in amphibians. *Ecology.* 36, 100 - 116.

Ulmer, M.S. and H.A. James (1976). Studies on the Helminth fauna of Iowa: II Cestodes of amphibia. *Proc. Helminthological Soc. Wash.* 43(2), 191 - 200.

van der Waaij, D. (1974). Colonization patterns of aerobic gram-negative bacteria in the cloaca of *Rana pipiens.* *Laboratory Animal Science.* 24(2), 307 - 317.

Walters, B. (1975). Studies on interspecific predation within an amphibian community. *J. Herpetology.* 9(3), 267 - 279.

Wassersug, R.J. and E.A. Seibert (1975). Behavioural responses of amphibian larvae to variation in dissolved oxygen. *Copeia.* 1975(1), 86 - 103.

Whitaker, J.O. (1961). Habitat and food of mouse-trapped young *Rana pipiens* and *Rana clamitan.* *Herpetologica.* 17(3), 173 - 179.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

VII THE CANE TOAD *(Bufo marinus)*

by

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ABSTRACT

The precise environment of the Cane Toad *(Bufo marinus)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as an AES Working Paper. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No 9/81. A revised version of this Working Paper will be available in 1983.

CONTENTS

A. INTRODUCTORY NOTE

There are many synonyms for *Bufo marinus*, most commonly *B. agua, B. horridus, Rana marinus*. Cochran and Goin (1970) for example, list 2 subspecies of *B. marinus* and 11 other species names.

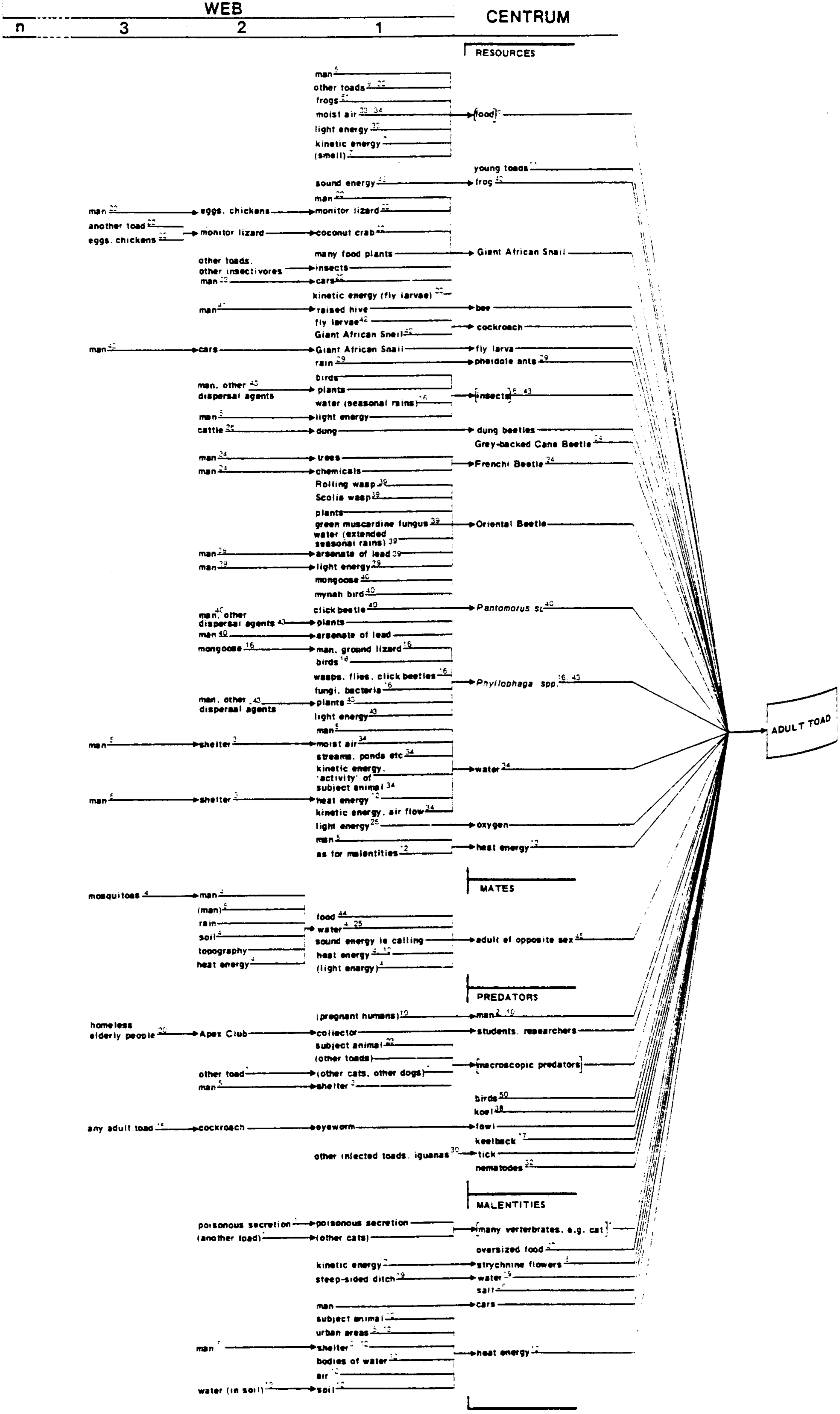
The toad's natural range is in South and Central America (see map), however it has been introduced to many countries, usually in an attempt to control pests of the sugar cane industry. The dates of introduction to various countries are given in Easteal (1981). However, this attempt at biological control has not always been successful and the animal itself has sometimes become a pest. The toad shows a marked ability to thrive in a wide variety of habitats. Covacevich and Archer (1975) cite the following range in Queensland alone: frontal dunes of ocean beaches, inland border of coastal mangroves, highly acidic areas of coastal wallum, *Melaleuca* swamps, open grassland, open sclerophyll forest, highland closed forest, dry sparse open plains, wet and dry creek beds and coastal towns and cities. The toad is usually a lowland animal, found below 1,000 m according to Zug and Zug (1979), the maximum height for population survival probably being determined by thermal tolerance limits. Zug and Zug also remark that they suspect that forests are marginal areas (see Section C n.3, n. 12). van Beurden and Griff (1980) report a spread of *B. marinus* along the coast of New South Wales and inland at rates which are sometimes as high as 3 km per year. However capture-mark-release-recapture data from van Beurden (1978) in Queensland indicate that the resident adult toad moves little from day to day or month to month.

Fully adult toads may reach a snout-vent length of 120 mm (females) and 110 mm (males) (Zug and Zug, 1979). Pemberton (1949) reports a captive toad living 15 years, during which time it ate an estimated 72,000 cockroaches.

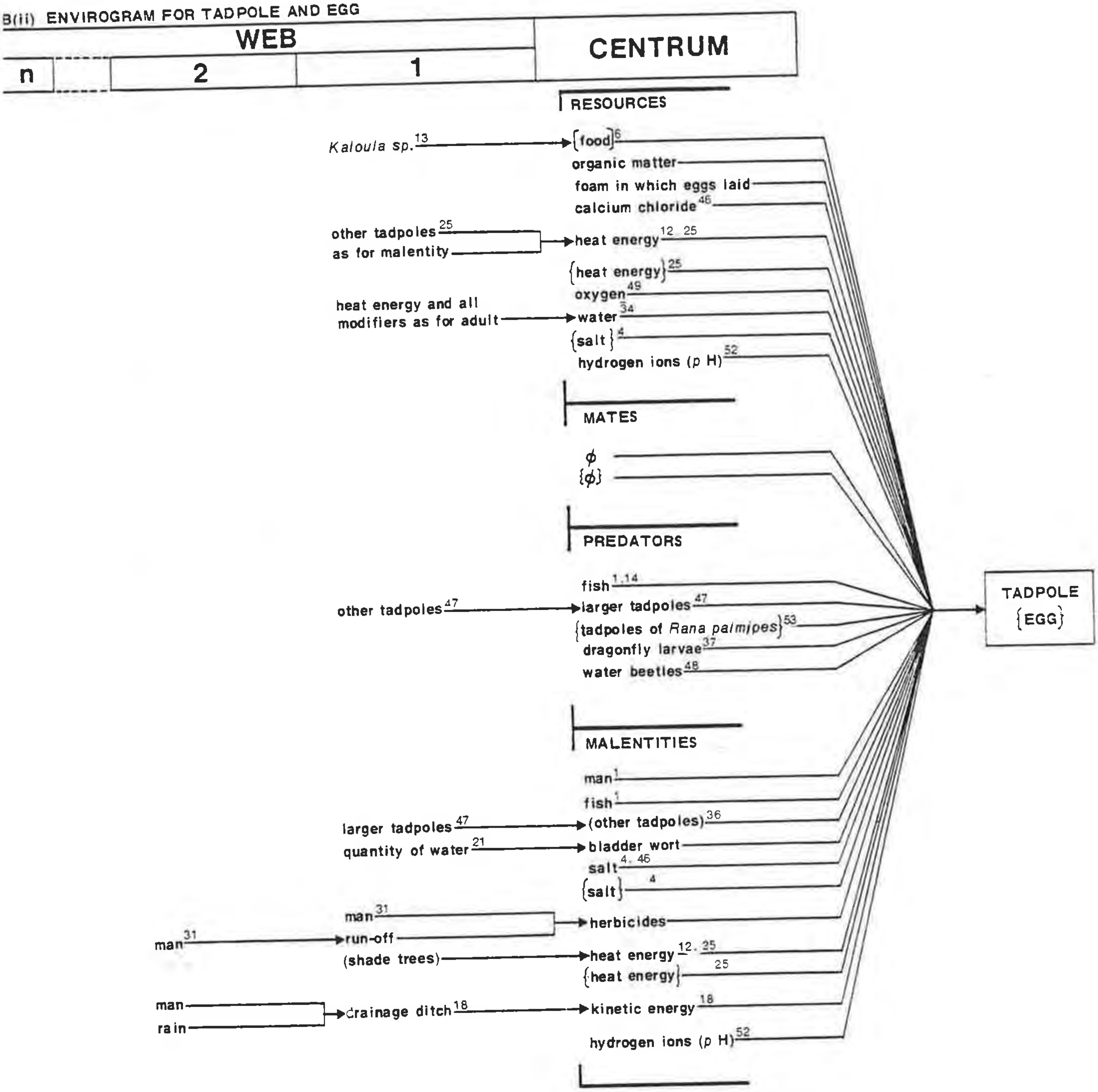
The work on the cane toad in the School of Australian Environmental Studies, Griffith University, was directed with skill and enthusiasm by the late Dr M.D. Sabath, whose tragic death at an early age dealt a heavy blow to the research activities of the School. We are indebted to his students, S. Easteal and R. Floyd for allowing us to use their bibliography, for lending us very many reprints and for freely providing us with large quantities of useful information about the animal.

The map is taken from Easteal (1982).

B(i) ENVIROGRAM FOR ADULT TOAD



B(ii) ENVIROGRAM FOR TADPOLE AND EGG



C. NOTES ON THE ENVIROGRAMS

1. Man and many other vertebrates have been known to mouth or ingest *B. marinus* and either die or become ill. Licht (1967) reports the death of some members of a Peruvian family after eating soup containing eggs of the toad. At least the following cases of death among animals have been recorded: domestic cats and dogs; pigs; rat *(Rattus rattus)*; western native cat *(Dasyurus geoffroii)*; Land Mullet *(Egernia bungana)*; goannas *(Varanus* spp.*)*; Slaty Grey Snake *(Stegonatus cucullatus)*; Brown Tree Snake *(Boiga irregularis)*; Red-Bellied Black Snake *(Pseudechis porphyriacus)*; Death Adder *(Acanthophis antarcticus)*; Brown Snake *(Pseudonaja textilis)*; Tiger Snake *(Notechis scutatus)*; crows *(Corvus* spp.*)*; Kookaburra *(Dacelo gigas)*; Tasmanian Devil *(Sarcophilus harrissi)*; turtle *(Kinosternon* sp.*)*.

   In all cases the animals listed above suffered from the effects of the poisonous milky secretion from the toad's parotid gland. Knowles (1964) gives Marino bufagin, bufotoxin and bufotenine as the active constituents; the mixture has a digitalis-like action (see D). Blair (1947) reports that on occasions the toad is capable of squirting its poison up to 15 inches. Chen and Chen (1933) report that the regeneration by the toad of its poisonous secretion after expression is apparently quite slow. One toad weighing 254 gms gave 0.71 gms of fresh secretion at the first expression and only 0.48 gms at the second expression 76 days later.

   Abel and Macht (1912) report that *B. marinus* is resistant, but not totally so, to its own poison. Under its influence the toad becomes sluggish.

   Clearly any animal species which is poisoned through contact with *B. marinus* is in considerable danger unless it learns to avoid toads. In all areas into which the toad has been introduced there have been reports of native species being affected e.g., Covacevich and Archer (1975) suggest that *Dasyurus* spp. (the marsupial 'cats' of Australia) are retreating to areas not populated by the toad. Alcala (1957) reports, however, that domestic cats in the Philippines have learned to avoid the toads.

In our opinion there are only two ways in which this can happen: (a) the 'cat-malentity', having had a previous encounter with a toad, almost dying and now knowing the necessity of avoiding further toads; (b) because (a) seems insufficient to explain the whole cat community's adaptation some method of communication is demanded. This may involve either the cat in (a) or the observation by cats of other cats dying from the effect of eating other toads.

Zug and Zug (1979) observe that young toads are distasteful but not toxic and thus the likelihood of death by predation is greater during this stage than it is for the adults, both because of smaller body size and lack of toxicity. Pearse (1980) has shown that, at least with respect to some fish *viz.* the Purple-spotted gudgeon *(Mogurnda mogurnda)* and the Fire-tail gudgeon *(Hypseleotris galli)* the tadpole is quite toxic. The mosquito fish *(Gambusia affinis)*, a native of Mexico like *B. marinus*, did not relish the tadpoles, but recovered from minor effects.

2. In order to classify 'man' as a predator, we require a suitable extension of the primitive term 'H' (see General Introduction).

   Toadskin has uses in classical Chinese medicine (still practised) and was also used in seventeenth and eighteenth century England and Germany for the treatment of dropsy. Some Amazon natives use toadskins to make poison for their arrows (Abel and Macht, 1911). In all cases some property of the digitalis-like poison is utilized (see n. 1 and §D).

3. The role of shelter in the environment is difficult to classify - with other animals we have usually classified it as a modifier of malentities and/or predators. In accordance with the suggestions below we have kept to this scheme, though here we also classify it as a modifier of a resource. However there is a case for shelter to be considered as a resource; the definitive experiment for *B. marinus* has not been done (see General Introduction to the series).

B. marinus is primarily though not exclusively nocturnal. During the day the species characteristically seeks cover (shelter) in thick growths of vegetation beneath rotting organic matter, within clods in ploughed fields, in holes and under houses. Alcala (1957) comments that *B. marinus* tends not to penetrate primary forest. He adds that the toad is most abundant in savannah country, grasslands, cultivated areas and near human habitation (see n. 5). On Barbados Mungomery (1936a) observes that the elimination of available day-time shelter resulted in a decrease in the toad population. Tyler (1940) reports that the toad is having difficulty in maintaining its population partly because of the clearing of suitable day and dry period shelter. Zug and Zug (1979) suggest that toads reduce water loss by retreating to sheltered areas during the day and at other times of low humidity. They suggest also that sub-adults and adults compete for sheltered retreats. The latter point is made more strongly by Straughan (1966) who suggests that juveniles are forced to migrate because of occupation by adults of suitable sheltering sites; this leads to the dispersal of the animal.

4. *B. marinus* is an opportunistic breeder, requiring only appropriate bodies of water into which the female, who nearly always carries mature eggs, lays. Almost any body of water, whether standing or running, fresh or brackish, will probably be satisfactory. The Queensland Museum has a photograph of eggs laid in salt water (in the wild) but it is not known if they survived and developed. However Ely (1944) conducted laboratory experiments which showed that eggs could survive and develop normally in solutions containing up to 20% sea water. A solution containing 15% sea water (approximately 0.5% salt) seemed to be the most favourable medium since the eggs developed more quickly than in either a 10% sea water solution (see n. 25 on rapid development) or in tap water. Takano and Iijima (1937) report that NaCl is fatal at a density above 0.7% but development proceeds naturally below 0.6%.

The only direct observation of the animal breeding in salty water in the wild which we have come across is that of Waite (1901), in Bermuda, who reports the toad, referred to as *'Bufo aqua'*, breeding in brackish water and marshes. Straughan (1966), in Queensland, writes that preferred breeding sites are in the shallows and that the presence of aquatic vegetation, grasses or weeds or whether the bottom is clear or covered with rocks, sand or vegetation has no effect on choice of breeding site.

Water, which is essential for breeding, may be removed from the toad's habitat in several ways, e.g., on Barbados many hundreds of estate ponds and low-lying areas where water may accumulate have been filled or drained for either aesthetic reasons or for mosquito control (Mungomery, 1936a and Tucker, 1940). Also water may simply evaporate (requiring heat energy), or seep away through the soil.

In the Barbados Tucker (1940) reports that the animal is having difficulty in maintaining its populations in part because of lack of suitable breeding water and oiling of water for mosquito control, thus farmers are being encouraged to build artificial breeding ponds.

B. marinus may breed twice a year, laying between 10,000 and 21,000 eggs each time according to Tyler (1976) - but Straughan (1966) observed 8,000 to 35,000 eggs being laid. Buzacott (1936) has recorded one female laying a clutch of 16,000 eggs and on another occasion nine females laying 125,000. When temperatures are sufficiently high and rainfall adequate the toad will reproduce all the year round, but in marginal habitats the breeding season usually coincides with the warmest and wettest time of the year (Oliver, 1949). Wilhoft (1965) mentions that there are always some unfertilized eggs and Tucker (1940) counted the number of toadlets surviving from an initial egg lay as ranging from 75 to 300, probably an underestimate, he reports, due to the difficulties of observation.

Zug and Zug (1979) report that eggs will hatch in 36 hours to 4 days. Floyd (pers. com. 1981) finds that the development time of the eggs falls from 155 hours at 18°C to about 1 day at 35°C.

Breeding success is aided by the animal's short development period - a larval (tadpole) life of between 25 days and 2 months, depending on water temperature (Tyler, 1976, see also n. 25). The following table is from Zug and Zug (1979).

TABLE 4: Development of *B. marinus* tadpoles from hatching to metamorphosis

Locality	Duration	Source
Oahu	30 days	Pemberton, 1934
Puerto Rico	60-70 days	Sein, 1937
Panama	4-6 weeks	Breder, 1946
Negros Island	7-8 weeks	Alcala, 1957
Queensland	75-80 days	Straughn, 1966
Trinidad	6 weeks	Kenny, 1969
Venezuela	29-32 days (experimental)	Durant, 1974
Venezuela	58 days (natural)	Durant, 1974

Despite some counter-examples of year-round breeding, Zug and Zug (1979) believe that bimodal reproduction is typical for most native populations. The following chart is from their article.

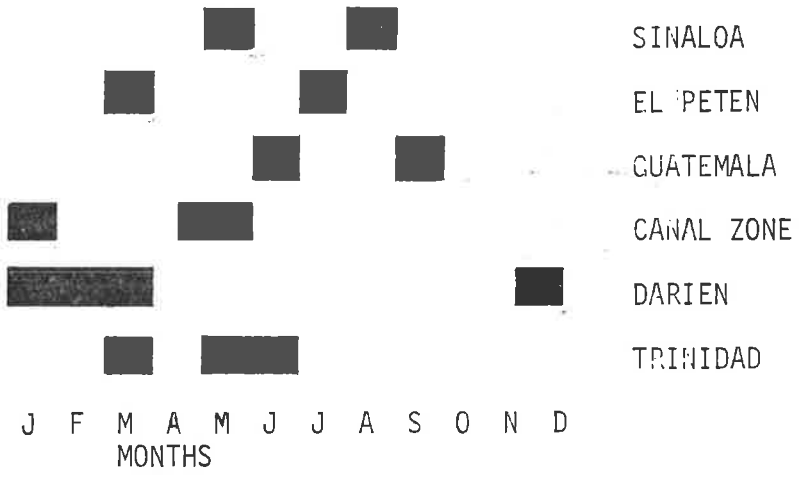


FIGURE 8: Breeding activity of *B. marinus* within its natural range. Data, top to bottom, are from Hardy and McDiarmid (1969), Duellman (1963), M. Dix (pers. comm.). Breder (1946) and our samples. Breder (1946) and C.W. Myers (pers. comm.), Kenny (1969).

Tyler (1975) remarks that some members of both sexes are found to be in breeding condition throughout the year, waiting for the right climatic conditions for breeding. Zug (1975), in Papua New Guinea, report that there in every month at least some of the females possess eggs ready for deposition. They suggest that the number of such females is partly dependent on the rainfall since it appeared that heavy rain preceding the sampling date reduced the number of gravid females because they had bred during that rainy period. The year round availability of eggs indicates that *B. marinus* is an opportunistic breeder. Wilhoft (1965) also found an inverse relation between the observed number of gravid females and the amount of rain. Straughan (1966), in Queensland, writes that the breeding season starts with the first summer storms in September. Oviposition may occur throughout the day as well as night although it was never observed to commence during the day.

In Australia, toads often atain adult length in their second summer (van Beurden, 1978). Zug and Zug (1979) record that in New Guinea females reach sexual maturity at a snout-vent length of 70-80mm; in the Canal Zone, Panama, the length is 90-100mm and males mature at 85-95mm. Zug *et al* (1975), in Papua New Guinea report no size difference between the (adult) sexes.

5. Many writers have noted the close association of *B. marinus* with man. The following reasons have been suggested:

(i) Lights (which attract insects);
(ii) Food (refuse and pet food);
(iii) Warmth;
(iv) Water;
(v) Shelter.

For example:

(i) Brattstrom (1962b) in studying homing observed that of 15 transported toads, 11 returned, all to the same light; he strongly suggests that the insects around the light were the main attraction. Dexter (1932) and many others concur. Oliver (1949) remarks that the animals characteristical return to good feeding sites.

(ii) Alexander (1964) observed toads eating (diurnally) canned dogfood remains and the following household refuse: raw lettuce, avocado, broccoli and carrot, cooked corn, rutagabas, black-eyed peas, and rice. No insects, which might have attracted the toads, were seen close by.

(iii) & (iv). R. Floyd (1981, personal communication) suggests that the greater warmth of urban areas (see note 12) and the greater availability of water for breeding (see note 4) attracts toads.

(v) Several writers including Krakauer (1968) and Alcala (1957) suggest that *B. marinus* prefers disturbed areas - around buildings, on farms, along canals and in secondary growth. The continued expansion of Miami seems to be destroying the habitat of *B. terrestris* while creating more disturbed areas for *B. marinus*. Such areas provide nooks and crannies for day shelter.

6. Adult toads are astonishingly catholic eaters (see §D, also notes 7 and 8).

In addition to the items mentioned in notes 5, 7 and 8, Krakauer (1968) found five toads in Florida with stomachs full of undigested grass (also Zug *et al*, 1975, for New Guinea).

Mungomery (1938a) reports that *B. marinus* can survive long periods without food. He kept several pairs of toads without food for one month and they showed no ill effects; one pair bred immediately upon release.

Oliver (1949) notes that if an abundant supply of insects is available the toad will only stop eating when gorged to the point of distending its body.

Zug, Lindgren and Pippet (1975) find that forest-dwelling toads are better fed and bigger, with more animals in the diet. The greater abundance of plants found in the stomachs of savannah-dwelling toads shows deliberate rather than accidental ingestion by these toads, presumably to supplement meagre insect resources.

Once the mouth is formed, tadpoles eat the foam they were laid in. When this is finished they eat organic matter in the water. *B. marinus* tadpoles show no preference in feeding from surface, mid-water or substrate, in contrast to other species of toads. However, this may be because the high clutch numbers force this wide range in feeding behaviour (Tyler, 1971). Zug and Zug (1979) remark that the ideal time for metamorphosis would seem to be at the beginning of the wet season (about May in the toad's native environment) when insects are abundant.

7. Many writers agree that the toads are carnivorous and feed only on moving organisms, however see notes 5(ii) and 8. Also, King (1969) comments that *B. marinus* can detect prey by smell alone. Clearly movement is often a factor in arousing feeding responses e.g., a toad has been recorded as pursuing and attempting to eat a ping-pong ball and Grant (1948) reports a toad consuming a lighted cigarette butt. Movement is suggested as the operative factor in toads eating strychnine flowers (note 8). F.A. Bianchi, in a personal communication to S. Easteal, mentions that when *B. marinus* was first introduced into Hawaii it would eat nothing but flying or moving insects, although the descendents will eat solid and liquid food. Ingle and McKinley (1978) find that two moving objects close together elicited more strikes than a single moving object. Fite (1973) comments that *B. marinus* never misses when it strikes, though frogs have error rates of 2% - 7%.

Most prey for large toads is in the 5.1mm to 10mm range (in length). The toads ignore anything less than 2mm long (Zug and Zug, 1979) (see Table in §D).

8. In the Foster Gardens in Hawaii a seasonally fatal epidemic occurs when blossoms fall from the strychnine trees. Toads, attracted by the movement, eat the blossoms and die of strychnine poisoning. Petals of the flowers contain 1.023% pure strychnine (Alexander, (1964).

9. Several authors, notably Boice and Boice (1970) have suggested that there is an hierarchical feeding order among toads, which correlates positively with size. Sometimes individuals will push others away from food in an extremely aggressive manner. Fellows (1969a) observed a number of toads sitting in a perfect circle around a straw-sized hole from which female termites were emerging. The toads struck at the emerging insects in a definite order and no two toads ever struck at the same time.

10. *B. marinus* males can be used for a simple human pregnancy test. We classify 'man' as a predator here with the understanding that some suitable interpretation of 'H' must be made (c.f. n. 20, see General Introduction).

11. Cannibalism has been observed by Hinckley (1962), Bailey (1976) and Tyler (1976). The latter records that a newly-metamorphosed toad is approximately 8mm in length and at constant risk of being eaten by larger toads. This risk diminishes with size.

12. There is a range of heat energy that can be considered beneficial or at least not harmful - this range will be a set of resources. Outside the beneficial range, both above and below, the animal will be increasingly disadvantaged to a point at which it will die - this range will be a set of malentities.

Brattstrom (1963) reports that in South America the average body temperature of the animal in the wild, calculated from all sources until 1963, was 25.2°C. Johnson (1972) in Australia gives 21.3°C ±2.4°C as the body temperature. van Beurden (   ) also in Australia, reports that when *B. marinus* is exposed to temperatures of 3°C, it takes from 1 to 2 hours for the animal's deep body temperature to fall from 20°C to 3°C. The raising of the deep body temperature occurs more quickly. He also found that toads from southerly (i.e. colder) areas recovered more quickly from exposure to very low temperatures of 0° - 2°C. Survival times of juveniles and tadpoles exposed to very low temperatures were short however all tadpoles survived at 8°C for 24 hours.

50% of newly metamorphosed toadlets die within 4 hours when exposed to temperatures of either 4.5°C or 40°C. "On dry sunny days the activity of these toadlets is restricted to 10m from the water edge - regular excursions are made every15-20 minutes to the water for water uptake. Deprived of their "drink" and remaining exposed to the sun they died within 40 minutes. Similarly deprived but not exposed to the sun they died in 50 minutes." (van Beurden, 1978). A 12-hour exposure of adults to 30°C and 40°C was not lethal, but exposure for 28 and 48 hours was. All adults survived at least 96 hours at temperatures above 4°C. In an outdoor experiment with 52 adults in an enclosure 9 toads died during the first frost of the season. (The temperature fell to -1°C for just over an hour). On the following day 10 toads died. (The temperature fell below 1°C for over 8 hours). The position of the animals in the enclosure was thought to be important in this experiment, since the temperature beneath litter was approximately 2°C higher (van Beurden, 1979). Warburg (1965) noted that *B. marinus* at a temperature of 37.5°C and very low humidity of 0-5% had a mean survival time of 4-6 hours (maximum 8 hours).

Krakauer (1968) argues that Miami (Florida), which experiences sub-zero temperatures about once very five years, is a marginal habitat for *B. marinus*. He comments that any nearby water will moderate the microclimate and that the most favourable habitat for *B. marinus* is the East Coast Rock Ridge where the climate is mitigated by the Atlantic Ocean. He also indicates that nocturnal temperature inversions will cause ground frosts more frequently in open areas than in urban areas and hence that toads are attracted towards urban areas. Zug and Zug (1979) note that the limit of the range of *B. marinus* in Texas corresponds to the 15°C isopleth. Stuart (1951) found Guatemalan toads only below 1,500 m which is the isopleth for the 15°C mean minimum temperature.

It seems almost certain that all anurans use evaporation from the skin as a cooling device, both in stress situations and for normal thermo-regulation. Other factors affecting body temperature will be the temperature of the surrounding air in the microenvironment and the temperature of the substrate; both of these involve conduction. A modifier of the substrate will be the amount of air it holds.

Duellman (1965) hypothesizes that the low density of *B. marinus* in well-shaded forests might be because the thermal requirements of embryos are unsuited by shaded pools. He notes that the animals are abundant in nearby clear areas.

Oviposition can be interrupted by a fall in temperature. Delays at up to 3 days were observed by Straughan (1966) when the water temperature dropped below 72°F. Oviposition continued once the temperature returned to 78°F.

13. This frog of the family Microhylidae shares the same breeding ponds as *B. marinus* in parts of the Philippines. *B. marinus* lays a much larger clutch of eggs so that we might expect it to consume most available organic matter, particularly in adverse conditions. However, food is so abundant that the competition has little noticeable effect (Alcala, 1957). Rabor (1952), also in the Philippines, observed *Kaloula conjuncta* (Peters) as a possible competitor.

14. Alcala (1957) reports that some fish eat *B. marinus* larvae but does not specify which ones (see n. 1).

15. Buzacott (1939) showed that domestic fowls could eat young toads (3/8in - 7/16in long) with impunity. He also records that the toad feeds on the cockroach which is an intermediate host for the fowl-parasite, the eye-worm.

16. In Puerto Rico the ground lizard *Ameiva exsul* (Wolcott, 1950) was useful in controlling the cane pests *Phyllophaga portoricencis* (the June Beetle) and *Cnemarachis vandinei*. The lizard was practically exterminated by the introduced mongoose and *B. marinus* was then introduced to control the cane pests. Any surviving lizards are competitors of *B. marinus* and their effectiveness is governed by the size of the mongoose population (Mettrick and Dunkley, 1968).

Smyth (1917) also records the lizard as feeding on the beetles. He lists the following *Phyllophaga* sp. on Puerto Rico: *P. vandine*, *P. portoricensis*, *P. guanicana* and *P. citri*, also *Phytalus insularis*. All these are eaten by the toad. The grubs are eaten by the Puerto Rican blackbird *Holoquiscalus brachypterus*, the bare-legged owl, 'mucaro' *Gymnasio nudipes nudipes*, the little blue heron 'garza axul', *Florida caerulea caerulescens* and the mangrove cuckoo *Coccyzus minor nesiotes*. On St. Kitts *Phyllophaga patruel* is a resource of *B. marinus* and on St. Vincent, *P. patens*. Wasps of the family Scoliidae and the click beetle family, Elateridae, also attack the grubs while flies, family Tachinidae, attack the adult beetles. The grubs are also susceptible to the fungus *Metarrhizium* and the bacterium *Micrococcus nigrofaciens* Nov. At the time of writing, man was also a significant modifier of this resource; during a seven-month period in 1914, 2,255,000 beetles were collected by paid workers on the sugar cane plantations. Other modifiers of the *Phyllophaga* spp. are mites, the humidity and texture of the soil, heat energy, and various fruits and plants (see n. 43). Many authors have suggested that insects are seasonally abundant in *B. marinus'* environment; many species of insect emerge only when favourable conditions such as seasonal rains, appropriate temperatures etc. occur. In some areas (Zug and Zug, 1979, see n. 34) this seasonal abundance results in greatly increasing activity among the toads.

17. The Common Keelback (a snake *Amphiesma mairii*) thrives in captivity on a diet of *B. marinus* and is the only Australian species of animal known to utilize the toad regularly for food.

18. Both Tyler (1976) and Brattstrom (1962b) note that flash floods in drainage ditches and other confined waterways are dangerous to tadpoles, although Breder (1946) remarks that tadpoles can stem a considerable current.

19. At metamorphosis young toads are at high risk of death by drowning if they are unable to climb from the water (Tyler 1976).

20. Tyler (1976) notes that the principal benefit of *B. marinus'* presence in Australia has been as an experimental animal for use in secondary schools, Universities and in a variety of medical research institutions to the extent of 100,000 animals per year. We class these students and researchers as malentities with the understanding that some suitable interpretation of 'H' must be

made. (c.f. n. 10. See General Introduction). The Innisfail Apex Club (in North Queensland) made enough money from the sale of cane toads to build an Old People's Home (known locally as 'Toad Hall'). On the envirogram 'Apex Club' is classified as a second-order modifier - strictly speaking this is not an object - we could, however, replace it with say the President or Secretary of the club.

21. Small tadpoles are 'eaten' (see General Introduction) by the aquatic insectivorous bladderwort plant *Utricularia* spp. The tadpoles are in danger particularly when water levels are low (Tyler, 1976).

22. Mead (1961)(also see Working Paper on *Achatina fulica* in this series) gives the following complex interaction on Guam and Ponape Island between *B. marinus* and several other introduced and native species. The Giant African Snail *(Achatina fulica)* was accidently introduced on boats with produce etc. and *B. marinus*, which was introduced effectively, to control the black garden slug *Veronicella leydigi*, also predated the young of the snail. In addition the toad predated the native snails *Opeas* spp. Furthermore, examination of the toad's stomach contents revealed flesh and shell fragments from much larger snails, usually in the presence of dead fly maggots. Apparently the toads were attracted by the movement of fly maggots to dead snails which had been crushed by cars. Cockroaches had thrived because of the large numbers of dead snails - and *B. marinus* thrives on cockroaches. Early traders had accidentally introduced rats; to control them the Monitor Lizard (*Varanus* spp.) was brought in. Unfortunately the lizard is diurnal and the rats nocturnal, so the lizard became a pest by predating eggs and chickens. The Monitor Lizard also ate *B. marinus* which poisoned it (see note 1). Cats and dogs were the best ratters on the islands, however they ate *B. marinus* and died. A beneficial consequence of the introduction of the Monitor Lizard was the predation of coconut pests: the coconut crab *(Birgus latro)* and grubs of the rhinoceros beetle; and the general agricultural pest, the Giant African Snail. The coconut crab also feeds on this snail.

Thus the introduction of *B. marinus*:

(i) Reduced the black slug population;
(ii) Reduced the Monitor Lizard population;
(iii) Reduced the cat and dog population;
(iv) Aggravated the rat problem (by killing lizards, cats and dogs);
(v) Reduced the natural control of coconut pests;
(vi) Had some effect on the Giant African Snail population;
(vii) Ameliorated the fly and cockroach problem (caused by the abundance of dead Giant African Snails).

Bailey (1976) and Tyler (1976) both comment on the extremely poor condition of many toads in New Britain (New Guinea). At that time, the toads had apparently eaten out almost the entire population of ground-dwelling insects. In consequence they began eating the introduced Giant African Snail *(Achatina fulica)*. This snail has a large and probably indigestible shell which has been known to puncture car tyres (c.f. note 24). We classify insects as first-order modifiers because in their presence the snail is less likely (unlikely) to be eaten but in their absence the probability of the snail being eaten increases markedly. (see General Introduction on disappearing or non-existent objects). (see also note 42).

23. When faced with an enemy *B. marinus* has a behaviour pattern which is apparently an attempt to convince the would-be predator that the toad is too large to eat. The toad drops the side of its body nearest the enemy and raises the other side, thus displaying the greatest possible surface area (Tyler, 1976).

24. The Frenchi beetle, *Lepidiota frenchi* feeds by preference on Moreton Bay Ash, Bloodwood and guava. Both the elimination of these trees and soil fumigation using carbon bisulphide and paradichlorobenzene were employed by farmers to help control this cane pest (in Queensland).

By 1941 it was apparent that *B. marinus* was playing only a minor role in controlling the Greyback and Frenchi beetles in Queensland (van Beurden, 1978).

Fellows (1969b) reports that *B. marinus* will not eat large hard-cased adult cane beetles although they will readily eat softer, younger cane beetles. Presumably the beetle in question is either the Grey-Backed beetle *Dermolepida albohirtum* or the Frenchi beetle *Lepidiota frenchi* (see note 44), (c.f. snail note 22).

25. The tadpoles are very dark in colour; this aids them in absorbing and maintaining high body temperature. It is to *B. marinus*' advantage to maximize growth and development rates to increase the probability of eggs surviving through the tadpole stage to metamorphosis before the pond dries up or flash floods sweep them away (Heatwole *et al*, 1968). (see also n. 12 and n. 18).

Tadpoles aggregate. Brattstrom (1962b) has done experiments which show that aggregated tadpoles absorb heat more readily than when dispersed, and convey heat to the surrounding water thus raising the temperature of their immediate surroundings.

Both Floyd (personal communication) and Mares (1972) remark that the tadpoles, often aggregated, vary their location in the pond in order to remain within their preferred temperature range.

Oliver (1949) lists the following as affecting tadpole development:

(i) Water temperature;
(ii) Amount and type of food;
(iii) Amount of light;
(iv) Number of tadpoles present.

Floyd (pers. com. 1981, thesis in prep.) reports that egg survival rises from an average of 60% at 18°C to over 90% at 27°C then falls to approximately 62% at 34°C.* He believes that eggs are less tolerant than tadpoles of temperature extremes. At 14°C eggs hatch after 155 hours; the hatching time decreases approximately exponentially to about 25 hours at 34°C.

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* Outside this temperature range survival is negligible.

26. Hinckley (1962), working in Fiji, reports that the animal eats dung beetles of the genera *Copris* and *Aphodius*. We have included cattle as second-order modifiers; almost any animal excreting faeces could be included here.

27. Hinckley (1962), in Fiji, reports that adult toads occasionally choked to death when trying to swallow young mynahs and chickens.

28. Hutchinson and Kohl (1971) measured metabolic rate in terms of oxygen consumption and found that changes in metabolic rate were governed by the photoperiod (i.e. no internal rhythmn was observed). Under various regimes of photoperiod a pronounced decrease in metabolic rate occurred in the two to three hours after onset of the photophase and a peak in metabolic rate in the corresponding two to three hours after darkness.

29. Illingworth (1941) reports that these ants, *Pheidole megacephala*, are eaten only on rainy nights, apparently giving away their position by throwing up mounds of soil.

30. Jakowska (1972), in the Dominican Republic, reports the tick *Amlyomma dissimile* as producing lesions on *B. marinus*. Female ticks will feed for five or six days on the toad, breed, then fall off. The young ticks may infest other toads so that infested toads, or the other known host, the iguana *Cyclura cornuta*, are first-order modifiers. The same tick was reported in Trinidad by Lever (1938).

31. Johnson (1976) gives the following TL_{50} (50% tolerance limit) concentrations in ppm. for tadpoles:

TABLE 2: TL_{50} values for herbicides with anurans in bioassays conducted at 21° to 22°C.

Toxicant	24h	48h	96h
Fenoprop	60	42	34
Sodium arsenate	195	150	123
2, 4, 5-T amine	425	382	340
2, 4D amine	346	333	288

Chemical compositions of these toxicants may be found in Johnson's article.

These herbicides may enter the locality in at least two ways: by direct spraying and through runoff from spraying of the littoral area.

B. marinus tadpoles were more resistant than other anurans tested.

32. Kloss (1974) reports the following four nematodes (Rhabditoidae) infesting *B. marinus* : *Rhabdias sphaerocephala* Goodey 1924; *R. fuelleborni* Travassos 1927; *R. elegans* Gutierrez 1945; *R. hermaphrodita* Kloss 1971. All species have a complex two-generation life cycle: a free-living generation in the excrement of the host which will penetrate the skin of almost any animal; and an hermaphroditic generation within the host, usually in the lungs.

33. Except for a few instances of diurnal feeding (e.g. see note 5, Alexander 1964) the usual adult cycle is one of nocturnal activity and diurnal disappearance. Zug and Zug (1979) found that not all individuals are active in feeding even during periods of optimum conditions and abundance, which suggests that toads feed maximally when active and then retire for several days to assimilate their food. In the wet season in Papua at least 31% of the population were active on any one night with a maximum of 50% on one particular night. Most toads reached a peak of activity about two hours after dusk.

34. It is not known whether *B. marinus* drinks; like all amphibians water is absorbed through the skin. Krakauer (1970) reports that *B. marinus* survived 140 days (i.e. to termination of experiment) immersed in distilled water. Heatwole and Newby (1972) determined that activity greatly influences evaporative water loss. In plotting activity against hydrated weight they found that *B. marinus* was most active between 50% and 59% of its fully hydrated weight and that it still remained active when its hydrated weight was as low as 30% - 39%. They concluded that the animal was well adapted to relatively dry conditions.

Krakauer (1970) tested the toad's dehydration tolerance. The following figures are from Table I of his article: (the figures in brackets are for *Rana pipiens*

Weight (g)	84.4	(10.4)
Body water (%)	77.2	(83.5)
Tolerance (%)	52.6	(52.2)
Essential water (%)	60.9	(70.8)

'Body water' is the difference between wet weight (empty bladder) and oven-dried weight, as a percentage of body weight. 'Tolerance' is the lethal limit of dessication i.e. the difference between wet weight and weight at death as a percentage of (wet weight - dry weight). 'Essential water' is the difference between weight at death and dry weight as a percentage of weight at death.

Machin (1969), in laboratory experiments, showed that low humidity and high air flow over the toad are important factors in evaporative water loss. He comments that toad skin acts as a diffusion barrier and that it becomes less permeable as the humidity drops. For tadpoles, heat energy can be a malentity in another way; Gomoll (1968) in Guam, and others, comment that occasionally *B. marinus* lays eggs in small puddles that are in danger of drying up.

Zug and Zug (1979) suggest that the ideal time for metamorphosis would be the beginning of the wet season when high humidity permits, rapid and distant dispersal. Takana and Iijima (1939) find that toadlets die quickly if the relative humidity is below 70 - 80%.

Of several species of tadpole tested Valerio (1971) reports *B. marinus* as being the second least resistant to being removed from water. (He used tadpoles which had reached a late stage). Of 10 *B. marinus* tadpoles all survived up to 7 hours and all were dead by 10 hours.

In Papua Zug and Zug (1979) noticed greatly reduced activity among the toads in the dry season. As the number of consecutive dry days increases the activity of the population decreases. They suggest two causes of this decrease: (i) during the dry season there are less prey available and (ii) there is a high water loss from the animal. They suggest that the toad uses a crouched posture to lessen the skin area through which water can evaporate (see also n. 3). They report also that hydration occurs faster in water than in saturated soil. The rate of water loss is size dependent. Large toads lose more water at a faster rate but because they have much more water to lose they survive better.

We have assumed above that we are discussing healthy animals. However in the case reported in note 22 near-starving toads that ranged too far from cover in search of food during the night died of dehydration in the morning sun, being too weak to return (Bailey, 1976 and Tyler, 1976).

35. Krakauer (1970) reports that toads placed in sea-water (15% NaCl) "thrashed around" immediately and all died within hours. At 10% NaCl there was 100% survival after 96 hours.

Curiously, Wingate (1965), in Bermuda, writes "adults occasionally swim across salt waters to the smaller islets and I once intercepted a large adult specimen swimming ashore on Nonsuch Island from the mainland 1,500 ft distant".

36. Mares (1972) comments that in experiments with tadpoles crowding inhibits growth. This has not been observed in the wild. We have tentatively classified 'other tadpoles' as malentities because inhibited growth may simply reduce 'H'.

37. Mares (1972) reports a tadpole captured by a dragonfly larva (Odonata) but released after a struggle.

38. There is an unknown (at time of writing, 1981) but significant predator of *B. marinus* in northern Australia. This predator disembowels the toad and consumes the viscera. Cassels (1970) reports a Koel *(Eudynamys scolopacea)* killing and eating two toads in this way. Several ecologists support the theory that the predator is the white-tailed water rat *(Hydromys chrysogaster)*. Frauca (1974) often observed the Australian crow *(Corvus orru)* eating dead toads from the road in similar fashion.

39. *B. marinus* in Hawaii eats the adults of the oriental beetle, *Ardoretus sinicus* Burm., which feed at night on many plants including rose, grape, cycad, okra, bean, soya bean, pigeon pea, sweet potato, asparagus, taro, banana, cotton, canna, acalypha, Mexican creeper. Many larvae and pupae of the beetle are killed by the green muscadine fungus *Metarrhiziun anisopliae.* Larvae are also parasitized by the Scolia Wasp, *Campsomeris marginella modesta* Smith and the Rolling Wasp *Tiphia segregata* Crawf. Lights discourage the beetle (contrast with note 5). Arsenate of lead is effectively used by gardeners (Fullaway and Krauss, 1945).

In Queensland, Mungomery (1936a) reports that the scarabaeid beetle population emerges in full force only during the wetter period of the year.

40. *B. marinus* eats the adults of this beetle (*Pantomorus* sp.) which feeds on at least the following: geranium, hibiscus, bean, alfalfa, citrus, boa (*Acacia koa*), ti (*Cordyline terminalis*), sugar cane. Larvae are eaten by the click beetle (*Monocrepidus exsul*) and adults are also eaten by mynah birds and mongooses. This beetle, like the scarab, is also controlled by arsenate of lead.

41. *B. marinus* is known to eat domestic bees. Goodacre (1947) reports finding 300 bees in the stomach contents of one toad. Apiarists have adopted the practice of raising their hives on stakes two feet in height to prevent this predation. The toads seem to suffer no ill effects from being stung.

42. Zug and Zug (1979) observed an instance of *B. marinus* following the calls of male frogs of the species *Physalaemus pustulosus* to their pool and later eating two of them. Other observations suggest that *B. marinus* recognises the various sounds made by prey. (However, vision appears to be the toad's primary sense).

43. The *Phylophaga* spp. listed in n. 16, often called the 'May' or 'June" beetles are attracted by at least the following fruit trees:

banana *(Musa* sp.*)*
casuarina *(Casuarina equisetifolia)*
flamboyant *(Delonix regia)*
almendro *(Terminalia catappa)*

guava *(Inga laurina)*
coconut *(Cocos nucifera)*
breadfruit *(Artocarpus communis)*
trumpet *(Cecropia peltata)*
(Dexter, 1932).

Smyth (1917) lists many other plants "greatly relished" by *Phyllophaga*, including: salcilla *(Schrankia portoricensis)*, quenepa *(Melia azedarach)*, tamarind *(Tamarindus indicus)*, jobo *(Spondias lutea)*, cecropia *(Cecropia palmata)*, pigweed, or bledo *(Amaranthus* spp.*)*, mallow *(Malachra rotundifolia)*, and *Petiveria alliacea*. He also mentions that adult *Phyllophaga vandinei* are strongly attracted to light.

Diaspore dispersal can be categorized by the operative energy source(s). The major division is between parent plant energy and external energy sources. The latter will include various agencies such as humans, animals, wind, water etc. (M.J. Liddle and A. Bulow-Olsen, personal communication), all of which appear in the environment of the toad as second-order modifiers. Some of these modifiers may work in combination, modifying each other, and thus entering the environment as third-order modifiers in the formal sense.

44. Zug and Zug (1979) suggest, from a study of fat body weight, that in some areas the females require a period of intense feeding to replenish their lipid stores before vitellogenesis can begin.

45. Mungomery (1936b)observes that male toads can change their sex, although the conditions (if any) which induce such a change are not known. The mechanism is as follows: a rudimentary ovary, the Bidders organ, is present in all young toads. Subsequently, it degenerates in females, but persists in males. Internal secretions may bring about a slow change from male to female with the Bidders organ functioning as an ovary. Eggs are normal but markedly fewer. Males to which this may happen are not classified as mates (for a male) because the primitive term 'ξ' requires that some response is evoked immediately (see General Introduction).

Zug and Zug (1979) report that in field data on *B. marinus* there is a marked tendency towards one sex only being observed - either male or female - and that there is no known explanation of this. However, Floyd (pers. com. 1981) suggests that collection time, site and method of collection all have a big influence on which sex is actually collected. van Beurden (1978) in Queensland reports a 1:1 sex ratio.

Lucas (1969) reports that at Stuttgart zoo a toad hydrid, *B. blombergi* X *B. marinus*, was raised.

46. Takano and Iijima (1937) find that the presence of $CaCl_2$ is essential for tadpole development.

47. Takana and Iijima (1939) note that in crowded conditions large tadpoles eat smaller ones.

48. The giant water beetles (Dytiscidae) *Hydrophilus ater* and *Megadytes giganteus* are reported by Tucker (1940) as attacking *B. marinus* tadpoles in Barbados.

49. Only older tadpoles have lungs; when a tadpole reaches this stage it is obliged to rise to the surface to breathe (Tyler, 1975).

50. Tyler (1975) reports that (in Australia) the Fork-tailed Kite and Ibis and (in Bermuda) Herons eat both juvenile and adult toads.

51. van Beurden (1978) showed that there was high dietary overlap of *Lymnodynastes terraereginae* and other frogs with *B. marinus* at Lake Ainsworth in Queensland. He remarks that the observed declining populations of the toad may be due to this competition.

52. Takano and Iijima (1937) observe that tadpoles will develop in pH range 4-9. If they mean by this that the tadpole will not develop outside this range then pH, like heat energy (see n. 12, page 1), will have a range that constitutes resources and another that constitutes malentities.

53. Breder (1946) reports tadpoles of *Rana palmipes* eating *B. marinus* eggs.

D. DETAIL

Poisonous secretion

The table is from Knowles (1964).

COMPOSITION OF BUFO SPECIES TOXIN

A. *Marino bufagin*

1. A bufagin, a steroid type compound
2. It has a digitalis-like action: causing emesis and ventricular fibrillation.
3. Toxicity (mg per kg) 0.555 .028

B. *Marino bufotoxin*

1. A bufo toxin a congegation product.
2. Digitalis-like action: systolic standstill of heart

C. *Marino bufotenine*

1. Oxytoeie there is little or no pressor action.
2. Produces cardiac arrest at dilution of 1:5000.

D. Others

a. Epinephrine
b. Cholesterol
c. Ergosterol
d. 5-hydroxytruptamine

Temperature tolerance

The following table is from Mares (1972):

Time	Temperature		Tadpole Position	
	Shallow Water	Deeper Water	Shallow Water	Deeper Water
0545	21.8	*	X	
0910	34.6	31.8		X
0930	37.0	33.6		X
1005	38.0	33.8		X
1100	37.4	37.0		X
1330	37.2	36.4		X
1400	34.0	34.4	X	
1445	34.6	32.5		X

* Although no measurements were made at this time, it was assumed that water temperatures of the two depths had equalized during a night's cooling.

The following table was provided by Floyd (Pers. com. 1981):

CTMax	Acclimation Temp	Time	Locality	Source
41.5	21	7 days	Puerto Rico	Heatwole et al 1968
41.6	23	NA	Florida	Krakauer 1970
42.5	25.6	NA	Florida	Krakauer 1970

The measurements which follow are from Brattstrom (1968):

Location: Panama, 9^{0}N.

Altitude: 1,000 ft

Critical thermal data: Maximum subject to acclimation. Giant toads acclimated for several weeks at 27°C and placed at 38°C changed their CTM from 39.2 to 41.0°C. If acclimated at 27°C and placed at 7°C they showed a drop in the CTM. After two days they could no longer survive the cold. The mean body temperature for a sample of 19 toads was 25.2°C (ranging from 24.2 to 27.0°C).

FOOD

The following table is from Mungomery (1936a):

The following represents the stomach contents of 50 toads, captured in different localities between 5/12/38 and 12/4/30, and presents a fair picture of what they had been eating during that period.

Family	Order	Species	No.	Common Name
Orthoptera	Blattidae	Periplaneta sp.	2	House Cockroach
Orthoptera	Gryllidae	Gryllus sp.	1	Mole Cricket
Isoptera	Termitidae	Eutermes sp.	50	Termites
Dermaptera	Forficulidae	Unidentified	3	Earwigs
Hemiptera	Pentatomidae	Nezera viridula	2	Shield bugs
Hemiptera	Cydnidae	Cyndus sp.	80	Black bugs
Coleoptera	Scarabaeidae	Lepidiota frenchi	37	Frenchi Cane Beatle
		Anoplognathus biosduvali	4	Christmas Beetle
		Neso ducalis	14	
		Onthoplagus sp.	8	Dung Beetle
		Epholcis bilobiceps	92	
		Phaeochrous hirtipes	25	
		Frenchella sp.	1	
		Isodon puncticollis	3	
		Repsimus aeneus	1	
		Bolboceros sp.	1	
		Unidentified	6	
	Leucanidae	Unidentified	5	
	Chrysomelidae	Unidentified	42	
	Coccinelidae	Coccinella 8-maculata	1	Ladybird
		Coccinella repanda	1	Ladybird
	Elateridae	Monocropidius Cairnsensis	11	Wireworm adults
		Unidentified	23	Wireworm adults
		Larva	1	Wireworm
Coleoptera	Carabidae	Unidentified	7	Ground Beetles
	Curculionidae	Rabdoenenis obscura	13	Cane beetle borer
		Lixus mastersi	1	Weevil
		Unidentified	7	Weevil
	Lagriidae	Unidentified	19	Leaf eating beetles
	Tenebrionidae	Gonocephalus sp.	4	False wireworm beetles
		Unidentified	7	

Family	Order	Species	No.	Common Name
Coleoptera	Dermestidae	Unidentified	2	Carrion beetles
	Hydrophilidae	Larva	1	Water beetle larva
Hymenoptera	Formicidae	Aphaenogaster sp.	Many	Mound building ants
		Pheidole sp.	Many	Common house ant
		Unidentified	6	Ants
	Mutillidae	Ephutomorpha sp.	1	Wasp or Velvet Ant
Lepidoptera	Noctuidae	Spodoptera exempta	180	Army worms
		Unidentified larvae	45	Army worms
	Pyralidae	Unidentified larvae	6	
Myriopoda (Class)			1	Millipede
Annelida (Class)			3	Earthworms
Mollusca (Phylum)			1	Small Snail

The following tables are from Pippet (1975):

Table 1: Stomach contents of *Bufo marinus* taken at Laloki between January and December, 1973. Number of individuals 351. Mean stomach contents 1.5g.

- ANNELIDA
  - OLIGOCHAETA
    - 1 earthworm
- MOLLUSCA
  - GASTROPODA
    - 1 snail
- ARTHROPODA
  - CRUSTACEA
    - ISOPODA
      - 2 slaters
- MYRIAPODA
  - CHILOPODA
    - 3 centipedes
- DIPLOPODA
  - 6 millipedes
- SCORPIONES
  - 1 scorpion
- ARACHNIDA
  - ARANEAE

- COLEOPTERA
  - 30 CARABIDAE including
    - 5 Cicindelinae Tiger beetles
    - 1 *Pheropsophus verticalis*
- 2 HYDROPHILIDAE
- 8 STAPHYLINIDAE
- 82 SCARABAEIDAE including
  - 3 Cetoniinae
  - 9 Melolonthinae Chafers
  - 30 *Aphodius*
  - 29 Hybosorinae
- 33 ELATERIDAE, Click beetles including
  - 17 *Lacon*
  - 2 *Heterodes*
  - 2 *Colacon*
- 4 BOSTRYCHIDAE
- 5 LANGURIIDAE
- 18 COCINELLIDAE Ladybirds
- 13 TENEBRIONIDAE

12 spiders
ACARINA
1 mite
INSECTA
BLATTODEA
BLATTIDAE
4 cockroaches
ISOPTERA
26 termites
ORTHOPTERA
GRYLLIDAE
64 crickets *Acheta commoda*
ACRIDIDAE
64 short-horn grasshoppers
TETTIGONIIDAE
4 long-horn grasshoppers
HEMIPTERA
2 FLATIDAE
5 CICADIDAE Cicadas
16 MIRIDAE
5 REDUVIIDAE Assassin bugs
1 ENICOCEPHALIDAE *Oncylocotis*
26 COREIDAE
1 PLATASPIDAE
45 CYDNIDAE
50 PENTATOMIDAE Shield bugs
4 LAGRIIDAE
2 ANTHICIDAE
16 CERAMBYCIDAE Longhorn beetles
54 CHRYSOMELIDAE including
3 Cassidinae Tortoise beetles
1 BRENTHIDAE
6 APIONIDAE *Cylas formicarius*
18 CURCULIONIDAE Weevils including
2 *Oribius*
2 *Leptopius squalidus*
DIPTERA
2 (1 larva, 1 adult)
LEPIDOPTERA
12 moths
290 Larvae, including
82 SPHINGIDAE including
59 *Herse convolvulus*
198 NOCTUIDAE including
152 *Spodoptera*
60 *Plusia*
17 GEOMETRIDAE *Ectropis*
HYMENOPTERA
395 including
2 VESPIDAE
4 SPHECIDAE
1 ICHNEUMONIDAE
385 FORMICIDAE mainly *Pheidole*
CHORDATA
SQUAMATA
SCINCIDAE
1 skink

Table 2: Stomach contents of *Bufo marinus* taken at Serovi Plantation, Popondetta, Northern District, from March to November, 1973. Number of individuals 405. Mean stomach contents 2.3g.

- ANNELIDA
  - OLIGOCHAETA
    - 3 earthworms
- MOLLUSCA
  - GASTROPODA
    - 17 snails, 2 spp
- ARTHROPODA
  - CRUSTACEA
    - ISOPODA
      - 2 slaters
  - MYRIAPODA
    - CHILOPODA
      - 2 centipedes
    - DIPLOPODA
      - 172 millipedes, 3 spp
    - ARACHNIDA
      - ARANEAE
        - 28 spiders
      - ACARINA
        - 2 ticks
      - PHALANGIDA
        - 1 harvestmen
- INSECTA
  - BLATTODEA
    - BLATTIDAE
      - 16 cockroaches
  - ISOPTERA
    - 94 termites
  - DERMAPTERA
    - 20 earwigs, including
      - 9 Forficulidae
      - 8 Labiidae
  - ORTHOPTERA
    - GRYLLIDAE
      - 48 crickets *Acheta commoda*

- COLEOPTERA
  - 67 CARABIDAE
  - 1 DYTISCIDAE
  - 4 HYDROPHILIDAE
  - 27 STAPHYLINIDAE Rove beetles
  - 3 LUCANIDAE Stag beetles
  - 2 PASSALIDAE
  - 220 SCARABAEIDAE including
    - 94 Hybosorinae
    - 4 *Aphodius*
    - 54 Coprinae
    - 5 Dynastinae *Papuana*
    - 57 Melolonithinae Chafers
    - 1 Rutelinae
  - 1 BYRRHIDAE Pill beetle
  - 1 HETEROCERIDAE
  - 1 RHIPICERIDAE
  - 123 ELATERIDAE Click beetles including
    - 4 *Aeolus*
    - 9 *Colacon*
    - 4 *Corodius*
    - 14 *Compsolacon*
    - 83 *Lacon*
    - 3 *Lanelater*
  - 18 EUCNEMIDAE
  - 1 LYCIDAE
  - 2 ANOBIIDAE
  - 10 BOSTRYCHIDAE
  - 42 NITIDULIDAE
  - 2 EROTYLIDAE
  - 5 COCCINELLIDAE
  - 19 LANGURIIDAE
  - 40 TENEBRIONIDAE
  - 2 LAGRIIDAE
  - 57 CERAMBYCIDAE Longhorn beetles

ACRIDIDAE
  2 short-horn grasshoppers
GRYLLOTALPIDAE
  1 mole cricket
PYRGOMORPHIDAE
  5 specimens
HEMIPTERA
  3 FLATIDAE
  1 CERCOPIDAE
  31 CICADIDAE emerging nymphs
  1 MEMBRACIDAE
  70 MIRIDAE
  8 REDUVIIDAE Assassin bugs including
    1 Emesinae
    1 PYRRHOCORIDAE
    248 DINIDORIDAE *Megymenum papuense*
    10 PLATASPIDAE
    12 PENTATOMIDAE Shield bugs
DIPTERA
  76 Larvae, including
    1 STRATIOMYIDAE
    3 TIPULIDAE Crane flies

14 CHRYSOMELIDAE Leaf beetles
2 ANTHRIBIDAE
10 APIONIDAE *Cylas formicarius* (Sweet Potato Weevil)
146 CURCULIONIDAE Weevils, including
  48 *Pantorbytes szent-ivanyi*
  25 Cryptorrhynchinae sp
  2 Cossoninae sp
  1 *Oribius* sp
  13 *Leptius* sp including
    10 *Leptopius squalidus*
LEPIDOPTERA
  105 moths
  348 caterpillars, including
    242 GEOMETRIDAE
      167 *Ectropis*
      75 *Hyposidra*
    8 NOCTUIDAE *Plusia*
    10 AGARISTIDAE
    23 LYMANTRIIDAE
HYMENOPTERA
  982 including
    1 VESPIDAE
    1 APOIDEA
    1 ICHNEUMONIDAE
  954 FORMICIDAE various spp
CHORDATA
  SQUAMATA
    SCINCIDAE
      2 skinks

In a personal comment to Pippet, F. Rather reported a marked reduction of the Papuan Black-Snake *Pseudechis papuanus* in the Port Moresby area which was possibly due to *B. marinus*. Pippet also reports *Dasyurus* spp. dying after attacking the toad.

The following table and pie charts are from Zug and Zug (1979):

Gamboa: urban sample, collected in November.

Cocole and Summit Hill: savannah country, collected in May. There are Zoological Gardens at Summit Hill where the lights attract insects.

BCI (Barro Colorado Island Research Station), collected in May.

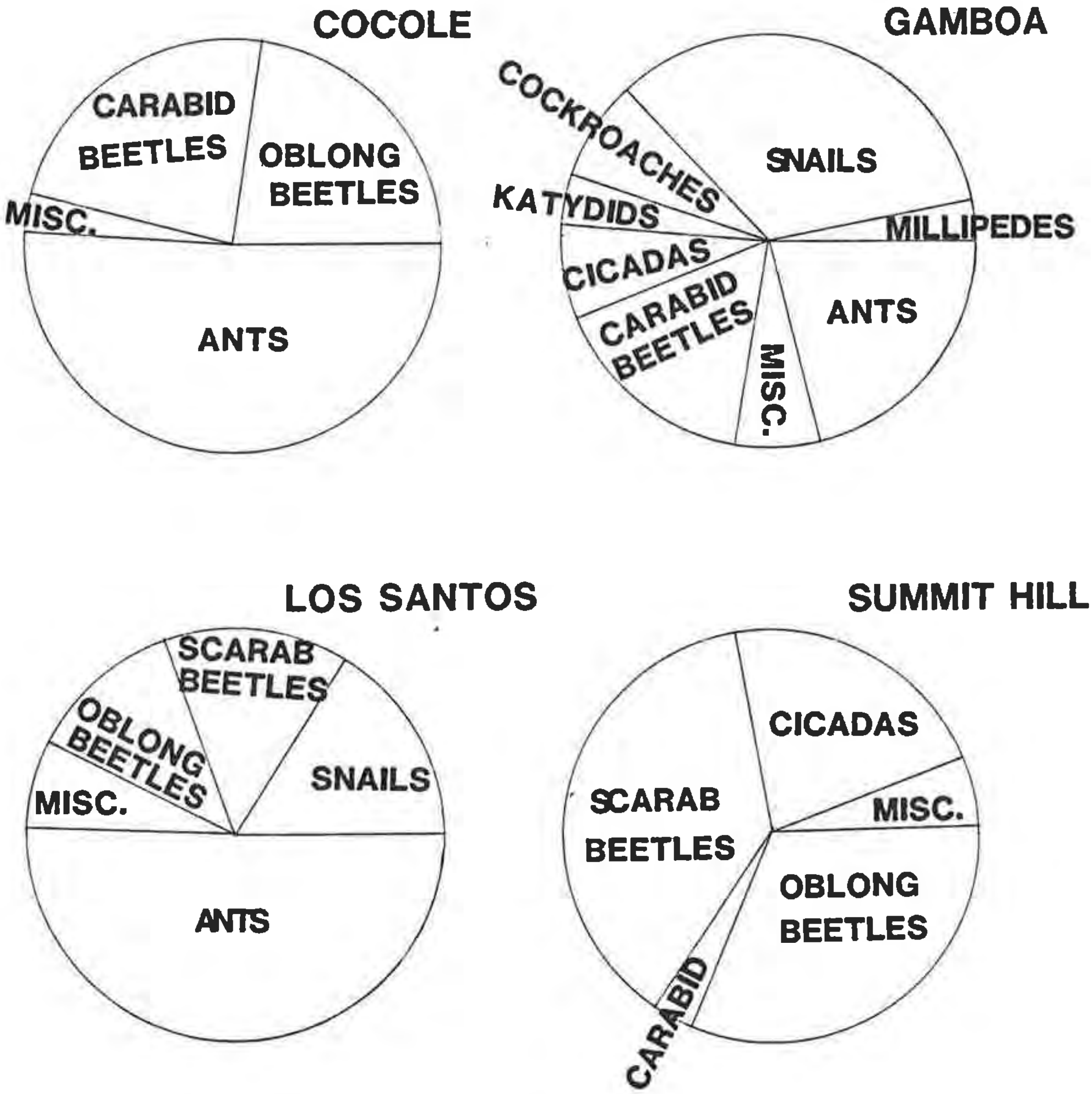
Cocole and Summit Hill results indicate the toad's diet prior to becoming a commensal of man.

The first figure in brackets is the number of toads with empty stomachs, the second the number of toads with stomachs which were not empty.

Prey	Cocole (2/9)	Gamboa (0/10)	Summit Hill (0/11)	Los Santos (3/12)	BCI (1/1)
Arthropoda					
Diplopoda (millipedes)		5			+
Arachnida					
Phalangida (daddy-longlegs)					+
Araneida (spiders)	1	2	2	1	
Insecta					
Odonata (dragonflies)				1	
Orthoptera					
Acrididae (grasshoppers)					+
Lettigoniidae (katydids)		2			
Gryllidae (crickets)		1	1		+
Blattidae (roaches)		3			+
Isoptera (termites)			1		+
Dermaptera (earwigs)		4	1		
Hemiptera					
oblong bugs (e.g., reduviids)			1		+
obovate bugs (e.g., pentatomids)		1	1		
Homoptera					
Cicadidae (cicadas)		1	3		
Neuroptera (lacewings)					+
Coleoptera					
Carabidae (ground beetles)	6	7	5		+
Curculionidae (weevils)	1	3	3	1	+
Scarabaeidae (scarabs)			9	3	+
oblong beetles (e.g. elaterids)	5	4	8	3	+
round beetles (e.g. chrysomelids)	2	1	2	1	

Prey	Cocole (2/9)	Gamboa (0/10)	Summit Hill (0/11)	Los Santos (3/12)	BCI (1/1)
Lepidoptera (moths)			1	1	
Hymenoptera					
Formicidae (ants)	9	8	6	10	+
winged hymenopterans			8	2	+
Annelida (earthworms)			1		
Mollusca					
Gastropoda (snails)		5		1	+

FIGURE 15: Prey preference of marine toads from four localities (Proportions calculated from prey biomasses and only those prey representing more than 2.7% - 10 or more degrees of circle - are plotted separately).



Zug and Zug (1979) also give the following table of prey sizes:

TABLE 12: Frequency of different sized prey in different sized marine toads from Gamboa (prey size classes selected to portray relative live weight: using equation $W = 0.0001L^3$, length classes approximately equivalent to <0.0001, 0.0001-0.001, 0.001-0.01, 0.01-0.1, 0.1-1.0 and >1.0 in grams respectively.)

Snout-vent length (mm)	Head Width (mm)	Prey classes					
		>1.0mm	1.1-2.0	2.1-5.0	5.1-10.0	10.1-22.0	>22.0mm
64	26	0	0	1	0	1	0
86	33	0	0	29	15	11	0
92	34	0	0	0	18	18	0
105	37	2	3	0	48	2	0
110	40	0	0	5	101	2	0

The following list of food for young toads is from van Beurden (1978):

DIETARY ITEMS OF JUVENILE TOADS

Showing the number of each taxa found in stomachs of 30 juveniles captured on grassy sand and 30 captured on leaf litter.

TAXON	Numbers in 30 Juveniles on grassy sand	Numbers in 30 Juveniles on leaf litter
GASTROPODA	1	0
AMPHIPODA	0	3
ISOPODA	0	5
CHILOPODA	0	4
ARANEIDA	0	7
ACARINA	154	584
THYSANURA	0	1
COLLEMBOLA	203	0
Orthoptera		
GRYLLIDAE	1	0
TETTIGONIIDAE	1	1
Dictyoptera		
BLATTIDEA	0	4
Hemiptera		
FULGORODEA	0	1
COCCOIDEA	1	4
SCHIZOPTERIDAE	6	0
ATHIDIDAE	193	5
LYCAEDAE	2	0
SALDIDAE	2	0
UNKNOWN	5	3
NEUROPTERA	0	1
LEPIDOPTERA	0	1
Diptera		
CULICIDAE	0	5
MYSETOPHILIDAE	0	1
DROSOPHILOIDEA	0	1
PHORIDAE	5	3
BIBIONIDAE	0	1
SCIARIDAE	1	1
CHIRONOMIDAE	67	6
CECIDOMIDAE	0	2
LARVAE	59	1
UNKNOWN	1	12

TAXON	Numbers in 30 Juveniles on grassy sand	Numbers in 30 Juveniles on leaf litter
<u>Hymenoptera</u>		
FORMICIDAE	75	143
CYNIPOIDAE	0	5
PROCTOTRUDOIDAE	0	1
SCELIONIDAE	4	1
MICROGASTRINAE	0	1
TRICHOGRAMMITIDAE	1	0
DIAPRIIDAE	1	0
UNKNOWN	1	1
<u>Coleoptera</u>		
CARABIDAE	0	11
ELATERIDAE	0	2
BIPHYLLIDAE	0	1
SPHAERIDAE	0	1
STAPHILINIDAE	7	16
BYRRHOIDAE	0	1
PHALACRIDAE	1	0
GEORYSSIDAE	3	0
PSELAPHIDAE	1	0
TENEBRIONIDAE	4	0
LARVAE	20	3
UNKNOWN	2	0
THYSANOPTERA	3	2

The following table is from Dexter (1932). 6 out of 20 insect orders are represented.

TABLE XI

SUMMARY OF ALL FORMS FOUND IN THE 301 SPECIMENS EXAMINED

Name of Specimen	No. of specimens eaten	Percent by bulk
Phyllophaga	635	28.9
Millipeds	570	26.3
Diaprepes	523	12.
Anchonus suillus Fabr	132	.6
Diptera larvae	125	2.8
Catapsomeris dorsata Fabr	111	5.1
Unidentified insect larvae	99	1.1
Ligyrus tumulosus Burmeister	91	12.
Metamesius hemipterus I.	70	1.6
Dyscinetus sp.	65	1.4
Tetraca infuscata Mannerheim	60	2.7
Nymph of Odonata	53	.8
Scapteriscus vieinus Scudder	52	2.4
Ataenius sp	46	.3
Lachnopus curvipes Fabr	41	.5
Lepidoptera larvae	34	.5
Exophthalmodes roseipes Chevr.	32	.5
Snails	28	.3
Euscepes sp.	27	.2
Coleoptera unidentified	25	.2
Shpenophorus sp.	23	.5
Gryllus assimilis Fabr.	20	.9
Aphodius	19	.1
Coleoptera larvae	17	
Unidentified Curentionid	17	.4
Centiped	13	
Spiders	13	.1
Roaches	11	.1
Stethorus sp.	10	.9
Slugs	10	.4
Heteroderes lauretis	9	
Hymenoptera	9	
Monocrepidus sp	8	.1
Periplaneta sp.	8	.1
Pyrophorus laminostus III	8	.37
Stratagus sp.	7	.6
Aeolus elegans Gab.	5	.04
Phalangids	5	.04
Seldistaecerca sp.	5	.04
Cosmopolites sordidus Germar	5	.09
Tarantula	8	.37
Trox suberosus Fabr.	4	.09
Dermaptera	3	.04
Hemiptera	3	
Neoconocephalus macropterus (L.) Redt	3	.04
Culsoma alternans Fabr.	2	.37
Haltica	2	.04

The following lists are from Zug et al (1975):

APPENDIX 2

IDENTITY AND NUMBER OF PREY OF THE *Bufo marinus* FROM THE SAVANNA SAMPLING SIT

MOLLUSCA

Gastropoda - 24 small forest snails

ARTHROPODA

- Chilopoda - 10 centipedes
- Diplopoda - 16 millipedes
- Arachnida
  - Araneae - 25 spiders
  - Acarina - 1 tick
- Isopoda - 1 slater
- Insecta
  - Blattoda
    - Blattidae - 7 cockroaches including 3 *Periplaneta grammea* and 1 *Periplaneta armericana*
  - Isoptera - 800 termites
  - Dermoptera - 3 earwigs
  - Orthoptera
    - Gryllidae - 40 *Acheta commoda*
    - Gryllotalpidae - 3 *Gryllotalpa africana*
    - Pyrgomorphidae - 11 *Desmoptera* sp.
    - Acrididae - 4 short-horned grasshoppers
  - Hemiptera (116 bugs total)
    - Cicadellida - 4 leafhoppers
    - Miridae - 8
    - Reduviidae - 5 assassin bugs
    - Pentatomidae - 19 shield bugs
    - Cydnidae - 51 *Adrisa* sp.
  - Coleoptera
    - Carabidae - 22 ground beetles
    - Dytiscidae - 1 water beetle
    - Curculionidae - 19 weevils including 8 *Apion* sp., 3 *Cylas formicarius*, 2 *Oribus* sp., 2 *Cryptorbinus* sp., and 1 *Pachyrhynchinis* sp.
    - Elateridae - 11 click beetles including 5 *Lacon* sp., and 3 *Aeolis* sp.
    - Tenebrionidae - 12
    - Lagriidae - 3
    - Anthicidae - 1

    Othniidae - 1
    Cerambycidae - 7 unidentifiable longhorns
    Chrysomelidae - 41 leaf beetles including 1 species of Cassidae
    Heterocidae - 4
    Hydrophilidae - 11 water beetles
    Scarabaeidae - 21 including 1 *Melolontha* sp. and 16 *Hybosorinas* spp.
    Staphylinidae - 4 rove beetles and 1 larva
    Erotylidae - 1 fungus beetle
    Coccindellidae - 10 ladybug beetles
Diptera - 12 flies including 5 Muscidae
Lepidoptera - 75 unidentified moths and 94 larvae including those listed below
  Geometridae - 35 looper caterpillars
  Nymphalidae - 1 *Hypolimnas* sp. caterpillar
Hymenoptera
  Vespoidae - 2 wasps
  Sphecidae - 1 *Sphex* sp.
  Formicidae - 680 ants including 269 *Polyrhachis* sp., 197 *Pheidole* sp., 81 *Oecophylla amaragdina* and 68 *Odontomachus* sp.

Note: Prey derived from all the toads (476) collected during the biweekly sampling of October 1971 through September 1972.

APPENDIX 3

IDENTIFY AND NUMBER OF PREY OF THE *Bufo marinus* FROM THE RAIN FOREST SAMPLING SITE

ANNELIDA

Oligochaeta
  Terricolae - 3 earthworms

ARTHROPODA

Diploda - 28 millipedes
Arachnida
  Arancae - 2 spiders
  Scorpions
    Scorpionidae - 1 scorpion
Insecta
  Blattodea
    Blattidae - 1 cockroach
  Dermaptera - 1 earwig
  Hemiptera
    Cicadidae - 1 cicada
    Miridae - 1

Coreidae - 4
Scutelleridae - 2 Harlequin bugs
Pentatomidae - 5 shield bugs
Cydnidae - 2 *Adrisa* sp.
Gerridae - 1 water strider

Coleoptera
Cicindelidae - 1 *Tricondyla aptera*
Hydrophilidae - 3 water beetles
Curculionidae - 49 weevils including 28 *Meroleptus squalidus*, 2 *Rhimoscapha funigris*, 1 *Rhabdoscermus obscurus*, 7 *Cryptorhinus* sp., and 2 *Oribus* sp.
Elateridae - 11 click beetles including 7 *Lacon* sp.
Cerambycidae - 12 unidentified longhorns
Chyrosomelidae - 4 leaf-eating beetles
Byrrhidae - 19 pill beetles
Scarabaeidae - 33 including 9 *Lepidiota* sp., 6 *Melolonthus* sp., and 16 Hybosorin
Passalidae - 1
Trogidae - 1 carrion beetle
Geotrupidae - 1 dung beetle
Staphylinidae - 7 rove beetles
Erotylidae - 1 fungus beetle

Lepidoptera
Geometridae - 11 unidentifiable larvae and 18 geometrid larvae

Hymenoptera
Ichneumonidae - 10 parasitic wasps
Formicidae - 366 ants including 169 *Odentomachus* sp., 123 *Pheidole megacephala*, and 22 *Oecophylla smargadina*

Note: Prey derived from all the toads (37) collected during the biweekly sampling of October 1971 through May 1972.

APPENDIX 4

IDENTITY AND NUMBER OF PREY OF THE *Bufo marinus* FROM THE SAMPLES COLLECTED AT DARU, TALASFA, AND WARIARATA

MOLLUSCA

Gastropoda - 34 small forest snails

ARTHROPODA

Chilopoda - 3 centipedes
Diploda - 24 millipedes
Arachnida
  Araneae - 2 spiders
  Scorpiones
    Scorpionidae - 1 scorpion
Insecta
  Isoptera - 10 termites
  Mantodea
    Mantidae - 1 praying mantis
  Orthoptera
    Gryllidae -11 *Acheta commoda* and 2 *Brachytrypes achatinus*
    Gryllotalpidae - 2 *Gryllotalpa africana*
  Hemiptera
    Cicadidae - 9 emerging cicada nymphs
    Pentatomidae - 3 shield bugs
    Cydnidae - 9 *Adrisa* sp.
    Gelastocoridae - 2 *Nerthra* sp.
  Coleoptera
    Haliphidae - 3 small water beetles
    Curculionidae - 11 weevils including 4 *Meroleptus squalidus*, 2 *Rhinoscapha* sp., 2 *Elytrochiclus graniger* and 2 *Cryptorhinus* sp.
    Elateridae - 6 *Lacon* sp.
    Tenebrionidae - 169 including 166 *Tribolium* sp. from Daru
    Lagriidae - 1
    Helodidae - 187 from Talasea
    Cerambycidae - 13 unidentifiable longhorns
    Chrysomelidae - 1 leaf beetle
    Byrrhidae - 2 pill beetles
    Chelonariidae - 2
    Scarabaeidae - 20 including 6 *Lepidiota* sp., 2 *Aromala* sp. and 9 Hybosorinae

Copridae - 2 dung beetles
Lucanidae - 1 stag beetle and 4 unidentifiable beetles
Diptera - 5 unidentified pupa
Statiomyidae - 1 horsefly larva
Trichoptera - 2 caddis flies
Lepidoptera - 9 unidentified larvae
Geometridae - 1 geometrid larva
Hymenoptera
Vespidae - 2 wasps
Fromicidae - 190 ants including 133 *Oecophylla smaragdina*, 26 *Pheidole megacephala*, and 31 *Polyrachis*

CHORDATA

Amphibia
Bufonidae - 2 *Bufo marinus* juveniles

Note: Samples collected at Daru and Wariarata during April 1972; samples collected at Talasea during May 1972. Sample sizes are: Daru, 90; Talasea, 31; and Wariarata, 17.

All four tables which follow are from Hinckley (1962);

TABLE II - ANALYSIS BY LOCATION

	Number per 10 Toads		
Location	Gastropods	Myriapods	Insects
Lawns and Gardens	7	2	51
Coconut Plantation	13	5	75
Banana Groves	6	30	69
Cane Roads	21	40	4
Rice Field	2	-	90
Percentage containing such prey	42%	40%	82%

TABLE V - SUMMARY OF ECONOMIC IMPORTANCE

Economic Classification	Number eaten by 114 toads	Percentage of toads with such prey
Phytophagous:		
slugs	32	62%
snails	17	
crickets	3	
roaches	6	
leafhoppers	23	
true bugs	48	
caterpillars	166	
beetles	19	
	314	
Scavenging:		
earthworms	15	66%
snails	71	
crabs	2	
mites	2	
pillbugs	3	
millipedes	146	
beetles	48	
	287	

Beneficial:

parasitic wasps	2	65%
predators	40	
ants	368	
bees	300	
	710	

TABLE 1: Identity and Number of Prey of the Giant Toad

PLATYHELMINTHES
TURBELLARIA
Tricladia
1 Land planarian
ANNELIDA
CHAETOPODA
Oligochaeta
15 earthworms
MOLLUSCA
GASTROPODA
Pulmonata
68 *Subulina octona*
17 Heliciform snails
32 Vaginulid slugs
Steptoneura
3 ?*Melania* sp.
ARTHROPODA
CRUSTACEA
MALACOSTRACA
Isopoda
3 Pillbugs
Decapoda
2 Crabs (1 hermit)
Lever (1944)
MYRIAPODA
CHILOPODA
5 Centipedes
DIPLOPODA
57 Yellow-spotted black millipedes, *Orthomorpha coarctata*
46 Small white millipedes
38 Large red millipedes *Trigoniulus lumbriciuus*
ARACHNIDA
ARANEIDA
5 Spiders (1 wolf)
ACARINA
39 Mites, most *Fuscuropoda* sp.
SCORPIONIDEA
1 Scorpion - Lever (1939)
INSECTA
PTERYGOTA
Orthoptera
3 Crickets (1 *Acheta oceanica*)
6 Cockroaches
2 Coconut Stick Insect *Graeffea crouani*, eggs (1 hatched, 1 inviable)
Dermaptera
3 earwigs, most *Chelisoches morio*
Hemiptera
48 True bugs, including
21 *Pachybrachius* sp.
1 *Brachyplatus pacificus*
1 Pentatomid
23 Leafhoppers, including
12 *Nilaparvata lugens*
2 *Chlorionafurcifera*
1 *C. kolophon*
2 *Tettigoniella spectra*
1 Derbid
Odonata
2 Dragonflies - Lever (1938a)
Neuroptera
1 Lacewing larva
Diptera
4 Maggots
1 Puparium
2 Red-eyed black flies
Lepidoptera
166 Caterpillars, including
1 *Humenia recurvalis*
127 *Pseudalotia separata*
16 *Spodoptera mauritia*
4 *Prodenia litura*
2 *Euclidisema alycone*

- 1 Pupa
- 1 Moth

Coleoptera

- 10 Curculionids, including
  - 4 *Cosmopolites sordidus*
  - 3 *Elutroteinus subtruncatus* (Lever (1938b))
  - 1 *Acalles* sp. - Lever (1938a)
  - 1 *Grochiesis* sp. - Lever (1938b)
- 4 Rutelids, *Adoretus versutus*
- 1 Helodid, *Scirtes natovensis*
- 4 Tenebrionids
- 1 Cerambycid
- 7 Hydrophilids, including:
  - 5 *Hydrophilus gayndahensis*
  - 1 Dytisid, *Hyphydrus lyratus*
  - 1 Nitidulid, *Carpophilus* sp.
  - 25 Aphodiids, *?Aphodius* sp.
  - 13 Scarabaeids, *Copris incertus prociduus*
  - 1 Carabid
  - 4 Coccinellids, including:
    - 3 *Coccinella transversalis*
  - 10 Elaterids, *?Simodactylus* sp.
  - 13 Unidentified beetles

Hymenoptera

- 62 *Odonotomacus haematoda*
- 56 *Tapinoma melanocephalum*
- 55 *Pheidole megacephala*
- 1 *Camponotus* sp.
- 4 Wasps including:
  - 2 *Polistes olivaccus*
  - 1 Ichneumonid, *Notalia* sp.
  - 1 Braconid

300 Bees, *Apis mellifera* Lever (1944)

CHORDATA

VERTEBRATA

AMPHIBIA

Young toads - Simmonds (1957)

AVES

Young chickens and mynahs - Simmonds (1957)

2 Mice, possibly regurgitated by cats)

TABLE IV - Economic Importance in Relation to Location

No. consumed per 10 toads in:	Important Pests	Millipedes	Ants	Beneficial Predators
Lawns and Gardens	8	2	31	2
Coconut Plantation	2	5	100	6
Banana Groves	15	30	50	3
Cane Roads	10	38	2	4
Rice Field	28		10	1
Percentage of toads consuming such prey in:				
Lawns and Gardens	40%	13%	80%	20%
Coconut Plantation	20%	45%	65%	35%
Banana Groves	65%	65%	65%	15%
Cane Roads	40%	87%	7%	33%
Rice Field	67%	0%	27%	7%

The following tables and quotation are from Krakauer (1955):

TABLE 1: The stomach contents of 85 *Bufo marinus* and 33 *Bufo terrestris*

	B. terrestris		*B. marinus*	
	N	%	N	%
Sex				
Male	23	69.7	63*	71.6
Female	10	30.3	21	28.1
Stomach				
Empty	3	9.1	10	11.8
Trace	8	24.2	14	16.5
Half-full	12	36.1	25	29.4
Full	10	30.3	36	12.3
Vegetation				
None	23	69.7	36	12.3
Trace	7	21.2	24	28.2
Quarter	3	9.1	25	29.4
Mollusks	1	3.0	16	18.8

* One animal could not be sexed.

TABLE 2: Percent of non-empty stomachs containing certain food items

Food item	*B. terrestris*	*B. marinus*
Coleoptera	60.0	61.2
Dermaptera	46.8	21.4
Hymenoptera		
Formicidae	66.7	28.0
Apoidea		5.3
Odonata		1.3
Orthoptera		
Blattidae	6.6	5.3
Gryllotalpidae	3.3	
Lepidoptera (adult)		2.7
Hemoptera		1.3
Crustacea		
Isopoda		6.7
Grapsoidea		6.7
Gastropoda	3.3	24.4

"Since the results of stomach content surveys are biased towards heavy-bodied prey, because chitin is digested slowly, and since the survey does not closely reflect the nutritive value of each food item, no volumetric analysis of the stomach contents was run. The analysis of stomach contents of indescriminate feeders is a "standing crop analysis" and reflects only the recent feeding history of each animal and the availability of specific food items at that time".

Rabor (1952) in an examination of contents of stomachs, in the Philippines reported 17 containing remnants of the small burrowing snake *Typhlops* and 5,000 containing remnants of the common field rat *Rattus rattus mindanensis*.

Weber (1938) lists the following foods, in Trinidad and British Guiana:

The leaf caterpillar *Mocis repanda*.
The ants *Ectatomma ruidum* Roger, *Odontomachus haemotoda, Pheidole fallax jelskii* Mayr, *Cyphomyrmex rimosus* Spinola, *Wasmannia auropunctata* Roger.

The army ants *Eciton burchelli* var. *urichi* Forel, *E. ierense* Weber, *E. postangustatum* Borgmeier.
The arboreal ants *Pseudomyrma elegans* F. Smith, *Procryptocerus goeldii guianensis*, *Cryptocerus varians* F. Smith, *Cephalotes atratus quadridens* de Geer.
The fungus-growing ants (Attini) *Cyphomyrmex*, *Tachymyrmex urichi* Forel, *Acromyrmex actospinosus* Reich, *Atta sexdens* (L.).
The ants *Gnamptogenys sulcatum* F. Smith, *Holcoponera striatula* Mayr, *Pachycondyla harpax* Fabr, *Anochetus inermis* Ern. André, *Crematogaster brasiliensis* Mayr, *Monomorium* sp., *Tranopelta gilva* Mayr, *Solenopsis altinodis* Forel, *S. geminata* Fabr, *Brachymyrmex cordemoyi* Emery, *Paratrenchina longicornis* Latr., *Nylanderia* sp., *Companotus abdominalis* Fabr, *C. rufipes* Fabr, *C. crassus* Mayr.
The mole cricket *Orthoptera-gryllotalpidae-scapteriscus victnus.*
O.-tettigoniidae.
Blattariae-epilampria abdomenigrum (De G.)
The soil mantid *Mantodea.*
Termites, *Isoptera.*
Hemiptera: Pentatomidae.
Coleoptera: *Opatrinus* sp. and *Sphenophorus* sp.

Weber (1945) reports the ant *Atta cephalotes* L. as being predated by *B. marinus* and the large silky ant-eater *Tamandua logicauda* Wagner; the latter animal is thus a first-order modifier in the toad's environment.

Walcott (1937), in Puerto Rico, reports the toad eating the following:
May-beetle
Scarab beetle *Parachalepus barbatus* F.
Cububanos *Pyropnorus luminosus* Illiger
Cockroach *Periplaneta americana* L.
Weevils *Diapreps abbreviatus* L.
Scarab beetle *Ligyrus tumulosus* Burmeister
Pentatomid bug *Nezara viridula* L.
Rotten cane-stalk weevils *Metamasius hemipterus* L.
Cicindelid beetle *Tetrachasobrina infuscata* Mann.

Various authors report *B. marinus* eating the following:

Tenebrionid beetles, *Eleodes* spp.
Carabid beetles, *Pasimachus* spp.
Two coleopterous pests of cane; *Diaprepes abbreviatus* and *Lachnosterna* (also called *Phytolus* and sometimes *Phylophaga*) *smithi*.
Probably the cane weevil *Metamasius sericeus*
The grey-backed cane beetle *Lepidoderma albohirtum* Waterh.
The scarab beetle *Dyscinetus* sp. in British Columbia
'White grub' cane pest in Barbados *Phytalus smithi* Arrow
Gonocephalum sp. in Hawaii
The sugarcane borer *Rhabdocnemis obscura* Bois. in Hawaii
Army worms
Christmas beetle *Anoplognathus borsduvali*
The black Pentodon beetle (a cane pest) *Metanastes vulvivagus*
The beetle *Lepidiota caudata*
Cydnid bugs
Black widow spider
The leaf caterpillar,*Mocis repanda* (Anon. 1902)
Leaf-cutting ants, *Atta* spp.
Marsupial mouse, *Planigale maculata*
Grasshopper, *Oxya chinensis*
The carpenter bee *Xylocopa varipuncta*
Centipede Scolopendra
Sweet Potato Moth, *Hippotion celerio*
Cockroach, *Periplaneta americana*
Burrowing roach, *Pychnocelus surinamensis* (Linn.)
Chinese rose-beetle *Adoretus sinicus* (Burm.)
Pheidole ants *Pheidole megacephala*
Ants, *Polyrachis* sp.
Rhinoceros beetle *Strategus barbigerus*
Cane pests, *Phyllophaga portoricencis*, *Cnemarachis vandinei*
Surinam roach *Pycnoscelus surinamensis* (L.)
Black garden slug, *Veronicella leydigi*
Scorpions
Snail, *Opeas* spp.
Black grass bugs *Geotonus pygmaeus*
Black wasp *Odynerus*
Fuller's rose-beetle *Pantomorus godmani* (Crotch)
Honey bee

A large caterpillar *Herse cingulata* (Fab.)
Scarabaeid adults
'Frenchi' beetle, a sugar cane pest.
A large centipede *Scolopendra subspinipes* (Leach)
The sweet potato hawk moth *Hoppotion celerio* (Szent-Ivany, 1972)
Ants, *Odontomachus simillimus* and *Oecophylla smaragdina*
Snails, *Subulina octina* and small specimens of *Achatina fulica*
Cacao weevil borer *Pantorhytes plutus*
Millipedes
Weevil *Orochlesis* sp.
Weevil *Elytroteinus subtruncatus* Frum.
Hornet *Polistes hebraens*
Laydbird *Coccinella transversalis* F.
Snail *Subulina octona* Breug.
Hermit crab
Weevil *Acalles* sp.
Banana-borer *Cosmopolites sordidus* Chevr.
Click beetles, Elaterids
Pentatomids, *Geotomus* sp.

PREDATORS

Caimans, *Caiman latirostris*

Snake *Helicops* sp.

Cat-eyed snake, *Leptodeira annulata* (ate a 20mm toadlet)

Domestic fowls and ducks.

Mongoose introduced into Hawaii

Eel, *Anguila* sp. (ate a young toad)

Dytiscid beetle, *Megadytes giganteus* Castelnau (predates immature stage of toad)

Candoia, a reptile.

Mosquito *Mimomya elegans* (Taylor); other mosquitoes suspected.

Turtle, *Kinosternon* reported by Blair (1947) as dragging a toad under water.

Rana palmipes tadpoles eat eggs of *B. marinus*

The following parasites are listed by Zug and Zug (1979):

Bacteria: *Salmonella* (7 species)
Protozoans: *Cytoamoeba bactipera*, the blood shizopod
Ochoterenella cf. *digicauda* (Mar-Kinelle 1970)
Tritrichomonas batrachorum, the gut flagellate
Helminths: *Creptotrema lynchi*
Cyclindrotaenia americana Jewell 1916
Glypthelmins robustus
Gorgoderina diaster Lutz 1926
Ophiotaenia borariensis Szidat and Soria 1954
Rhabdias fuelliborni
R. sphaerocephala
Arthropods: *Amblyomma dissimile*
A. humerale
A. rotundum
A. testudinis

Other authors mention:

Rhabdias elegans
R. hermaphrodita
An unknown virus or bacterium causing atrophied liver and death.
Bacteria similar to *Sphaerophorus necrophorus*
Zelleriella opisthocarya
Z. antillensis
Z. artagasi
Mesocoelium sociale, in the small intestine
Catadiscus cohni
Choledocystus intermedius
C. vesicalis
Distoma linguatula
Glypthelmins intermedia
G. palmipedis
Gorgoderina cryptorchis
G. megalorchis
G. parvicava
Haematoloechus fuelleborni
Langeronia macrocirra
Mesocoelium sp. Ucros' Guzman 1959.
M. incognitum

M. travassosi
M. waltoni
M. sociale, in the small intestine
Plagiorchis hepaticus
Pneumonoeces fuelleborni
Schistosoma mansoni
Trypanosomes
Cytamoeba bacterifera Labbé
Trematode, *Mesocoelium danforthi* Hoffman 1935
Protozoans: myxosporidium *Cystodiscus immersus*
    gut balantidium *Nosema balantidii*

E REFERENCES

Abel, J.J. and D.I. Macht (1911). The poisons of the tropical toad, *Bufo agua*. *J. Am. Med. Assoc.* 56, 1531-1536.

Abel, J.J. and D.I. Macht (1912). Two crystalline pharmacological agents obtained from the tropical toad, *Bufo agua*. *J. of Pharmacology and Experimental Therapeutics* 3, 319-377.

Adams, N.G.K. (1967). *Bufo marinus* eaten by *Rattus rattus*. *North Queensland Naturalist* 34, 5.

Alcala, A.C. (1957). Philippine notes on the ecology of the Giant Marine Toad. *Silliman Journal* 4, 90-96.

Alexander, T.R. (1964). Observations on the feeding behaviour of *Bufo marinus* (Linne). *Herpetologica* 20(4), 225-259.

Allen, E.R. and W.R. Neill (1956). Effect of Marine Toad toxins on Man. *Herpetologica* 12, 1150-151.

Anon. (1932). Toads introduced into Hawaii. *Proc. Hawaii Ent. Soc.* 8, 229.

Anon. (1938). Toads introduced into Mauritius.

Bailey, P. (1976). Food of the Marine Toad, *Bufo marinus*, and six species of skink in a cacao plantation in New Britain, Papua New Guinea. *Aust. Wildl. Res.* 3, 185-188.

Baldwin, P.H., C.W. Schwartz and E.R. Schwartz (1952). Life history and economic status of the mongoose in Hawaii. *J. Mammology* 33(3), 335-356.

Beebe, W. (1927). In *Studies of a tropical jungle, Zoologica* 6(1), 1-193.

Bianchi, F.A. and S. Easteal (1981). Eating habits of *Bufo marinus*. Pers. comm.

Blair, A.P. (1947). Defensive use of parotid secretion by *Bufo marinus*. *Copeia* 2, 137.

Boice, R. and C. Boice (1970). Interspecific competition in captive *Bufo marinus* and *Bufo americanus* toads. *J. Biol. Psychol.* 21, 32-36.

Brattstrom, B.H. (1960). Thermoregulation in tropical amphibians. *Year Book of American Philosophical Society 1960*, 284-287.

Brattstrom, B.H. (1962a). Thermal control of aggregation behaviour in tadpoles. *Herpetologica* 18 (1), 38-46.

Brattstrom, B.H. (1962b). Homing in the Giant Toad *Bufo marinus*. *Herpetologica* 18, 176-180.

Brattstrom, B.H. (1963). A preliminary review of the thermal requirements of amphibians. *Ecology* 44(2), 238-255.

Brattstrom, B.H. (1968). Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol.* 23, 93-111.

Brattstrom, B.H. and N.B. Adis (1952). Notes on a collection of reptiles and amphibians from Oaxaca, Mexico. *Herpetologica* 8, 59-60.

Brattstrom, B.H. and T.R. Howell (1954). Notes on some collections of reptiles and amphibians from Nicaragua. *Herpetologica* 10, 114-123.

Breder, C.M. (1946). Amphibians and reptiles of the R.W. Chucunaque Drainage, Darien, Panama, with notes on their life histories and habits. *Bull. Amer. Museum Nat. History* 86, 394-397.

Brooks, D.R. (1976). Five species of platyhelminthes from *Bufo marinus* L. (Anura: Bufonidae) in Colombia with descriptions of *Creptotrema lynchi* sp. N. (Digenea: Allocreadiidae) and *Glypthelmins robustus* sp. N. (Digenea: Macroderoididae). *J. Parasitol.* 62(3), 429-433.

Buzacott, J.H. (1936). How frequently do Giant Toads produce eggs? *Cane Growers Quarterly Bulletin*, July 1936, 25.

Buzacott, J.H. (1939). Toads and fowls. *Proc. Cane Pests Board Conference,* Mackay 1939, 28-29.

Camhi, J.M. (1980). The escape system of the cockroach. *Scientific American* 243(6), 144-154.

Cassels, A.J. (1966). Disembowelled toads near water. *North Queensland Naturalist* 34, 6.

Cassels, M. as told by Dr Watsford (1970). Another predator on the Cane Toad *(Bufo marinus). North Queensland Naturalist* 37, 6.

Catalogue of Medical and Veterinary Zoology (1969). (U.S. Department of Agriculture).

Cei, J.M. (1968). Remarks on the geographical distribution and phyletic trends of South American toads. *Perace-Sellars Series Texas Memorial Museum* 13, 3-20.

Chen, K.K. and A. Ling Chen (1933). Notes on the poisonous secretions of twelve species of toads. *J. Pharm. and Exptl. Therapeutics* 47, 281-293.

Cochran, D.M. and C.J. Goin (1970). Frogs of Columbia. *U.S. Nat. Mus. Bull.* 228.

Covacevich, J. and M. Archer (1975). The distribution of the Cane Toad, *Bufo marinus*, in Australia and its effects on indigenous vertebrates. *Mem. Queensland Museum* 17(2), 305-310.

Dexter, R.R. (1932). The food habits of the imported toad, *Bufo marinus,* in the sugar cane sections of Puerto Rico. Bulletin No. 74, *Proc. Fourth Cong. International Society of Sugar Cane Technologists,* San Juan, 2-6.

Duellman, W.E. (1965). A biogeographic account of the herpetofauna of Michoacan, Mexico. *Univ. Kans. Publ. Mus. Nat. Hist.* 15, 627-709.

Easteal, S. (1981). The history of introductions of *Bufo marinus* (Amphibia: Anura); a natural experiment in evolution. *Biological J. of the Linnean Soc.* 16, 93-113.

Easteal, S. (1982). (Thesis). The genetics of introduced populations of the Marine Toad, *Bufo marinus* (Linneaus), (Amphibia: Anura); a natural experiment in evolution (Griffith University, Nathan, Queensland).

Ely, C.A. (1944). Development of *Bufo marinus* larvae in dilute sea water. *Copeia* 1944(4), 256.

Fellows, A.G. (1969a). Toads and termites. *Victorian Naturalist*, 86, 136.

Fellows, A.G. (1969b). Cane beetles and toads. *Victorian Naturalist*, 86, 165.

Fite, K.V. (1973). The visual fields of the frog and toad: a comparative study. *Behav. Biol.* 9, 707-718.

Floyd, R. (1982). Untitled thesis in preparation.

Frauca, H. (1974). Crows, Channel-bill Cuckoos and Cane Toads. *Aust. Birdlife* 1 (6), 112-114.

Fullaway, D.T. and N.L.H. Krauss (1945). *Common Insects of Hawaii* (Tongg Pub. Co., Honolulu).

Gomoll, L. (1968). Terrestrial animals. Chapter 3 in *A Naturalists Guide to Guam,* Ed. R.E. Key (Agana, Guam).

Goodacre, W.A. (1947). The Giant Toad *(Bufo marinus)* an enemy of bees. *The N.S.W. Agricultural Gazette* 58, 374-375.

Grant, C. (1948). Selection between armed and unarmed arthropods as food by various animals. *J. Ent. Zool. Clarmont. Cal.* 40, 66.

Heatwole, H. and R.C. Newby (1972). Interaction of internal rhythm and loss of body water in influencing activity levels of amphibians. *Herpetologica* 28, 156-162.

Heatwole, J., D.S. Sade and R. Hildreth (1963). Herpetogeography of Puerto Rico. I. Herpetofauna of Cayo Santiago and Cayo Batata. *Carib. J. Sci.* 3(1), 1-5.

Heatwole, H., S. Blasini de Austin and R. Herrero (1968). Heat tolerances of two species of tropical anurans. *Comp. Biochem. Physiol.* 27, 807-815.

Hill, W.C.O. (1954). Report of the Society's Prosector for the year 1953. *Proc. Zool. Soc. London* 124, 304-311.

Hinckley, A.D. (1962). Diet of the Giant Toad *Bufo marinus* (L.), in Fiji. *Herpetologica* 18(4), 253-259.

Hutchings, R.W. (1979). A native predator of the cane toad *(Bufo marinus)*. *North Queensland Naturalist* 45 (124), 4-5.

Hutchinson, V.H. and M.A. Kohl (1971). The effect of photoperiod on daily rhythms of oxygen consumption in the tropical toad, *Bufo marinus*. *Zeitschriff fur Vergleichende Physiologie* 75, 367-382.

Hutchinson, V.H., W.G. Whitford and M. Kohl (1968). Relation of body size and surface area to gas exchange in Anurans. *Phys. Zool.* 41, 65-85.

Illingworth, J.F. (1941). Feeding habits of *Bufo marinus*. *Proc. Hawaiian Ent. Soc.* 11(1), 51.

Ingle, D. and D. McKinley (1978). Effects of stimulus configuration on elicited prey catching by the Marine Toad *(Bufo marinus)*. *Anim. Behav.* 26, 885-891.

Jakowska, S. (1972). Lesions produced by ticks *Amblyomma dissimile* in *Bufo marinus* toads from the Dominican Republic. *American Zoologist* 12, 731.

Johnson, C.R. (1972). Thermal relations and daily variation in the thermal tolerance in *Bufo marinus*. *J. of Herpetology* 6(1), 35-38.

Johnson, C.R. (1976). Herbicide toxicities in some Australian Anurans and the effect of subacute dosages on temperature tolerance. *Zool. J. Linnean Soc.* 59, 79-83.

King, W. (1969). Adaptions for nocturnal survival. *Animal Kingdom* 22(3), 29-32.

Kloss, G.R. (1974). *Rhabdias* (Nematoda, Rhabditoidae) from the *Marinus* group of *Bufo*. A study of sibling species. *Arg. Zool.* 25(2), 61-120.

Knowles, R.P. (1964). The poison toad and the canine. *Small Animal Clinician* 59, 39-42.

Krakauer, T. (1968). The ecology of the neotropical toad, *Bufo marinus* in South Florida. *Herpetologica* 24(3), 214-221.

Krakauer, T. (1970). Tolerance limits of the toad *Bufo marinus,* in South Florida. *Comp. Biochem. and Physiol.* 33, 15-26.

La Rivers, I. (1948). Some Hawaiian ecological notes. *Wassman Collector* 7(3), 85-110.

Lehmann, D.L. (1966). Two blood parasites of Peruvian amphibia. *J. Parasitology* 52, 613.

Lever, R.J.A.W. (1937). The giant toad. *Fiji Agricultural Journal* 8, 36.

Lever, R.J.A.W. (1938). The giant toad - distribution, diet and development. *Fiji Agricultural Journal* 9, 28.

Lever, R.J.A.W. (1944). Food of the giant toad. *Fiji Agricultural Journal* 15, 28.

Lever, R.J.A.W. (1945). The giant toad in the Solomon Islands. *Fiji Agricultural Journal* 16, 88.

Licht, L.E. (1967). Death following possible ingestion of toad eggs. *Toxican* 5, 141-2.

Licht, L.E. and B. Low (1968). Cardiac responses of snakes after ingestion of toad paratid venom. *Copeia* 1968, 547-551.

Lucas, J. (Ed.) (1969). *International Zoo. Yearbook*, Vol. 9, (Zoo. Soc., London).

Machin, J. (1969). Passive water movements through skin of the toad *Bufo marinus* in air and in water. *Am. J. Physiology* 216(6), 1562-1568.

Mares, M.A. (1972). Notes on *Bufo marinus* Tadpole aggregations. *Texas Journal of Science* 23(3), 433-435.

Marinkelle, C.J. and N.J. Williams (1964). The toad *Bufo marinus* as a potential mechanical vector of eggs of *Ascaris lumbricoides. J. Parasitol.* 50(3), 427-428.

Mead, A.R. (1961). *The Giant African Snail: A problem in economic malacology* (University of Chicago Press).

Mettrick, D.F. and L.C. Dunkley (1968). Observations on the occurrence, gorwth and morphological variation of the trematode, *Mesocoelium danforthi* Hoffman 1935, in Jamaica. *Carib. J. Sci.* 8(1-2), 71-75.

Mungomery, R.W. (1935). The Giant American Toad *(Bufo marinus). Cane Growers Quarterly Bulletin (Qld.)* July 1935, 21-27.

Mungomery, R.W. (1936a). A survey of the feeding habits of the Giant Toad *(Bufo marinus* L.*)*, and notes on its progress since its introduction into Queensland. *Proceedings of the Queensland Society of Sugar Cane Technologists* 1936, 63-74.

Mungomery, R.W. (1936b). Sex reversal in the Giant Toad. *Cane Growers Quarterly Bulletin (Qld.)* July 1936, 7.

Mungomery, R.W. (1938). Toad protection. *Minutes Cane Pests Board Conference, Meninger,* 36-37.

Mungomery, R.W. (1940). Frenchi grub depredations and suggestions for control. *Cane Growers Quarterly Bulletin* April 1940, 171-174.

Mungomery, R.W. and J.H. Buzacott (1935). Control of the "Greyback Cane Beetle" *(Lepidoderma albohirtum* Waterh.*)* in north Queensland. *Proc. 5th Cong. Int. Soc. Sugar Cane Technologists, Brisbane,* 456-464.

Myers, J.G. (1931). *A preliminary report on an investigation into the biological control of West Indian insect pests.* (Empire Marketing Board PUbl. No. 42, London July 1931).

Niven, B.S. (1980). The formal definition of the environment of an animal. *Australian Journal of Ecology*, 5, 37-46.

Oliver, J.A. (1949). The peripatetic toad. *Natural History* 58(1), 30-33.

Pearse, B.W. (1980). The effect of toad poison on vertebrates. Unpublished paper available Griffith University Library.

Pearse, B.W. (1980). The effects of feeding on *Bufo marinus* by native and exotic fishes. Unpublished paper available Griffith University Library.

Pemberton, C.E. (1934). Local investigations on the introduced tropical American Toad *Bufo marinus*. *Hawaii Planters' Record* 38, 186-192.

Pemberton, C.E. (1949). Longevity of the tropical American Toad, *Bufo marinus* L. *Science* 110, 512.

Perez, M.E. (1951). The food of *Rana castebeniana* Shaw in Puerto Rico. *Herpetologica* 7, 102-104.

Pippet, J. (1975). The Marine Toad, *Bufo marinus*, in Papua New Guinea. *Papua New Guinea Agricultural Journal* 26(1), 23-30.

Rabor, D.S. (1952). Preliminary notes on the Giant Toad, *Bufo marinus* (Linn.), in the Philippine Islands. *Copeia* 1952(4), 281-282.

Richardson, C.L. ( ). The stomach contents of Giant Toads.

St. Cloud, S.F. (1966). Observation of J. James at Tinaroo Creek, Feb., 1966. *North Queensland Naturalist* 34, 6.

Sabath, M.D., W.C. Boughton and S. Easteal (1981). Expansion of the range of the introduced toad *Bufo marinus* in Australia from 1935 to 1974. *Copeia* 1981 (3), 676-680.

Schwartz, A. and R. Thomas (1975). *A checklist of West Indian amphibians and reptiles.* (Carnegie Museum of Natural History, Pittsburgh).

Sein, F. (1937). The development of the Giant Surinam Toad, *Bufo marinus* L. *Puerto Rico University Journal of Agriculture* 21(1), 77-78.

Simmonds, H.W. (1937). The Giant Toad. *Fiji Agricultural Journal* 8, 45-46.

Simmonds, H.W. (1957). The Giant Toad - *Bufo marinus* - in Fiji. *Fiji Agricultural Journal* 28, 77-78.

Simmons, M. (1980). A study of *Bufo marinus* to discern its movement patterns and the possible factors which regulate its movements via the use of a trailing device. Unpublished paper. Available Griffith University Library.

Smith, S.W. (1950). Chloromycetin in the treatment of "Red Leg". *Science* 112, 274-275.

Smyth, E.G. (1917). The white-grubs injuring sugar cane in *Porto Rico. Puerto Rico University, Journal of Agriculture* 1, 141-169.

Straughan, I.R. (1966). The natural history of the "Cane Toad" in Queensland. *Australian Natural History* 15, 230-232.

Stuart, L.C. (1951). The distribution implications of temperature tolerances and haemoglobin values in the toads *Bufo marinus* and *Bufo bocourti* Brocchi. *Copeia* 1951, 220-229.

Takano, S. and K. Iijima (1937). Studies on the life history and habits of *Bufo marinus* L. in Formosa. Part I. The relation between the growth of the tadpole and the quality of the breeding water. *Taiwan Gov. Sug. Exp. Stat. Report Japan* No. 9.

Takano, S. and K. Iijima (1939) - Part II. Ecology of the tadpole and the toadlet. *Taiwan Govt. Sug. Expt. Stat. Report Jap.* No. 4.

Taylor, E.H. and J.S. Wright (1932). The toad *Bufo marinus* (Linneaus) in Texas. *The University of Kansas Science Bulletin* 20(12), 247-249.

Tucker, R.W.E. (1940). *Bufo marinus* L. in Barbados. *Agric. J. Barbados* 8, 145-150.

Turbet, C.R. (1938). The Giant Toad I. Food. *Fiji Agricultural Journal* 9, 29.

Tyler, M.J. (1975). The Cane Toad *Bufo marinus*. An historical account and modern assessment. A report to the Vermin and Noxious Weeds Destruction Board, Victoria and the Agricultural Protection Board, W.A.

Tyler, M.J. (1976). *Frogs*. (Collins, Sydney).

Valerio, C.E. (1971). Ability of some tropical tadpoles to survive sithout water. *Copeia* 1971, 364-375.

van Beurden, E. (1978). Report on the results of stage I of an ecological and physiological study of the Queensland Cane Toad *Bufo marinus*. Report to the Aust. Nat. Parks and Wildl. Service, Canberra.

van Beurden, E. (1979). Report on the results of stage 2 of an ecological and physiological study of the Queensland Cane Toad *Bufo marinus*. Report to the Aust. Nat. Parks and Wildl. Service, Canberra.

van Beurden, E. (19). Tolerance of Australian *Bufo marinus* to low temperature. Unpublished.

van Beurden, E. (1980). Mosquitoes *(Mimomya elegans* (Taylor)*)* feeding on the introduced toad *Bufo marinus* (Linnaeus): implications for control of a toad pest. *Aust. Zool.*, 20(3), 501-504.

van Beurden, E.K. and G.C. Griff (1980). An isolated and expanding population of the introduced toad *Bufo marinus* in New South Wales, Australia. *Aust. Wildl. Res.* No. 7, 305-310.

van Volkenberg, H.L. (1935). Biological control of an insect pest by a toad. *Science* 82(2125), 278-279.

Waite, F.C. (1901). *Bufo agua* in the Bermudas. *Science* 13, 242-243.

Warburg, M.R. (1965). Studies on the water economy of some Australian frogs. *Aust. J. Zool.* 13, 317-330.

Watson, J.M. (1960). Notes on wildlife in Fiji and its conservation. *Fiji Agricultural Journal* 30, 67-70.

Weber, N.A. (1938). The food of the giant toad, *Bufo marinus* (L.), in Trinidad and British Guiana with special reference to the ants. *Ann. Ent. Soc. America* 31, 499-503.

Weber, N.A. (1945). The biology of the fungus-growing ants. Part VIII. The Trinidad, B.W.I., species. *Revista de Entomologia* 16, 1-88.

Wilhoft, D.C. (1965). The annual reproductive cycle of *Bufo marinus* in Australia. *Amer. Zool.* 5(2), 259.

Wingate, D.B. (1965). Terrestrial herpetofauna of Bermuda. *Herpetologica* 21, 202-218.

Wolcott, G.N. (1937). What the Giant Toad *Bufo marinus* L. is eating now in Puerto Rico. *University of Puerto Rico J. Agriculture* 21(1), 79-84.

Zug, G.R., E. Lindgren and J.R. Pippet (1975). Distribution and ecology of the Marine Toad, *Bufo marinus*, in Papua New Guinea. *Pacific Science* 29(1), 31-50.

Zug, G.R. and P.B. Zug (1979). *The Marine Toad, Bufo marinus, a natural history resume of native populations* (Smithsonian contributions to Zoology No. 284. Smithsonian Institution Press, Washington).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS
XXII THE ATLANTIC FULMAR *(Fulmarus glacialis glacialis)*

by

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ABSTRACT

The precise environment of the Atlantic Fulmar *(Fulmarus glacialis glacialis)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in AES Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

A INTRODUCTORY NOTE

The Atlantic Fulmar, *Fulmarus glacialis glacialis* (Linnaeus) is widely distributed over the North Altantic. The name 'Fulmar' is derived from Icelandic and means 'foul-gull', referring to the birds' habits of vomiting when startled. Fulmars have been sighted as far north as 86° 35'N. The southernmost sighting was at a point just north of Madeira and due west of Casablanca, approximately 34°N, 17°W.

The Atlantic Fulmar has two colour forms, with breasts either white or grey, head white (or near-white) or grey and wings mouse-grey or dark grey. The wing-tips are always chaetura-drab. A few albinos have been recorded; they are white with pink eyes and legs and dull-crimson beaks. The 'light' and 'dark' forms sometimes occupy the same areas, as shown in the table below. However the 'dark' form is always more northerly in the Atlantic both at sea and in colonies. In England virtually 100% of Fulmars are the 'light' form. The table summarizes the lengthy discussion given by Fisher (1952) of the Fulmar's distribution.

WATERS	JAN & FEB	MAR & APR	MAY & JUNE	JULY & AUG	SEPT & OCT	NOV & DEC
WEST ARCTIC Nos quite high. Light and dark forms approx 1:1. Dark predominates in the west, light in the east, but feeding grounds are shared.	From mid-Oct till early Apr there are no certain records for these birds. Birds withdraw to the east to be near the ice edge and winter feeding grounds. (see also Oct, Nov, & Dec)	Returning birds begin to reach their still iced in breeding colonies	Birds now common near all breeding colonies (see note 4). Present on the Queensland coast to 78^{0}N. Northerly record 82^{0}N.	The breeding concentration around the colonies diffuses to an extent and any suitable water within 700 miles of a colony will be utilized.	12th Oct is the late date record - otherwise as for Jan, Feb & Mar. Note that the lack of records could be because of the absence of humans - cf. the East Arctic situation	
EAST ARCTIC The dark form outnumbers the light in both east and west, but the light form predominates in the centre.	The first probings over pack-ice towards breeding colonies begin.	First birds appear at Franz Joseph Land (400 miles onto the ice). All colonies are occupied by late Apr. Birds vary common on the North. Norway feeding grounds	Birds very common at all breeding station. (The most northerly colonies still ice bound). North.Norway waters still occupied and now common in the Barents Sea.	The ice slowly retreats and reaches its greatest extent by mid-Oct. Birds abundant, especially on the ice edge and in the Barents Sea - also the most northerly distribution northerly record being 86^{0}N.	Re-freeze begins in mid-Oct. Information is scanty but generally the greatest retreat from the pole has occured by late Dec.	
ICELANDIC The light form predominates, especially in the south. Most dark occur in the north-west.	Birds present throughout the year in great numbers, both on the sea and around colonies: only in the summer (Mar-May) breeding season is the density discernably greater and then only near the larger colonies					
NORWEGIAN Light dominate in the south, dark in the north. Both move north in the warm months.	Present all year, particularly near the larger colonies and on the important feeding grounds near the Varanger Fjord. Even during the Oct withdrawal, the birds do not get very far away from the northern colonies and remain common in the south.					
LABRADOR The dark form comprises 2-10% although it predominates in patches in the north.	Birds not present on the iced-in coast but common on the ice edge. Numbers steadily increase with latitude on the transect from Newfoundland to South Greenland.		Access to the coast begins. Numbers greatest in the North and steadily increasing.	Birds common and in places abundant on the Labrador coast. Numbers dwindle, particularly in Oct.		Coast again ice-bound (see Jan-Apr)
MID-OCEAN Dark form between 5 and 20% though usually low on this range.	Not present south of 51^{0}N. Numbers low, and decreasing.	Withdrawal to about 53^{0}N. Numbers low.	Southerly limit about 48^{0}N in the west and 50^{0}N in the east. Numbers moderate.	Southerly limit. 50^{0}N. Numbers increasing.	Maximum southerly penetration - to about 43^{0}N. Greatest numbers.	Retreat to about 51^{0}N or further. Numbers rapidly dwindle.
HOME Dark form exceptional	Not south of 50^{0}N i.e. Cornwall. West of Ireland, the Southerly limit is 51^{0}N.	Penetrate to about 1^0 further south than in Jan-Feb. Numbers not high.	Similar southerly limits to Mar-Apr. Numbers rise steadily in abundance around the colonies.	Again similar southerly limit to Mar-Apr. Numbers rise steadily to abundance around the colonies.	Penetration to 48^{0}N with numbers high north of 50^{0}N.	Withdrawal to about 53^{0}N.
NORTH SEA Dark form very rare.	Birds quite rare. No sea records, but coastal strandings indicate a presence north of 54^{0}N.		Numbers steadily increase over this 6 month period with slightly more southerly penetration. Maximum numbers in Oct., many being newly fledged young birds.			Numbers dwindle. Young birds head to open oceans.
GREAT BANKS Light form in the great majority. In autumn and winter the dark form makes up about 10%.	These notes refer to the quadrants named Newfoundland Bank and Outer Banks, as the birds are rare south of 40^{0}N, all seen occasionally on the Nova Scotia Banks and very rarely on the Long Island quadrant. These banks are the Fulmar's richest feeding grounds					
	Moderate numbers in the north east of Newfoundland Banks and north-west of Outer Banks. Birds rare below 45½^{0}N.	Numbers increase rapidly. High concentrations down to 42^{0}N between 55^{0}W and 45^{0}W.	Maximum population reached. Southerly penetration continued, with concentrations down to 40^{0}N between 56^{0}W & 44^{0}W.	Still abundant east of Newfoundland though the Southern Banks are distinctly deserted, withdrawal to 46½^{0}N	Partial return to the Banks - down to 43^{0}N. The distribution is narrower than Jan-Feb, but otherwise similar.	Moderate numbers north of 44^{0}N, with a broader distribution than Sept-Oct.

The following diagram is from Fisher (1952).

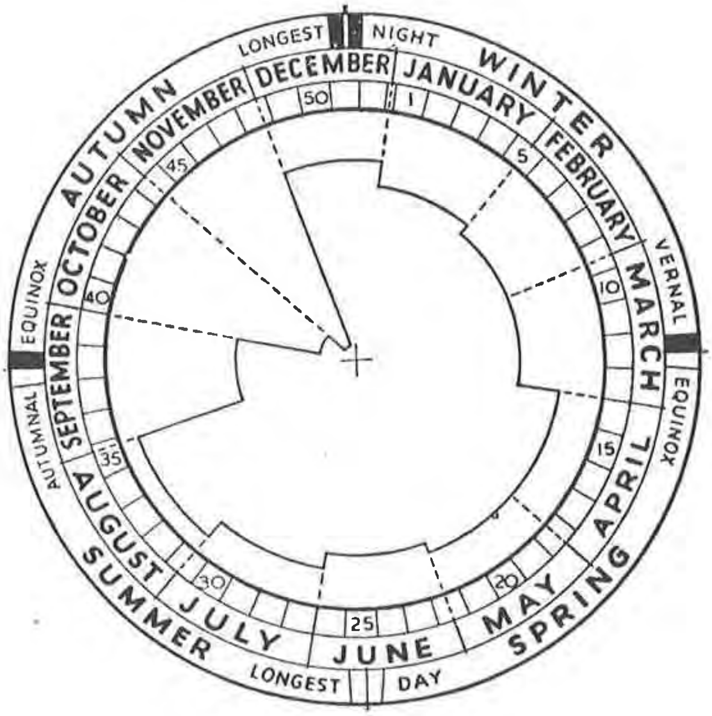


FIG. 46
Chart of the relative numbers of inland occurrences of the fulmar in Britain in the different months

Chick weight at hatching is about 75-80 gm. They grow extremely rapidly, sometimes approaching the adult weight of about 650 gms after only 2 weeks. From the third week most chicks will outweigh their parents. The time from hatching to departure from the nest is about 7 to 9 weeks, about the same as the hatching period (see n. 3).

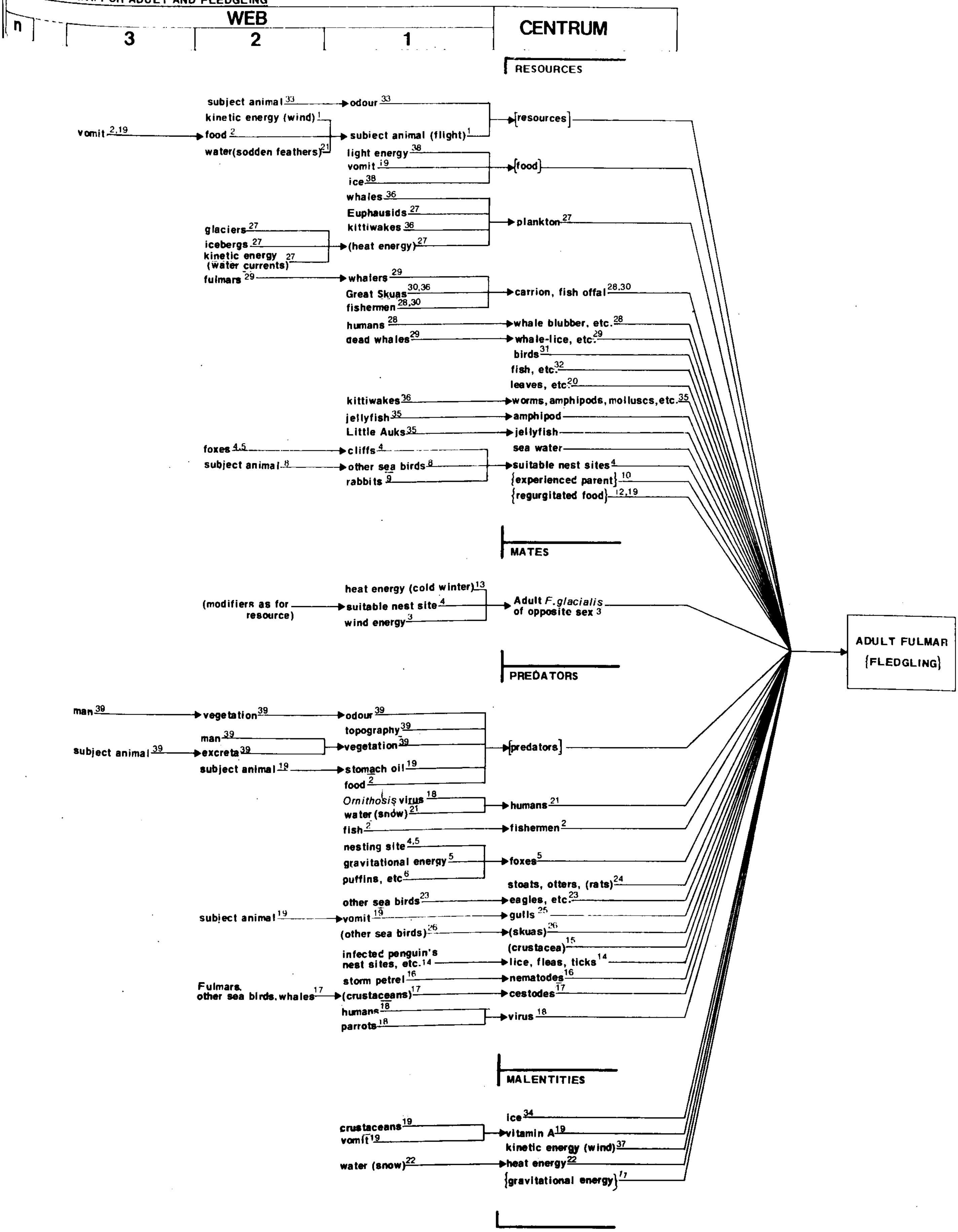
Fisher (1952) believes that the potential length of life of a Fulmar may be as much as 50 years.

It seems certain that each year there is a very large population of adult birds which do not breed, thus the area of the Great Banks off Newfoundland, 1,700 miles from the nearest breeding colony and therefore too far for parent birds to vist, is heavily utilized as a feeding ground in all seasons.

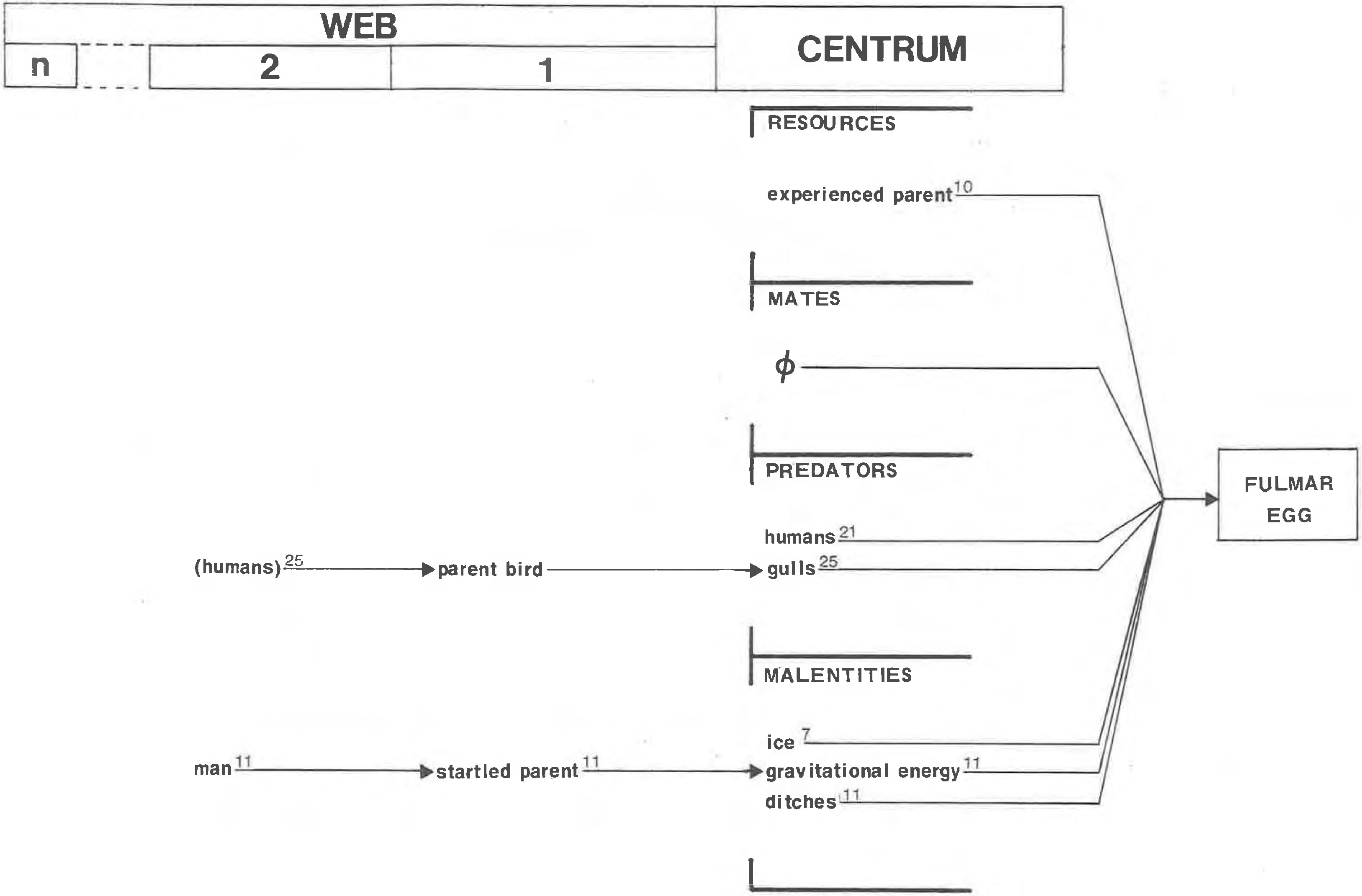
The following quotation is from Fisher (1952).

> "This picture is undoubtedly one if a dispersive rather than a migratory animal. Elsewhere I make the tentative suggestion that the Newfoundland Banks, and perhaps also the Varnager Fjord, may act as "nurseries" for young fulmars. Apart from the migrations that the young fulmars, and perhaps also some adults, may make to these special places, the species is certainly dispersive. It goes where its food goes. It seeks leads in the polar ice, hundreds of miles from base, when there is summer light to hunt the abundant food to be found in such places during the period of light. It avoids the ice when it is dark and unprofitable. It hunts the plankton areas of the open Atlantic; and the plankton content of this ocean steeply declines, as does the fulmar, south of about 50^0N. It goes now, also very much where the trawlers take it. Its distribution at sea can be compared with submarine isotherms, surface isotherms, air isotherms, isobars, isohyets, indeed, all kinds of isopleths - and has been compared with many of them, by the present writer amongst others. All such comparisons have proved fruitless, for the fulmar's distribution is controlled by the abundance of food, by its availability, by its accessibility, by the time the fulmar has to find it and gather it. The amount of food available to a bird with a food-list, and preferences, such as are described in Chapter 18 (p. 409) is controlled by no single factor in the environment."

B(ii) ENVIROGRAM FOR ADULT AND FLEDGLING



B(ii) ENVIROGRAM FOR EGG



C NOTES ON THE ENVIROGRAM

1. The Fulmar is one of the most accomplished fliers among birds and is well able to range far from its nesting site in search of food. During rough weather it is able to reach the middle of the ocean. Given a wind of force 4 or 5 on the Beaufort Scale a Fulmar can fly as far as needful without much apparent effort. "They can fly to windward in the highest storms and rest on the water, with great composure, in the most tremendous seas." (Fisher, 1952). One writer alleged a Fulmar to have glided half a mile in 12 seconds (i.e., at a speed of 150 m.p.h.) though he says nothing of wind-speed, other conditions or place. In calm conditions a Fulmar is reliably reported to have "with exertion" kept pace with a steamer travelling at 17 knots.

   The animal has also been sighted far inland. A Fulmar was found dead, tangled in fishing lines, on the shores of Lake Huron, Ontario, nearly 600 miles from the open sea. Another was found near Graz, Austria, over 500 miles from the Atlantic.

2. The Fulmar is gluttonous; they have been seen to feed continuously for 24 hours. When presented with abundant food they may feed so immoderately that they have difficulty in rising from calm water or flat ground. Sick adults or the very heavy young of late summer also have this difficulty. A Fulmar in this state is in greater danger from macroscopic predators. They may vomit (see n. 19) to reduce their weight.

   Because of their excessive weight Fulmars (in circumstances like the above) which follow fishermen and steal their fish are often easy for the fishermen to hook.

3. There is little external difference between the sexes; males are on average slightly larger and heavier and have a slightly bigger bill.

   It is particularly noticeable that Fulmars, who begin to occupy their breeding sites from December or sometimes November, only do so in calmer weather, at least up to mid-April when the parental demands of breeding begin. When the wind blows they go on their travels (see also n. 1).

Both females and males possess an 'incubation-patch', i.e. a bare patch low towards the legs that fits quite tightly around the egg. They take turns in incubating the egg, usually for about 4 days at a time, for an average period of about 50 days.

Eggs are laid in May or early June (1 egg per pair). If an egg is lost very few females will lay a replacement except in Iceland where colonies are recorded in which up to 10% of nests have 2 eggs, probably (but not certainly) laid by one hen. In such cases only 1 egg can fit into an incubation patch. The young hatch in late June and through July. They are tended continuously by the parents for about 2 weeks then left alone for gradually increasing periods, after which they moult and go to sea. The young leave the nest from late August through late September.

4. The Atlantic Fulmar breeds in the North Atlantic and Arctic from 50^0 to 80^0N at Jan Mayen, Bear Island, Novaya Zemlya, Franz Joseph Land, Sptizbergen, Ellesmere Island (southern end), Greenland (north, east and west), Disko Island, Devon Island. Some reports have been made of nests on other islands of the Canadian Archipelago i.e., within the Arctic Circle, also on many islands off Britain and Norway.

In the Arctic Fulmars invariably nest on rock though in more southerly parts it occasionally nests on soil or vegetation. Everywhere else it shows an almost complete preference for cliffs, usually high ones (e.g. a cliff at Spitzbergen which is 600 - 800 feet high). On Jan Mayen it nests on laminated cliffs, made of eroded lava layers, in great numbers, while only occasional colonies nest on terraced cliffs. It seems likely that the Fulmar's preference for high, sheer nesting sites is to escape predation by foxes (see n. 5). On Bear Island and the Orkneys Fulmars are recroded as nesting on flat ground but there are no foxes on these islands.

Fulmars prospect for, and choose, a nesting site when still non-breeding juveniles. They may occupy their site for several years, on average over 4 years, before laying any eggs there.

Nearly all Icelandic Fulmar colonies are coastal but in places they do nest up to 11 miles inland. On Spitzbergen the Fulmar usually nests at the head of a fjord or else on mountains up to 18 miles from the sea. However in Faeroe and in Britain the exposed oceanic islands and headlands were the first to be colonized.

On some ledges Fulmars will nest within one foot of each other while in others looking equally suitable the nests might be over 20 feet apart. On a cliff on Jan Mayen 100 yards long and 300 feet high 500 pairs of Fulmars were estimated to be nesting.

There is some evidence that Fulmars, once they begin breeding, return annually to precisely the same nest-site. A Fulmar will breed every year if its health and external circumstances permit and if it finds a mate.

5. The arctic fox *(Alopex lagopus)* is a predator of Fulmars throughout the arctic. In Britain the red fox *(Vulpes vulpes)* is also a predator. Foxes eat young Fulmars that have fallen from nests. Fox 'earths' have been found above cliffs only a few yards from the inaccessible nests; the foxes' presence seems to have stopped the spread of the Fulmar onto the sloping ground just above such cliffs.

6. Foxes will take other birds e.g., the puffin, thus such other sea-birds are modifiers of the fox in the environment of the Fulmar. We have found no information on the foxes' preferences.

7. On Bear Island, eggs have been laid where ice was still covering the rock of the cliff. In one instance a bird sitting on its nest had the egg frozen into the ice.

8. On Bear Island Fulmars have been seen nesting side by side with common guillemots, *Uria aalge* (Pontoppidon), Brunnich's guillemots, *U. lamvia* (Linnaeus) and glaucous gulls, *Larus hyperboreus* (Gunnerus). The Fulmar is usually capable of displacing its nesting-site competitors; part of the reason may be its vomiting-defence reaction (see n. 19).

The results of competiton for nesting-sites have been most obvious during the Fulmars' spread in the Faeroes and in Britain. There are recorded interactions between Fulmars and the following:

jackdaws, *Corvus monedula* (Linnaeus),
terns, *Sterna hirunda* (Linnaeus) and *S. macrura*,

herring gulls, *L. argentatus* (Pontoppidan)
kittiwakes, *Rissa tridactyla* (Linnaeus)
razorbills, *Alca torda* (Linnaeus)
guillemots, *U. lamvia* (Linnaeus)
puffins, *Fratercula arctica* (Linnaeus)

There is no evidence that the Fulmar has driven cormorants, shags or gannets away and occupied their nesting-sites.

9. On the Fair Isle and the Orkneys and in Norfolk and Yorkshire, Fulmars have taken the entrances to burrows of the European rabbit *Oryctolagus cuniculus* (Linnaeus) as nesting-sites. It is not clear whether the rabbits are driven out. Rabbits have been seen passing Filmars on cliffs without eliciting the vomit-defence response (see n. 19), thus they could not have been regarded as intruders or any danger or even a surprise.

10. The following table is from Fisher (1952).

REPRODUCTIVE OUTPUT OF COLONIES OF DIFFERENT SIZES, PER HUNDRED OCCUPIED SITES AT SPRING OR SUMMER PEAK

	No. of sites	Eggs Laid	Eggs Hatch	Young Fledge
Order 1 (under 10 eggs)	100	30	?	18.5
Order 2 (under 100 eggs)	100	51	40	37
Larger colonies ...	100	over 90	70 or over	over 50

The percentage of eggs hatched in the larger colonies has been as high as 93%, resulting in a percentage of fledged young well above 50%.

Part of the reason for the very large increase in efficiency of reproduction in the larger colonies is that the smaller colonies have younger and hence less experienced parent birds.

11. On occasions a startled bird has flown from its ledge with its egg embedded in its feathers so that it falls and smashes on the rocks. Usually the observer has been responsible for startling the bird.

During the last 10 to 14 days of the fledgling period the young birds have been known on rare occasions to fall from the cliffs, struggle towards new ledges and fall and also sometimes to wander inland up grassy banks and fall into ditches and other traps from which they cannot escape.

12. The chick is fed by both parents by regurgitation, to begin with once a day and after a few weeks once every two days.

13. The birds may be prevented from laying eggs by hard winters in the Arctic, with huge areas being iced up by seasonally abnormal temperatures, so that birds belonging to some colonies are outside the operational distance from feeding waters.

14. Five species of feather-lice or bird-lice are known to infest the Fulmar, also 3 species of bird-flea and 2 species of tick (see §D for a list of names).

The 2 species of tick, both *Ixodes* spp., are also found on other birds - ravens, crows, penguins, shags and others. It seems clear that such external parasites are transferred through a population by contact between infected birds and/or infected nest sites.

15. Clusters of barnacles of the species *Lepas hillii* Leack have been found attached to the outer barbs of the belly feathers of the Pacific Fulmar, *Fulmarus glacialis rodgersii* Cassin. There is no suggestion of true parasitism in this case and we do not know if the barnacle would interfere with the Fulmar's flying ability.

16. Nematodes (round-worms) belonging to the genera *Anisakis* and *Stegophorus* have been found in Fulmars on Jan Mayen and other areas.

S. stellae-polaris was found by one worker to infest both Fulmars and storm-petrels.

17. The cestode (tapeworm) *Tetrabothrius cylindraceus* (Rudolphi) has been found in the Manx shearwater and the herring-gull as well as in Fulmars. *T. monticellii* Fuhrmann was found in the Fulmar in Greenland and *T. neteroclitum* Diesing in the Antarctic Fulmar. Members of the genus are thought to have crustaceans as their intermediate hosts; they have also been found in ducks, other sea-birds and whales.

18. *Ornithosis* virus causes psittacosis in Fulmars and humans. Many Fulmars suffer from the disease. Sick birds are observed floating on the water. It is doubtful that many are killed by it. Following outbreaks of the disease among humans Fulmar fowling was made illegal in Iceland in 1939.

In 1929 psittacotic parrots were imported into Europe from the Argentine, some to Denmark, the Hebrides and Faeroe. The first outbreak among Fulmars was observed in Faeroe.

19. The name 'Fulmar' is derived from the Icelandic word for 'foul-gull' and refers to the defensive-vomiting habit of the bird.

The stomach-oil is a secretion of the preventriculus (the anterior part of the stomach). The oil has many uses:

(i) for ceremonial display purposes;

(ii) mixed with food it facilitates feeding young;

(iii) for preening and oiling feathers;

(iv) for defence.

The oil is rich in vitamins A and D.

The colour depends on the food eaten by the Fulmar. The most common colour is red, probably derived from planktonic crustaceans, or squids that have been eating planktonic crustaceans. The red colour is due to a substance called 'astacin' found in crustaceans and is a vitamin A source. Thus vomiting enables the Fulmar to excrete vitamin A (which can be poisonous if in excess).

When threatened a Fulmar will vomit or spit oil without consciously directing it at the intruder, but simply in the direction in which it is looking at the time. Recently consumed food will also be vomited. The range is from over 2 to 4 feet. A baby Fulmar not yet out of its shell has been observed to vomit through a small chink at an observer.

Fulmars also vomit in emergency situations if they have overfed and need to lighten themselves in order to take off.

Very young Fulmars even vomit at their parents.

Vomiting plays a role in the bird taking over birds' nests.

This behaviour is particularly effective against potential avian predators such as Great Blackbacks, glaucous gulls, herring gulls and other large members of the genus *Larus*.

20. A miscellany of objects has been found in Fulmar stomachs - signs of leaves, snails, seeds, worms, squid and stones.

Fulmars often eat the leaves of nearby plants e.g., sorrel leaves *(Rumex acetosa)*. They will also eat grass or spoonwort *(Cochlearia officinalis)* and a sedge *(Carex* sp.*)*, brown algae *(Ascophyllum nodosum)*, smartweed or viviparous polygonum *(Polygonum viviparum)*, cinquefoil *(Potentilla* sp.), and common seaweed *(Enteromorpha compressa)*.

21. Man eats, or kills without eating, far more Fulmars than any other predator. The birds are killed by North Pacific Islanders, Eskimos, northern whalers, fishermen and arctic travellers generally. In at least one case this predation has led to the decline of a Fulmar colony. Nowadays it is predominantly the eggs that are taken, especially in Iceland. The regular taking of eggs over years can cause birds to desert a colony, whereas taking fledglings has no known effect.

Fulmars are commonly shot. They are also easily caught on fishing lines with appropriate bait.

In Greenland Eskimos are more able to catch Fulmars if there has been a sudden snowfall, particularly in the spring when the snow melts quickly, since the birds' sodden feathers prevent them from taking off.

22. Occasionally Fulmars may become waterlogged at sea, especially after snowfalls in the spring when the snow melts quickly. Their feathers become so sodden that they are unable to take off and may die of cold (or hunger).

23. The white-tailed eagle *(Haliaeëtus albicilla)* is present although not common in Iceland. It takes sea-birds generally but seems to prefer the Fulmars.

The gyrfalcon *(Falco rusticolus)* also takes Fulmars. On two occasions, female peregrines *(F. peregrinus)* were seen to attack Fulmars, once successfully.

On one occasion a group of rooks *(Corvus frugilegus)* was seen to mob and kill a lone Fulmar; this occurred some way inland and is probably rare.

24. In Britain there is one record of a stoat *(Mustela erminea)* running amok in a Fulmar colony.

In the Shetland Islands the European otter *(Lutra lutra)* has been seen catching and eating a Fulmar.

Also in Britain 2 Fulmars in captivity were killed by a rat *(Rattus* sp.*)* and partly eaten.

25. Gulls of the genus *Larus*, particularly the Great Blackback *L. marinus* and the glaucous gull *L. hyperboreus* will readily eat Fulmar eggs and fledglings if they get the chance, usually when the parents are away from the nest, possibly after being frightened off by men either shooting or climbing.

26. The Great Skua *(Stercorarius skua)*, the arctic skua *(S. skua)* and the long-tailed skua *(S. longicaudus)* probably occasionally predate Fulmars at sea, but seem to prefer kittiwakes and other sea-birds.

27. Surface plankton is the main food of the Fulmars. They can consume plankton in any part of the ocean - deep water or inshore. The plankton consists mainly of Krill, *Euphausia superba*, and other crustaceans.

The bird has also been known to eat 'remnants of crayfish' (probably a Decapod), also *Oniscus pulex* which collects on the beach at low tide, the rare large Amphipod *Euryporeia gryllus*, the Amphipod *Halirages* and the large crustaceans *Hyperia* sp. and *Gammarus* sp. The shrimp *Hymenodora glacialis* is a major food which normally lives in deep water but comes to the surface to breed.

Fulmars also feed off the planktonic creatures in the detritus-laden run-off streams at the edges of glaciers. The most common of these are the two Copepods *Calanus finmarchicus* and *C. hyperboreas*, eaten by the larger crustacean, the Euphausid Schizopod *Thysanoessa inermis* (replaced in some glacial streams by *Euthemisto libellula*).

Particularly in the summer plankton seems to come to the surface at glacier faces and in the neighbourhood of large icebergs. Since the mechanism is not clear we have tentatively classified 'heat energy' as a first-order modifier of plankton. This phenomenon also occurs in almost any sort of turbulent water due to tides and currents or a mixing of warm and cold waters such as occurs on the Great Banks off Newfoundland, near the coast of Norway in the Barents Sea, or near the edges of pack ice.

28. Fulmars attend whale flensing in astonishing numbers. They disregard the men and gorge blubber and oil. Dead or stranded whales also attract them.

They also follow fishing boats that carry out gutting at sea.

29. Fulmars on dead whales have been reported as searching out and eating the whale-lice *Cyramus* spp. and barnacles.

In turn, whalers have claimed that congregations of Fulmars have led them to schools of live whales. Thus the Fulmars act as modifiers of whalers which in turn provide the carrion on which the subject animal may feed.

30. Fulmars seek carrion other than whales (n. 28, n. 29). They have been reported as feeding on the carcasses of bears, Rhinocerous auklet, puffin, snow-bunting, eider, redwing, kittiwakes, guillemot and herring-gull, fighting off Great Skuas and Great Blackbacks to eat the latter three (which had originally been killed by the Great Skuas but then stolen by Fulmars).

In one study 28% of the stomach contents consisted of carrion.

The bird also readily eats dead fish; a Fulmer has been observed eating a dead floating halibut, probably *Reinhardtius hippoglossoides*.

Fulmars obtain most of their fish by following fishermen and stealing their fish, even off lines.

31. Fulmars have been known to prey on small live birds.

32. Fulmars eat a small amount of fish but it is not a major part of their diet. They will also eat mussels, crabs *(Eupagurus* sp.*)* and fish roe, all unidentified. Stomach remains have included a Clupeoid, *Clupea harengus* and a sand-eel, *Ammodytes* sp. One rather unusual stomach analysis showed as much as 22% fish, including Gappids - the pollack *Gadus pollachius* and a doubtful identification of *Urophycis* sp.

33. Smell is important for Fulmars in detecting food. Procellariiforms, unlike most other birds, have a good olfactory sense. The olfactory lobe takes up about 4.5% of the total brain.

34. Many sea-birds, including Fulmars, are attracted to glacier run-off streams in order to feed on the planktonic creatures. (see n. 27). Occasionally some are killed by ice falls.

35. In the glacier run-off streams the Fulmar has been observed eating:

the Chaetognath worms
nereids (rag worms), *Sagittaelegans*
nematodes,
Amphipods: *Pseudaclibrotus littoralis, Euthemisto libellula, Hyperoche kroyeri, Parathemisto oblivia,*
molluscs: *Clione limacina*, other *Clione* spp., *Margarites heligini, Limacina limacina, Sepia* spp., possibly *Loligo* sp., the tectibranch (pteropod) mollusc *Limancina arctica,* and pelagic snails
the Schizopod *Mysis oculata*
and the jellyfish *Cyanea cappilata, Aurelia aurita, Chrysaora* sp., and *Medusa* sp.

The Amphipod *Hyperoche kroyeri* is parasitic on the jellyfish *Cyanea capillata*.

The Little Auk *(Alle alle)* competes with the Fulmar for jellyfish.

36. Whales, bearded seals and many sea-birds, especially kittiwakes and Great Skuas, compete with the Fulmar for much of its food, particularly the plankton.

37. Fisher (1952) reports many Fulmars were found dead after a hurricane in the North Atlantic.

38. We have recorded 'light energy' and 'ice' as modifiers of a large class of food since both factors operate in affecting the distribution of the Fulmar - see table in §A.

39. Topography and vegetation assist in hiding the nesting Fulmars from predators. In particular in the Westmann Islands the garden angelica *Archangelica officinalis* not only conceals the bird directly but also produces an odour, from its crushed leaves and flowers, which can drown the musk of the Fulmars and thus make them harder to locate. The Icelanders cook and eat this plant, thus acting as second-order modifiers by removing it from the environment of the Fulmar; they also trample it, thus releasing the odour; in this latter sense they act as third-order modifiers. The bird itself acts as a third-order modifier in its own environment by producing excreta which fertilizes the plant.

D DETAIL

FOOD

Plankton: krill *(Euphausia superba), Oniscus pulex, Euryporeia gryllus, Hyperia* sp., *Gammarus* sp., shrimp *Hymenodora glacialis*, the Copepods *Calanus finmarchicus* and *C. hyperboreas*, also isopods, amphipods, schizopods and crustaceans.

Carrion: bear *(Thalarctos maritimus)*, rhinoceros auklet *(Cerorhinca monocerata)*, puffin *(Fratercula arctica)*, snow-bunting *(Plectrophenax nivalis)*, eider *(Somoteria mollissima)*, redwing *(Turdus musicus)*, kittiwake *(Rissa tridactyla)*, guillemot *(Uria* spp.*)*, herring-gull *Larus argentatus)*.

Chaetognath worms: *Sagittae legans*

Amphipods: *Euthemisto libellula, Hyperoche kroyeri, Parathemisto oblivia, Pseudaclibrotus littoralis*

Molluscs: *Clione limacina* and other *Clione* spp., *Limacina limacina, L. arctica, Margarites heligina, Sepia* spp., possibly *Loligo* sp. and pelagic snails

Jellyfish: *Cyanea capillata, Aurelia aurita, Chrysaora* sp., *Medusa* sp.

Schizopod: *Mysis oculata*

Nereids (ragworms)

Nematodes

Sorrel leaves *(Rumex acetosa)*

Spoonwort *(Cochlearia officinalis)*

Sedge *(Carex* sp.*)*

Brown algae *(Ascophyllum nodosum)*

Smartweed or viviparous polygonum *(Polygonum viviparum)*

Cinquefoil *(Potentilla* sp.*)*

Common seaweed *(Enteromorpha compressa)*

PREDATORS

Homo sapiens

Foxes: the arctic fox *(Alopex lagopus)* and the red fox *(Vulpes vulpes)*

Stoat, *Mustela erminea*

Birds: White-tailed eagle *(Haliaeëtus albicilla)*, gyrfalcon *(Falco rusticolus)* peregrine *(F. peregrinus)*, Great Blackback *(Larus marinus)*, glaucous gull *(L. hyperboreas)*, rook *(Corvus frugilegus)*.

Crustacean, *Lepas hillii* Leack

Ticks: *Ixodes caledonicus, I. putus*

Bird fleas: hen-flea *(Ceratophyllus gallinae)*, moorhen-flea *(Dasypsyllus gallinulae)*, vagabond flea *(C. vagabunda)*

Mallophaga (feather-lice or bird-lice): *Austromenopon brevifimbriatum, A. numerosum, Ancistrona vagellia, Saemundssonia occidentalis, Perineus nigrolimbatus*

Nematodes: *Anisakis* spp., *Stegophorus stellae-polaris,* other *Stegophorus* spp.

Cestodes: *Tetrabothrius cylindraceus* (Rudolphi), *T. monticellii* Fuhrmann

Virus: *Ornithosis* virus

E REFERENCE

Fisher, James (1952). *The Fulmar.* (Collins, London).

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

V. THE KING PENGUIN. *(Aptenodytes patagonica)*

by

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ABSTRACT

The precise environment of the King penguin (*Aptenodytes patagonica*) is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

CONTENTS

The map and diagram below are from B. Stonehouse (1967).

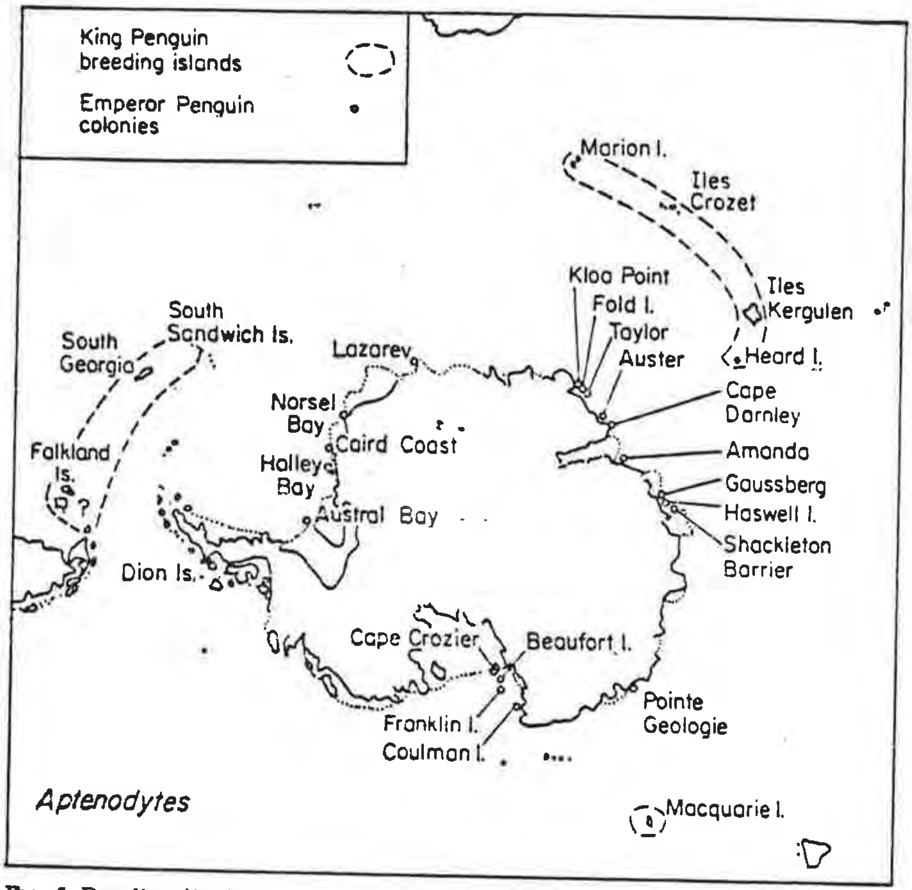


Fig. 5. Breeding distribution of *Aptenodytes*.

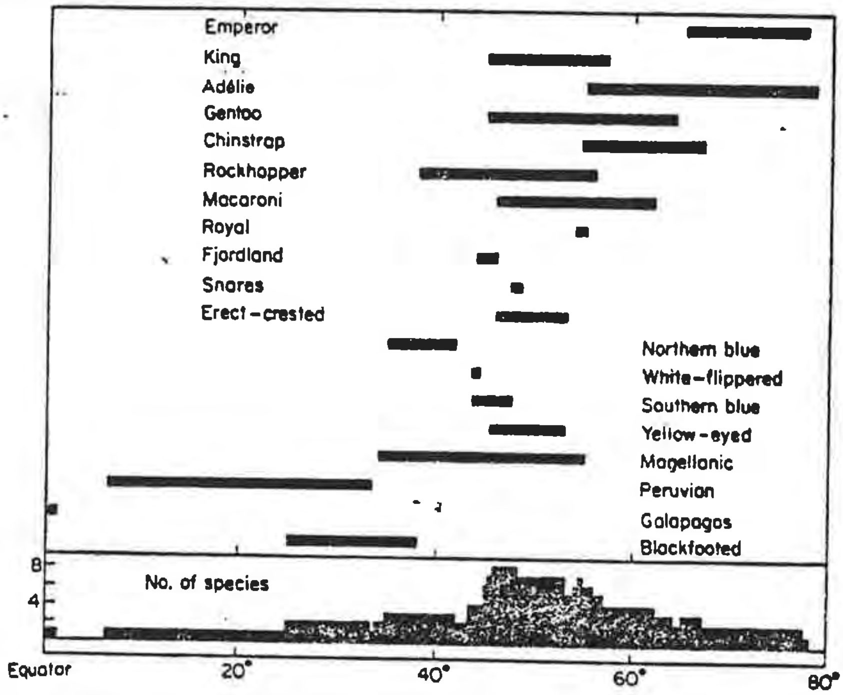


Fig. 6. Latitudinal spread of penguin breeding areas.

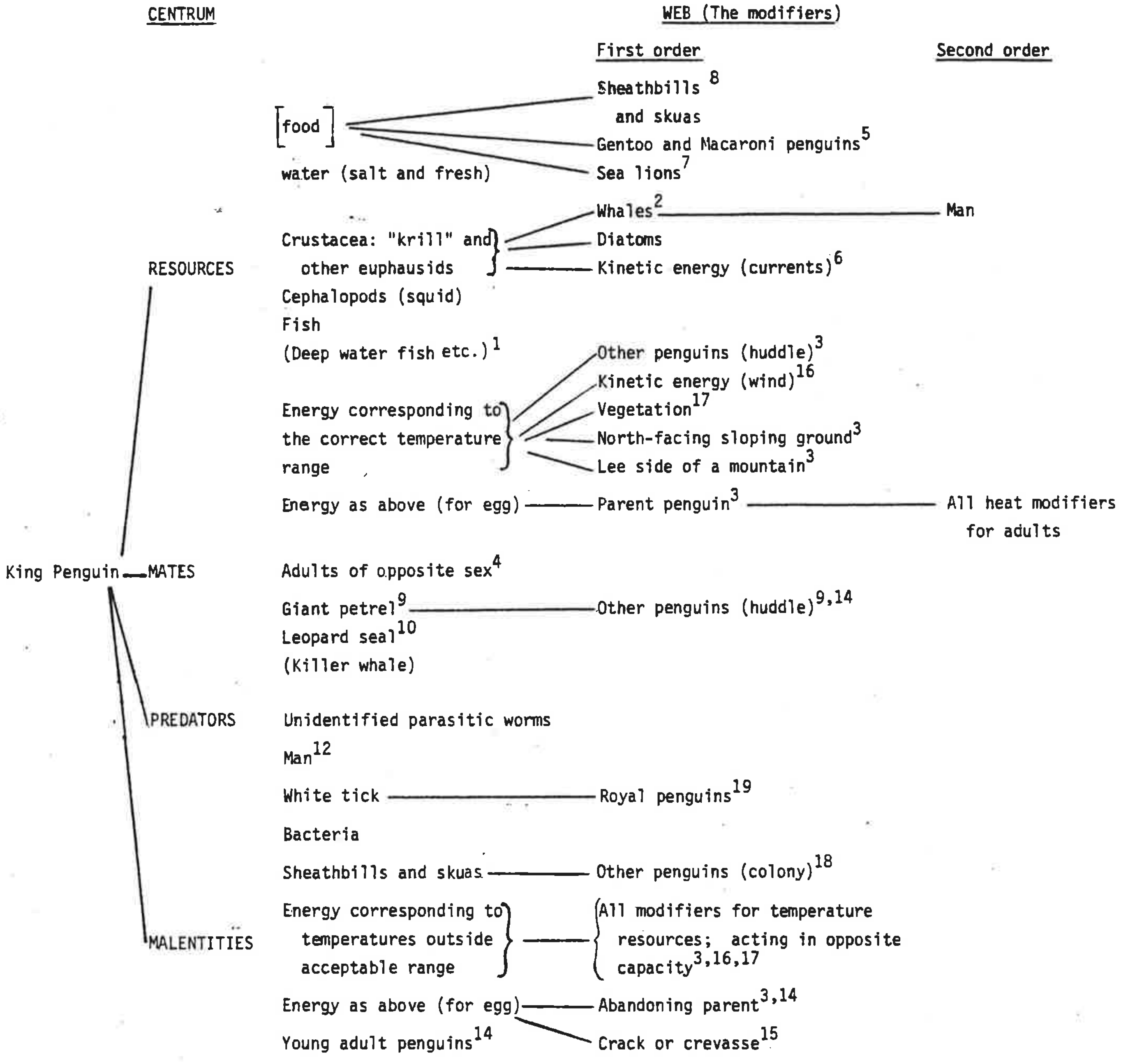
A INTRODUCTORY NOTE

As indicated in sections B, C and D we have sometimes used information on other penguins. In particular the King and Emperor Penguins are very similar.

The map and diagram are both from Stonehouse (1967).

The methodology used in the construction of the envirogram is explained in detail in the general introduction to the series (AES Working Paper 9/81). The defining equations for the environment of an animal are also given in the general introduction, together with some indications as to the place of the present study within the development of a mathematical theory of ecology.

B ENVIROGRAM



CENTRUM		WEB (The modifiers) First order	Second order
King Penguin — RESOURCES	[food]	Sheathbills[8] and skuas Gentoo and Macaroni penguins[5] Sea lions[7]	
	water (salt and fresh)		
	Crustacea: "krill" and other euphausids	Whales[2]	Man
		Diatoms	
		Kinetic energy (currents)[6]	
	Cephalopods (squid)		
	Fish		
	(Deep water fish etc.)[1]		
	Energy corresponding to the correct temperature range	Other penguins (huddle)[3] Kinetic energy (wind)[16] Vegetation[17] North-facing sloping ground[3] Lee side of a mountain[3]	
	Energy as above (for egg)	Parent penguin[3]	All heat modifiers for adults
MATES	Adults of opposite sex[4]		
PREDATORS	Giant petrel[9]	Other penguins (huddle)[9,14]	
	Leopard seal[10]		
	(Killer whale)		
	Unidentified parasitic worms		
	Man[12]		
	White tick	Royal penguins[19]	
	Bacteria		
	Sheathbills and skuas	Other penguins (colony)[18]	
MALENTITIES	Energy corresponding to temperatures outside acceptable range	All modifiers for temperature resources; acting in opposite capacity[3,16,17]	
	Energy as above (for egg)	Abandoning parent[3,14] Crack or crevasse[15]	
	Young adult penguins[14]		

C NOTES ON THE ENVIROGRAM

1. Kooyman (1975) has observed that the Emperor penguin can dive to 265m and can change depth at a rate of 120m/min. Comparable measurements for the King penguin are not available, however, it seems likely that this animal also is able to feed relatively deep, unlike other penguins which probably confine their feeding to the upper layers of the sea.

2. There is probably an abundance of Krill available for penguins following the excessive hunting of whales (by man).

3. King penguins have no nest. The parent bird carried a single egg on its feet during the summer and raises the chick during the following winter. The egg has further protection from the cold when the penguins huddle in large colonies, a common habit of both King and Emperor penguins. Thus, an adult parent will appear in the envirogram as a first-order modifier for the egg's heat resources; consequently any modifiers of the adults heat resources appear as modifiers of one order higher. Yeats (1975) remarks that penguins never huddle on the lee side of a mountain, where the winds are gusty and variable, thus creating snow drifts. Also they tend to use the northern slopes which "have a considerable radiation advantage over horizontal surfaces".

4. There is vocal dimorphism between sexes and efficient recognition of the partner's call. King penguins moult into adult plumage at the end of their second year but probably do not attain full sexual maturity for at least two more years.

5. Gentoo and Macaroni penguins breed as neighbours in many areas and may compete with the King penguin for food.

6. An enormous quantity of food is consumed daily by the large penguin colonies and replaced by the influence of the ocean currents; this applies particularly to small organisms e.g. Krill.

7. Sea lions eat squids, fish and crustacea which are also eaten by penguins.

8. Sheathbills and skuas are able to steal regurgitated food when the penguin chicks are being fed.

9. Giant petrels attack and kill the penguin chicks. They do not eat the flesh of their catch, but the contents of the stomach only. The habit of the King penguins of huddling (see note 3) helps to protect the chicks from these predators.

10. Probably the main predator at sea (Budd, 1975 and Spellerberg, 1975).

11. Sheathbills have been observed eating parasitic worms which are numerous in the droppings of penguins.

12. King penguins were attacked for their oil. According to Conroy (1975) the numbers are now increasing following the cessation of attacks by man.

13. After hatching chicks are brooded by parents until they can maintain body temperature:

    Hatching temperature : 34.3°C
    After 20 days : 39.2°C

    During this period the average air temperature was 16°C. (Barre, 1978).

14. Giant petrels attack only isolated overfed chicks. Young breeding birds frequently abondon eggs and this accounts for a high percentage of egg mortality. These same young birds will fight over abandoned chicks - frequently killing them - they will also take chicks from the feet of their parents only to abandon them a few hours later. This behaviour is facilitated by lack of defended breeding territories (necessitated by huddling, see note 3) and generally accounts for about 6% of chick mortality (Jouventin, 1975).

15. Ambulatory incubation and brooding leads to egg losses in cracks, crevasses etc. which thwart recovery attempts (about 5%, Jouventin, 1975).

16. Arctic winds are the greatest potential hindrance to the maintenance of survival temperatures by penguins (see also note 3).

17. Vegetation absorbs and emits radiation and maintains temperatures considerably above the ambient temperature. It also permits air circulation while reducing wind velocity (see notes 3,16).

18. Skuas are more likely to predate well-fed isolated chicks.

19. The white tick *Ixodes uriae* is an ectoparasite of the King penguin, however, the Royal penguin is the preferred host.

D DETAIL

Resources

The range of food for many species of penguins includes almost the entire span of prey taken by the family as a whole. We have listed only those directly confirmed for the King penguin.

Fish

Notothenidae (small transparent fish), in particular *Notothenia rossi.*
Pleuragramma antarcticum.

Cephalopods

According to Stonehouse (1967) to staple food.
Unidentified species, possibly *Onychoteuthis* spp.
Moroteuthis spp.

Crustacea

Euphausia superba, the opossum shrimp, "Krill".
E. crystallorophias
Other unidentified Euphausiacea.
Unidentified Amphipods.
Possibly *Arctomysis marina*, the swarming mysid.

Predators

Macronectes giganteus, the giant petrel.
Catharacta skua, Chionis minor and *C.* spp.; (sheathbills) both occasionally take young chicks and eggs.
Hydruga leptonyx, the leopard seal.
Stercorarius skua lommbergi, (the southern skua).
Ixodes uriae, the white tick.

The following table is from Soucek and Mushin (1970).

Table 6: Frequency of isolation (aerobically at 37 C) of gram-negative bacteria from the gut of penguins in various locations.

Location	Species and no. of penguins	No. of sterile birds	Total no. of isolations	No. of isolations of bacterial strains							
				Coliforms				Paracolons and nonlactose-fermenters			
				E. coli	*C. freundii*	*Emterbacter*	Irregular	Paracolon	*Alcaligenes faecolis*	*Proteus vulgaris*	*Pseudomonas*
Antarctic	Adélie(95)	19	335	46	7	7	220	12	43	0	0
	Emperor(8)	2	21	14	0	0	7	0	0	0	0
	Chinstrap(3)	1	7	2	0	0	5	0	0	0	0
Sub-Antarctic	Rockhopper(10)	0	114	53	0	1	59	0	1	0	0
	King(8)	2	144	75	2	0	67	0	0	0	0
	Gentoo(10)	2	45	25	0	0	13	4	1	0	2
	Royal(13)	0	88	55	0	0	33	0	0	0	0
Phillip Island	Fairy(11)	1	162	116	0	0	45	1	0	0	0

Saez (1968) records four species of fungi found in the King penguin: *Pencillium* spp. (intestine), *Scopulariopsis brevicaulis*, *Aspergillus niger* and *A. versicolor* (buccal cavity). We are unable to place them on the envirogram since their function is not recorded.

* * * * *

Budd (in Stonehouse 1975) records the following plants in and around King penguin colonies on Heard Island: tussock grass *(Poa cookii)*, azorella *(Azorella selago)* and Kerguelen cabbage *(Pringlea antiscorbutica)*.

E REFERENCES

Arnaud, P.M. (1973). (In French). Ecological notes on *Zanclorhynchus spinifer* (Teleosteen, congiopodidae) of the Kerguelen Islands and on their predation by species of the giant petrel Macronectes. *Tethys* 4(3), 757-760.

Barre, H. (1978). Energy metabolism of the King penguin chick during growth. *J. Physiol. (Paris)* 74(6), 555-562.

Budd, G.M. (1968). Population increase in the King penguin at Heard Island. *Auk* 85(4), 689-690.

\- (1973). Status of the Heard Island King penguins in 1971. *Auk* 90(1), 195-196.

Derenne, M., P. Jouventin and J.-L. Mougin (1979). The King penguin call and its evolutionary significance. *Gerfaut* 69(2), 211-224.

Fogg, G.E. (1970). Biolggical productivity in the Antarctic. *Med. Biol. Illus.* 20(2), 100-105.

Murray, M.D. and W.J.M. Vestjens (1967). Studies on the ecoparasites of seals and penguins: III. The distribution of the tick *Ixodes uriae* White and the flea *Parapsyllus magellanicus Heardi* de Meillon on Macquarie Island. *Aust. J. Zool.* 15(4), 715-725.

Saez, H. (1968). (In French). Contribution to the ecological study of subantarctic media: I. Fungi isolated from Spenisciformes in the Kerguelen Islands. *Vie Milieu* 19(1c) 1-9.

Soucek, Z. and R. Mushin (1970). Gastrointestinal bacteria of certain antarctic birds and mammals. *Appl. Microbiol.* 20(4), 561-566.

Sparks, J. and T. Soper (1967). *Penguins* (Angus and Robertson, Melbourne).

Stonehouse, B. (1967). The general biology and thermal balance of penguins. *Advan. Ecol. Res.* 4, 131-196.

Articles by the following authors are in B. Stonehouse (Ed.); *The Biology of Penguins* (Macmillan, 1975):

Budd, G.M.
Conroy, J.W.H.
Jouventin, P.
Kooyman, G.L.
Spellerberg, I.F.
Stonehouse, B. (Introduction)
Yates, G.W.

Voisin, J.F. (1972). Notes on the behaviour of the Killer whale, *Orcinus orca*. *Norw. J. Zool.* 20 (1), 93-96.

Young, E.C. (1967). Skua studies. *Tuatara* 15 (3), 142-148.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS
XII THE ROTTNEST QUOKKA *(Setonix brahyurus)*

by

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ABSTRACT

The precise environment of the Rottnest quokka *(Setonix brachyurus)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis,* 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

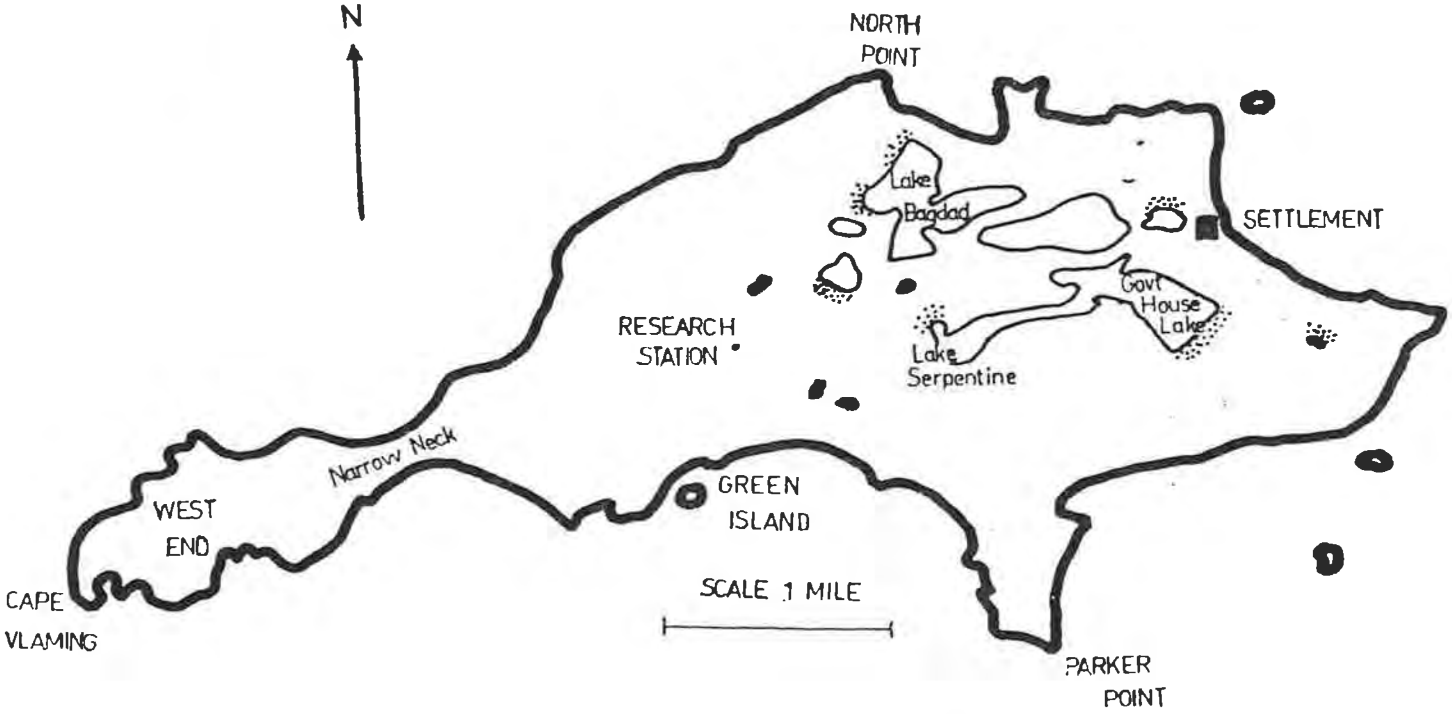
* * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed disucssion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in A.E.S. Working Paper No. 9/81; an improved and extended version will be available in 1983.

CONTENTS

ROTTNEST ISLAND WESTERN AUSTRALIA



Stippling indicates fresh water soaks bordering salt lakes

● indicates fresh water swamps which dry up in summer

A INTRODUCTORY NOTE

The quokka is a rabbit-sized wallaby confined to Western Australia. Most of the ecological work has been done on Rottnest Island, about 15 km off Fremantle particularly on West End (see map). There seems to be little movement of the animals on Rottnest across Narrow Neck. The quokka, like other marsupials, is nocturnal in its habits.

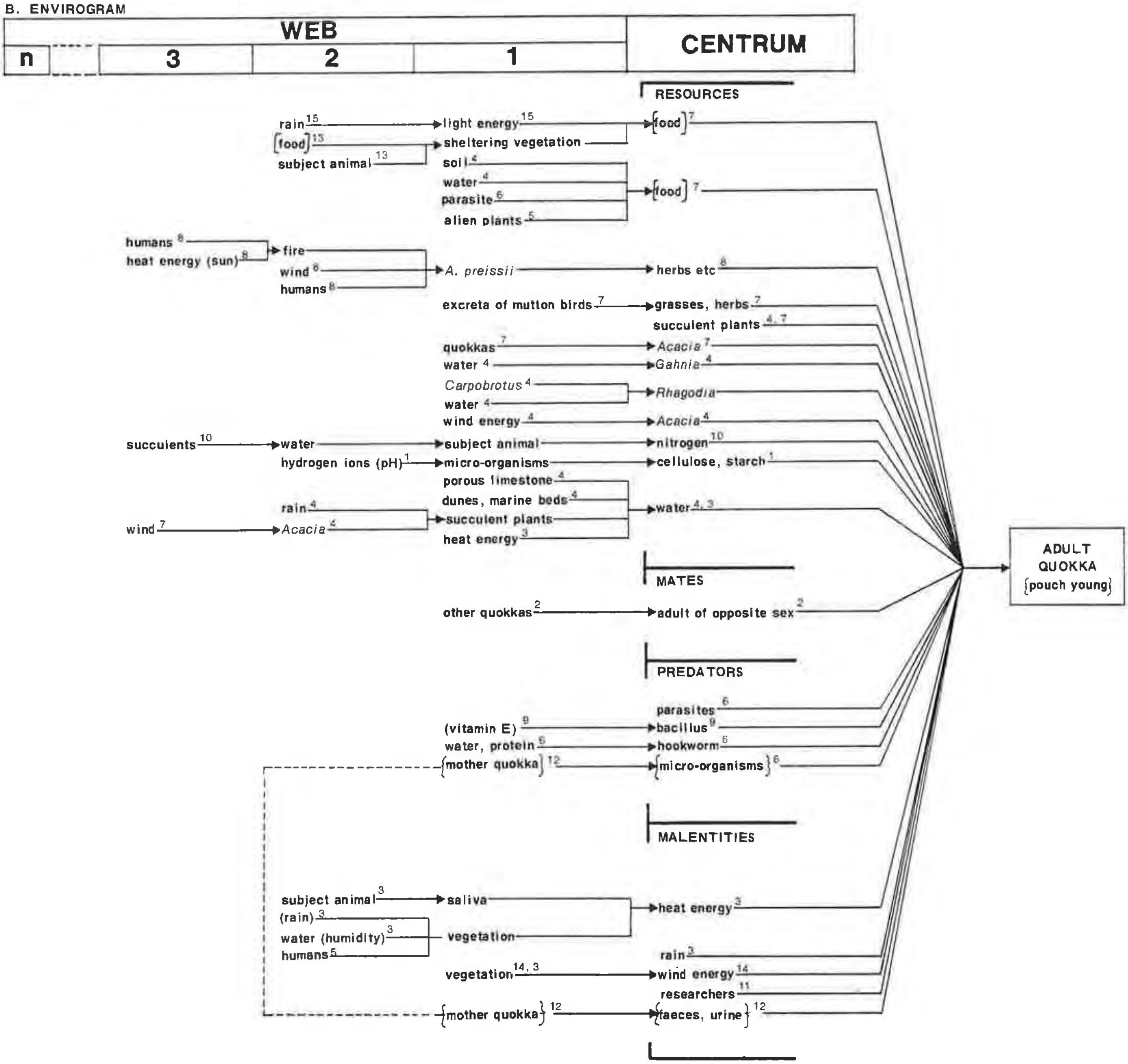
Females in the study compounds become sexually mature at about 18 months by which time they weigh approximately 2kg; the length from nose to base of tail is about 45 cm; the tail length is about 25 cm (short for a macropod marsupial). Females have an oestrous cycle of about 28 days which is interrupted in the wild for about 3-5 months between late August and late January. The anoestrous period is reduced in domesticated quokkas and after one year or more disappears. Sharman (1955a) suggests that the anoestrous period is affected by such factors as diet, availability of water and length of day. The duration of oestrous is rarely longer than 12 hours.

After its birth the foetus climbs immediately into the pouch. The passage of the foetus to the pouch after birth is reported as hazardous, but we cannot enter these hazards on the envirogram since no details are given in the literature. At birth the animal weighs approximately .07% of the adult weight, with a length of about 3 cm. The forelimbs are well developed, but the hind limbs only rudimentary. After 25 weeks it leaves the pouch and is capable of swift movement, but returns to the pouch if alarmed; it is heavily furred, weighs about 600 g and is about 35 cm long.

An interesting mechanism for emergency replacement of young is reported by Sharman (1955b). Shortly after parturition ovulation occurs; if the egg is fertilized as a result of a post-partem copulation the resulting blastocyst may remain quiescent for up to 5 months, proceeding with development only if the pouched young is lost.

The map is from Main *et al* (1959).

B. ENVIROGRAM



C. NOTES ON THE ENVIROGRAM

1. Moir *et al* (1954) record the presence of an unidentified microbial population in the stomach of the quokka which causes extensive erosion of cellulose material, thus making it available for digestion. Moir, Somers and Waring (1956) report that 15 types of bacterium were found in the stomachs of quokkas. The bacterial population consisted mainly of Gram-negative rods and cocci, with a few spiral forms. There were no ciliates. Bacteria were observed to attack both cellulose and starch enabling them ot be used as food. When the pH was below 5.5 Gram-positive rods dominated the bacterial population. Above pH 5.5 these bacteria were present only in small numbers.

2. The oestrus period for the female quokka is short - rarely longer than 12 hours. During this time the female will accept a series of males or the same male repeatedly. When several males are present severe fighting may occur between them at each attempt to copulate with the female. Only on rare occasions does the male attempt to mate with a non-oestrous female and at such times is rejected. Ovulation occurs 12-24 hours after the beginning of oestrous, independently of the occurrence of copulation (Sharman 1955).

3. The average body temperature of the quokka is from 37.5°C to 38°C. Even when subjected to temperatures of 44°C the animals maintain their normal skin temperature 7°C below the ambient temperature and their deep body temperature 5°C below. Quokkas salivate heavily and lick their front and hind feet, legs, tails, and sometimes bellies until the fur is dripping wet. The evaporation of this saliva is the main thermoregulatory mechanism at high ambient temperatures. When subjected to -10°C adult quokkas, even those crouching motionless, managed to maintain their deep body temperature 1°C - 2°C above normal body temperature; the thermoregulatory mechanisms are shivering and peripheral vasoconstriction. It is extremely rare for such temperatures to occur in the quokka's native habitat. Thus extremes of heat are an insignificant cause of mortality (Bartholomew, 1956).

   During the day, the quokkas lie up in the shade of vegetation, which is primarily an open heath formation of low shrubs with occasional *Acacia* spp. thickets. Rain and strong, especially cold, winds may prevent the emergence of the animals during the evening (Main, Shield and Waring, 1959).

Storr (1964) reports that in the region of Lake Bagdad (see map) there are thickets of *Solanum simile* which afford the quokkas good daytime shelter. To the west of the lake the quokkas spend the day under tussocks of *Gahnia*.

Kitchener (1972) also stresses the importance of shelter from the late summer heat on Rottnest Island. Around Barker's Swamp (in the centre of the island) the animals used fallen *Melaleuca* trees and *Acanthrocarpus* bushes for shelter. But when temperatures rise to about 32°C they shift to shelter provided by *Arthrocnemum* and *Gahnia* bushes. The shade of the latter is consistently 2°C - 4°C cooler than the shade of the other bushes, however quokkas in *Gahnia* shade retreat to *Arthrocnemum* later in the day, presumably because the humidity is 7% less than the humidity in *Gahnia* shade.

4. The annual precipitation on Rottnest Island is 29 inches, but in summer (December-March) only 1.5 inches falls. The island is composed of porous limestone and this allows rain to soak away rapidly. Only where there are recent or Pleistocene dunes over impervious marine beds is water available to the animals in a series of soaks wherever there are outcrops of marine beds, commonly around the salt lakes in the centre of the island (see map). (Main, Shield and Waring, 1959).

When surface water is not available on West End (where there are no soaks) quokkas obtain water from succulent plants such as *Carpobrotus* available only on Cape Vlaming (see map). Quokkas on other parts of Rottnest (apart from West End) also have access to these plants but they tend, in dry months, to aggregate around soaks. When water is freely available they are widely dispersed (Main, Shield and Waring, 1959).

These remarks are born out by Storr (1964) who records *Carpobrotus acquilaterus* as the only permanent water source for the quokkas in the West End and Cape Vlaming areas. Shrubs are not available for food in the Cape Vlaming area. Such vegetation as occurs is markedly modified by the soil structure - damp or drained, saline or not.

The following table is from Storr (1964). (Measurements from faeces analyses).

TABLE 4

WATER AND NITROGEN CONTENT OF FOOD PLANTS ON ROTTNEST I.

Collections made at Cape Vlaming and West End indicated by asterisk, all other collections from the lakes. Values given as percentage wet weight for water and percentage dry weight for nitrogen.

Food Plants	Jan-Mar		Apr-June		July-Sept		Oct-Dec	
	Water	Nitrogen	Water	Nitrogen	Water	Nitrogen	Water	Nitrogen
Succulents								
Arthrocnemum halocnemoides	82	1.1	83	1.2	93	2.9	87	1.7
*Atriplex cinerea**	74	1.3	78	1.3	86	3.5	71	1.7
Atriplex paludosa	77	1.5	78	1.8	86	2.7	80	1.9
*Carpobrotus aequilaterus**	88	0.8	89	0.9	93	2.0	90	1.1
*Rhagodia baccata**	76	1.0	79	1.2	88	2.4	83	1.9
Rhagodia baccata	71	1.8	74	2.0	85	3.3	76	2.2
Salicornia australis	84	1.0	84	1.0	94	2.7	88	1.4
*Threlkeldia diffusa**	85	1.7	84	2.0	91	3.1	82	1.9
Shrubs and trees								
*Acacia rostellifera**	67	1.2	65	1.2	75	2.4	73	2.0
Acacia rostellifera	63	1.3	63	1.4	74	2.1	71	1.6
*Diplolaena dampieri**	49	1.2	53	1.3	68	1.5	57	1.3
*Frankenia Pauciflora**	36	0.7	35	0.9	56	1.8	47	1.1
Guichenotia ledifolia	38	0.8	40	1.1	58	1.9	46	1.2
Melaleuca pubescens	59	1.5	55	1.5	66	1.9	63	1.7
*Olearia axillaris**	36	0.9	53	1.1	66	1.7	45	1.2
Samolus repens	48	1.3	50	1.2	76	1.6	65	1.4
*Scaevola crassifolia**	70	0.9	75	1.0	83	1.6	79	1.3
Solanum simile	79	2.7	84	2.8	85	4.5	77	3.3
*Westringia dampieri**	28	0.5	30	0.5	54	1.2	38	0.8
Forbs								
Average of 11 species	75	2.1	86	3.0	86	2.9	78	2.3
Sedges								
Carex preissii	-	-	75	2.6	69	2.0	29	1.1
Gahnia trifida	31	0.9	38	0.9	40	0.9	36	0.8
Grasses								
*Poa caespitosa**	35	1.2	41	1.4	67	1.8	50	1.4
Sporobolus virginicus	53	1.7	52	1.7	72	2.5	65	2.5
*Stipa variabilis**	31	1.5	38	1.8	60	2.3	44	1.9
Stipa variabilis	41	1.6	41	1.6	53	2.1	42	1.7
Average of five annual species	62	1.2	77	2.6	81	2.6	66	1.5

(see also n. 7).

5. Since the settlement of Rottnest Island in 1831 many alien species of plants have become established. We have classified them as modifiers of all food, since they tend to replace the native plants which are eaten by the animals.

6. Main, Shield and Waring (1959) report that quokkas are heavily infested with the intestinal parasite *Austrostrongylus thylogale*, a hookworm. Storr (1964) reports that this parasite, when present in high numbers, slows digestion to a minor extent, thus we have entered it on envirogram as a modifier of all food.

Gibb *et al* (1966) report an unidentified parasite which produces toxoplasmosis. The source of this infection in the quokkas is unknown; local mice were uninfected; the infection is confined to quokkas near the settlement. Other parasites which they report are a cestode *Progamotaenia* sp. in the bile duct, the nematode *Austrostrongylus thylogale* and a filaroid *Dipetalonema annulipapillata* (both the latter being frequently found in the peritoneal cavity and the duodenum). Also a *Cloacina* sp. was found in the foregut.

Iveson and Bradshaw (1973) report *Salmonella jauiana*, other species of *Salmonella* and *Arizona* spp. in Rottnest quokkas. They found that the effect of the hookworm *Austrostrongylus thylogale* is increased, possibly enough to cause the death of the animal, by shortage of protein and free water in summer. The effects of *S. jauiana* and *Arizona* spp. are also increased during summer. The mechanisms by which these parasites have reached Rottnest are unknown; suggestions are via droppings of migratory birds or via animal foodstuffs, organic fertilizers and domestic animals and birds brought on to the Island by people during the past century.

7. *Acacia* is a preferred item of diet. Main, Shield and Waring (1959) report that acacia is in decline on Rottnest Island. Semi-starvation which occurs to varying degrees each summer is closely tied to quokka grazing pressure on the *Acacia* seedlings. This is thought to be the main cause of death among quokkas. Thus the quokkas themselves act as first-order modifiers.

The following tables are from Storr (1964). (Measurements from faeces analyses).

TABLE 1

CAPE VLAMING: ITEMS IN FOOD

Values given as percentage dry weight

Food Plants	Jan-Mar	Apr-June	Oct-Dec
Succulents			
Corpobrotus aequilaterus	69	80	52
Rhagodia baccata	27	13	26
Threlkeldia diffusa	1	Trace	1
Shrubs			
Acacia rostellifera	-	1	-
Frankenia pauciflora	-	Trace	-
Olearia axillaris	Trace	-	Trace
Scaevola crassifolia	1	2	1
Westringia dampieri	1	-	9
Forbs	Trace	3	Trace
Grasses	1	1	11

TABLE 2

WEST END: ITEMS IN FOOD

Values given as percentage dry weight

	Jan-Mar	Apr-June	July-Sept	Oct-Dec
Succulents				
Atriplex cinerea	-	-	Trace	-
Carpobrotus aequilaterus	1	6	-	Trace
Rhagodia baccata	47	18	19	43
Threlkeldia diffusa	Trace	-	-	1
Shrubs				
Acacia rostellifera	21	35	36	30
Diplolaena dampieri	-	1	3	-
Guichenotia ledifolia	-	-	Trace	-
Olearia axillaris	Trace	1	1	Trace
Scaevola crassifolia	6	12	10	11
Solanum simile	1	-	-	-
Westringia dampieri	-	-	Trace	1
Forbs	6	16	9	4
Grasses	17	11	22	10

TABLE 3

MUD LAKE: ITEMS IN FOOD

Values given as percentage dry weight.
Data from West Bagdad in brackets.

Food Plants	Jan - Mar	Apr-June	July-Sept	Oct-Dec
Succulents				
*Arthrocnemum halocnemoides**	70 (32)	41	47	47
Atriplex paludosa	2 (3)	Trace	-	-
Rhagodia baccata	4 (7)	5	4	4
Suaeda australis	Trace (-)	1	-	Trace
Threlkeldia diffusa	1 (Trace)	1	-	1
Shrubs and trees				
Acacia rostellifera	- (-)	-	3	1
Guichenotia ledifolia	2 (Trace)	5	4	9
Hemichroa pentandra	Trace (1)	1	-	-
Melaleuca pubescens	1 (-)	2	1	4
Samolus repens	Trace (5)	-	-	Trace
Solanum simile	8 (12)	5	1	2
Forbes	1 (4)	9	8	3
Sedges				
Carex preissii	- (-)	2	-	-
Gahnia trifida	4 (15)	2	1	2
Grasses	7 (21)	26	31	27

* Includes *Salicornia australis* (the epidermis of these samphires is frequently indistinguishable).

Storr remarks that only animals with no water problems could eat large quantities of the "tough, dry sedge" (*Gahnia*) located to the west of Lake Bagdad (see map). In this neighbourhood grasses and herbs are fertilized by mutton-bird excreta and grow luxuriantly in winter and spring but after flowering they die off quickly on the exposed plateau; they are thus only a minor component in the animals summer and autumn diet.

In the seepage area on the west shore of Lake Bagdad only half as much samphire was eaten in summer as at Mud Lake (a small lake west of L. Bagdad), but three times as much grass and sedge. These differences can be explained partly by reference to the relative availability of the plants and partly to the water requirements of the animals. Palatable grasses, especially *Sporobolus*, are much more plentiful on the west shore of Lake Bagdad, where samphires are relatively scarce.

In summer succulents comprise almost half the animals' diet in the Mud Lake area. The scarcity of *Carpobrotus aequilaterus* in areas away from Cape Vlaming means that *Rhagodia baccata* becomes the dietary mainstay and water source in summer. Storr (1964) in a study at Mud Lake, reports that at no time did the consumption of succulents fall below 48% in this area - whereas at West End it falls as low as 19%. The explanation for this is the presence in the Mud Lake area of samphires such as *Arthrocnemum halocmemoides* and *Salicornia australis*. Storr claims that this "indicates the superior palatability of the samphires as compared to *C. aequilaterus* ", however it is not clear to us exactly how the animal could make such a comparison, since *C. aequilatureus* does not seem to occur in the Mud Lake area, nor do the samphires seem to occur in the Cape Vlaming and West End areas (as far as we can judge from the literature).

In sheltered situations *Acacia rostellifera* grows into a small tree with most of its foliage inaccessible to the animals. Thus it plays a minor role in the diet of the Mud Lake quokkas even though it is abundant in this area. In West End, on the other hand, *A. rostellifera* occurs mainly as low wind-pruned thickets, and thus it is able to play a major role in the diet of those quokkas. The inaccessibility of *A. rostellifera* foliage also forces the Mud Lake quokkas to depend more heavily on succulents for food than their West End counterparts (Storr 1964).
(see also n. 4).

8. A factor contributing to the greater consumption of shrubs at West End is the scarcity of alternative foods. Storr (1964) found that the peninsula had not been burnt for many years, hence much of the grassland was overgrown by tangled masses of *Acanthrocarpus*. In contrast, recent burning of the country found the lakes had favoured the tussock grasses over the slower-growing *Acanthrocarpus* and provided more space for annual herbs and grasses and for such short-lived shrubs as *Solanum simile* and *Guichenotia ledifolia*.

Holsworth (1967) remarks that *Acanthrocarpus preissii* is markedly modified by wind, varying from a dense tangle 2 or 3 ft deep in sheltered areas to small discrete bushes in exposed areas. He remarks that in sheltered areas it provides "ideal" cover for the quokkas, but it is not clear to us whether this is from rain or sun or some other object. He suggests, however, that it provides 'escape' cover from people.

9. Kakulas (1964) reports an atypical acid-fast bacillary infection, the end result of which is death due to nutritional myopathy. In a previous paper (1961) he reports that nutritional myopathy in captive quokkas always leads to death and that the disease is linked with deprivation of vitamin E. Possible sources of vitamin E on Rottnest Island are unknown.

Gibb *et al* (1966) observed nutritional myopathy and bronchogenic adenocarcinoma linked to vitamin E deficiency.

10. Quokkas have the ability to recycle nitrogen. Holsworth (1967) suggests that this ability is increased in an animal which is deprived of water. Quokkas on Cape Vlaming, where succulents are readily available even in the hot dry summers, can maintain a high water intake during the summer when nitrogen is in short supply; this is suggested as the cause of the low survival rate of the Cape Vlaming quokkas; the animals die of (nitrogen) starvation because they eat succulents to obtain water.

11. From 1973 the quokka is being used more and more as a laboratory animal, particularly by clinical workers doing medical research. We have classified 'researchers' as malentities here; the difficulty with the interpretation of 'H(researcher)' is discussed in the General Introduction.

12. Yadau *et al* (1972) report the following microflora commonly present in the gut of the pouch young: *Escherichia coli*, *Streptococcus faecalis*, *Aerobacter aerogener*. Less frequently present are: *Klebsiella* sp., *Salmonella newport*, *Pseudomonas aeruginosa*, *Staphylococcus albus*, *Proteus* sp., *Streptococcus lactua*, *Clostridium* sp. and yeasts. The mother provides protection from bacteria both through antibodies in her milk and in antibacterial secretions from glands in the skin of her pouch. The mother introduces bacteria into the pouch when she licks it to remove faeces and urine. Thus, by the same behaviour, the mother quokka modifies both predators and malentities.

13. Diurnal shelter is changed for only a short period in the year - from April to June. At this time the weather is mild, quokkas are in their poorest condition and are unable to travel between shelter and food. We have classified the subject animal itself as a modifier of shelter in the following sense: consider a particular bush, potentially useful as shelter; it will be removed from the animal's environment if the animal itself is (at that particular time) too weak to reach it from the food sources. Conversely, a bush further away from food may enter the animal's environment if the animal itself is strong enough to reach it. Since it also happens that the nocturnal feeding area is markedly reduced during the wet season (Nicholls, 1971) we classify all food (i.e. [food]) as a modifier of shelter.

14. Nicholls (1971) reports that the West End quokkas appear to seek shelter from wind. They crouch, particularly during the day, in the *Acacia* scrub and the more sheltered clumps of *Thomasia* and *Acanthrocarpus*. He remarks " ... a quokka has a nocturnal feeding area with a nearby diurnal shelter." He argues that there can be, in any one area, only a limited number of convenient combinations of food and shelter, which restricts the movement of the animals.

15. Quokkas are usually nocturnal but rain in the long dry periods during the summer may cause the animals to emerge during daylight and drink from roadside pools and other temporary waters (Main, Shield and Waring, 1959).

E. REFERENCES

Bartholomew, G.A. (1956). Temperature regulation in the macropod marsupial, *Setonix brachyurus*. *Physiol*. *Zool*. 29, 26-40, 1956.

Gibb, D.G.A., B.A. Kakulas, D.H. Perret and D.J. Jenkyn (1966). Toxoplasmosis in the Rottnest quokka (*Setonix brachyurus*). *Aust. J. Experimental Biol. and Med. Sc.* 44, 665-672.

Holsworth, W.N. (1967). Population dynamics of the quokka, *Setonix brachyurus*, on the West End of Rottnest Is., Western Australia. I. Habitat and distribution of the quokka. *Aust. J. Zool.* 15, 29-46.

Iveson, J.B. and S.D. Bradshaw (1973). *Salmonella jaurana* infection in an infant associated with a marsupial, the quokka, *Setonix brachyurus*, in Western Australia. *J. Hygiene*, 71, 423-432.

Kakulas, B.A. (1961). Myopathy affecting the Rottnest quokka (*Setonix brachyurus*) reversed by -tocopherol. *Nature* 191, 402.

Kakulas, B.A. (1964). Atypical acid-fast bacillary infection in the Rottnest quokka (*Setonix brachyurus*). Aust. J. Sc. 27, 115-116.

Kitchener, D.J. (1972). The importance of shelter to the quokka, *Setonix brachyurus* (Marsupialia) on Rottnest Island. *Aust. J. Zool.* 20, 281-299.

Main, A.R., J.W. Shield and H. Waring (1959). Recent studies on marsupial ecology. In *Biogeography and Ecology in Australia* (Eds. A. Kreast, R.L. Crocker and C.S. Christian), in *Monographiae Biologicae* (Eds. F.S. Bodenheimer and W.W. Weisbach).

V.8, 315-331.

Moir, R.J., G. Sharman and H. Waring (1954). Ruminant-like digestion in a marsupial. *Nature* 173, 269-270.

Moir, R.J., M. Somers and H. Waring (1956). Studies on marsupial nutrition I. Ruminant-like digestion in a herbivorous marsupial (*Setonix brachyurus* Quoy and Gaimard). *Aust. J. Biol. Sc.* 9, 293-304.

Nicholls, D.G. (1971). Daily and seasonal movements of the quokka, *Setonix brachyurus* (Marsupialia) on Rottnest Island. *Aust. J. Zool.* 19, 215-226.

Sharman, G.B. (1955). Studies on marsupial reproduction 2. The oestrous cycle of *Setonix brachyurus*. *Aust. J. Zool.* 3, 44-55.

Sharman, G.B. (1955). Studies on marsupial reproduction 3. Normal and delayed pregnancy in *Setonix brachyurus*. *Aust. J. Zool.* 3, 56-70.

Storr, G.M. (1964). Studies on marsupial nutrition. IV. Diet of the quokka *Setonix brachyurus* (Quoy and Gaimard), on Rottnest Island, Western Australia. *Aust. J. Biol. Sc.* 17, 469-481.

Waring, H., G.B. Sharman, D. Lovat and M. Kahan (1955). Studies on marsupial reproduction I. General features and techniques. *Aust. J. Zool.* 3, 34-43.

Yadau, M., N.F. Stanley and H. Waring (1972). The microbial flora of the gut of the pouch-young and the pouch of a marsupial, *Setonix brachyurus*. *J. Gen. Microbiol*. 70, 437-442.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS

VI THE BOTTLENOSE DOLPHIN *(Tursiops truncatus)*

by

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ABSTRACT

The precise environment of the bottlenose dolphin *(Tursiops truncatus)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis,* 1982). A diagram developed by H.G. Andrewartha, called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

This paper is part of a larger theoretical study, the methodology for which is set out in A.E.S. Working Paper No.9.

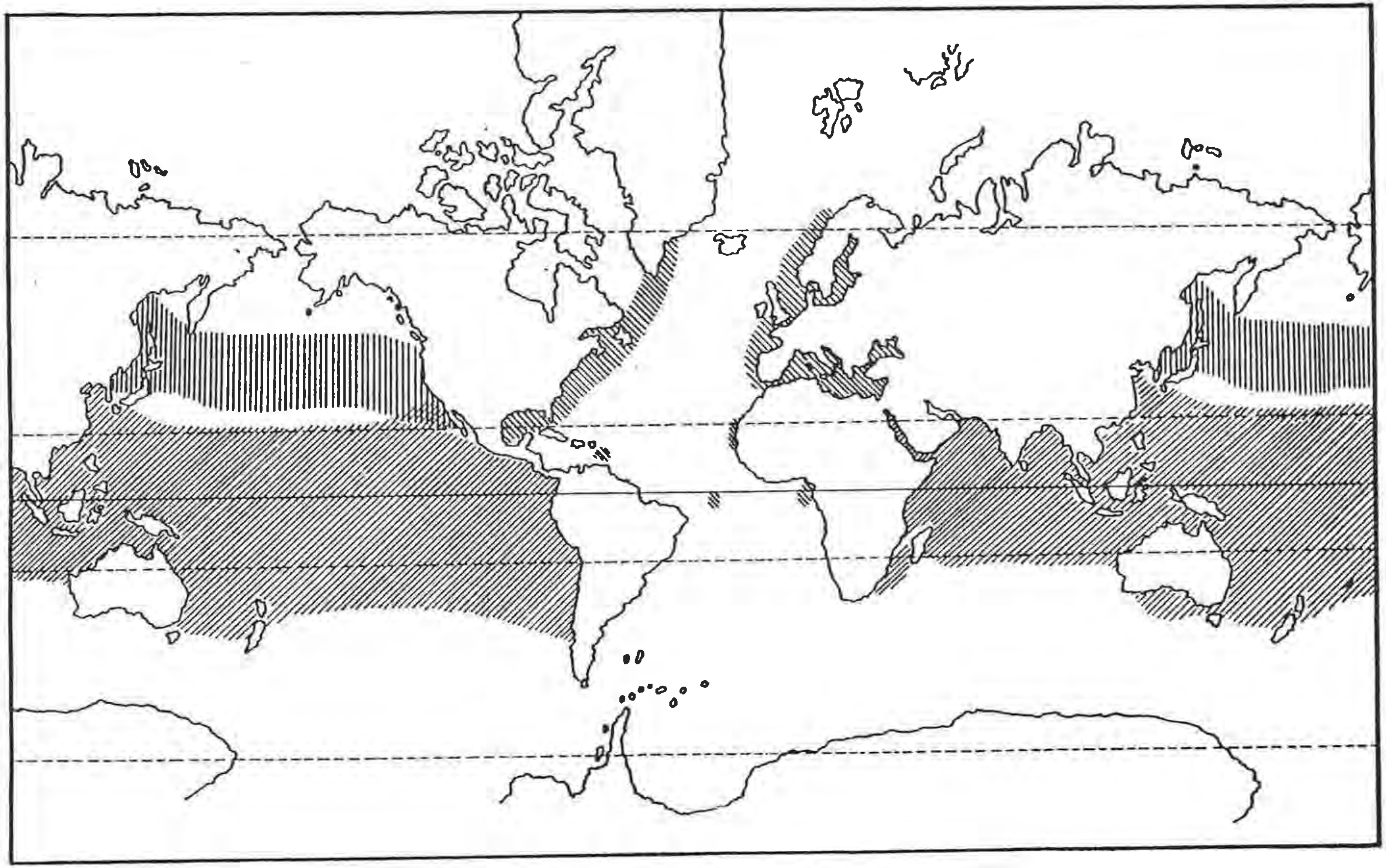


Fig. 38. Distribution of *Tursiops truncatus* (▧ *t. truncatus*, ▨ *t. aduncus*) and *Tursiops gilli* (▥).

CONTENTS

A. INTRODUCTORY NOTE

Various authors have reported migrations by populations of *Tursiops truncatus*, however the majority of more recent authors have concluded that for the particular population under study there is no migration. Extensive on-shore off-shore and coastal movements are recorded but none of these fit a regular or seasonal pattern.

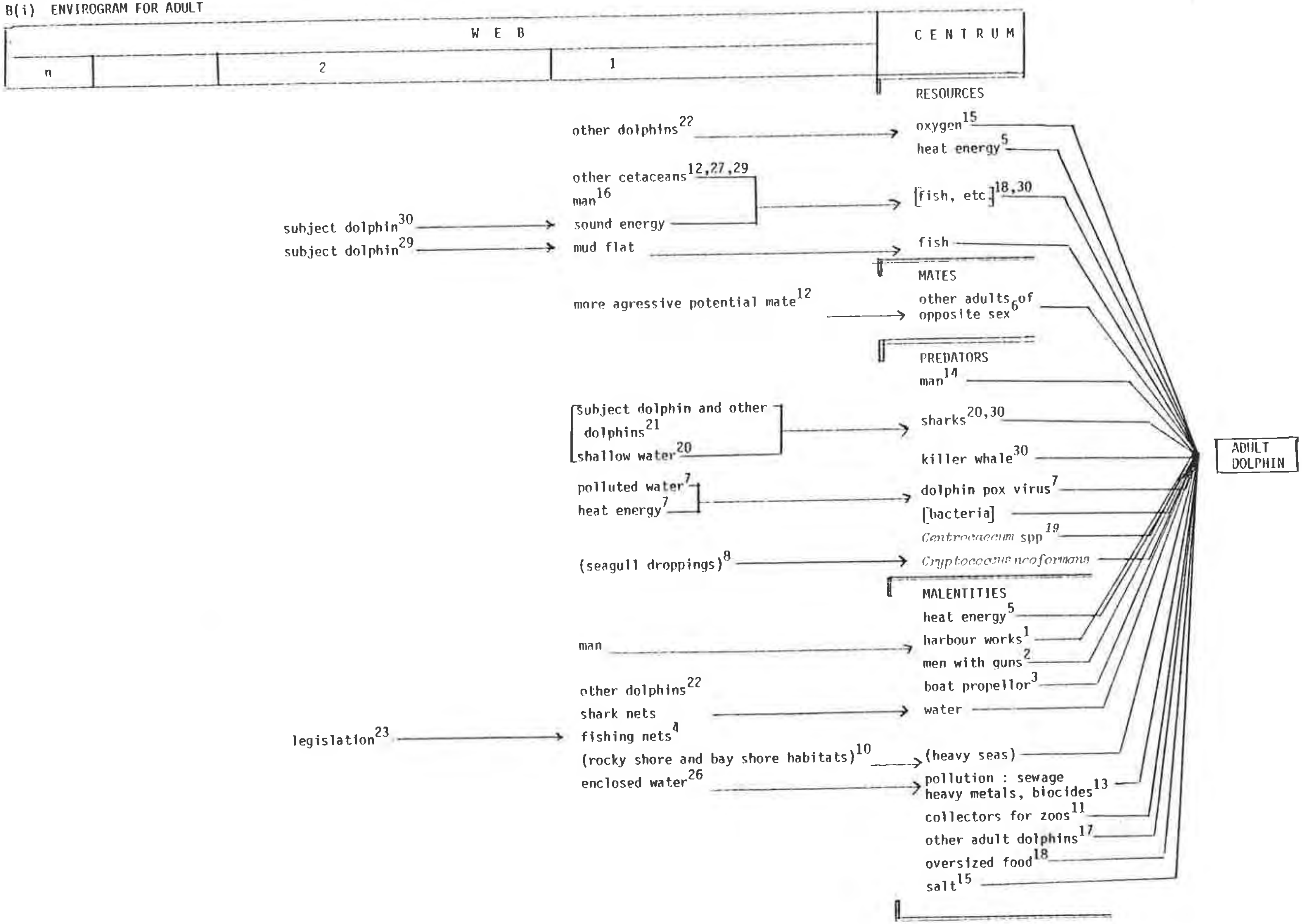
The taxonomy is still uncertain. There are many sharply-defined local populations. We have followed the advice of Dr M.M. Bryden in not differentiating among reported subspecies of *Tursiops truncatus*.

The following quotation, from Chapter 8 in the book by L. Harrison Mathews (1978) is relevant to some of the literature:

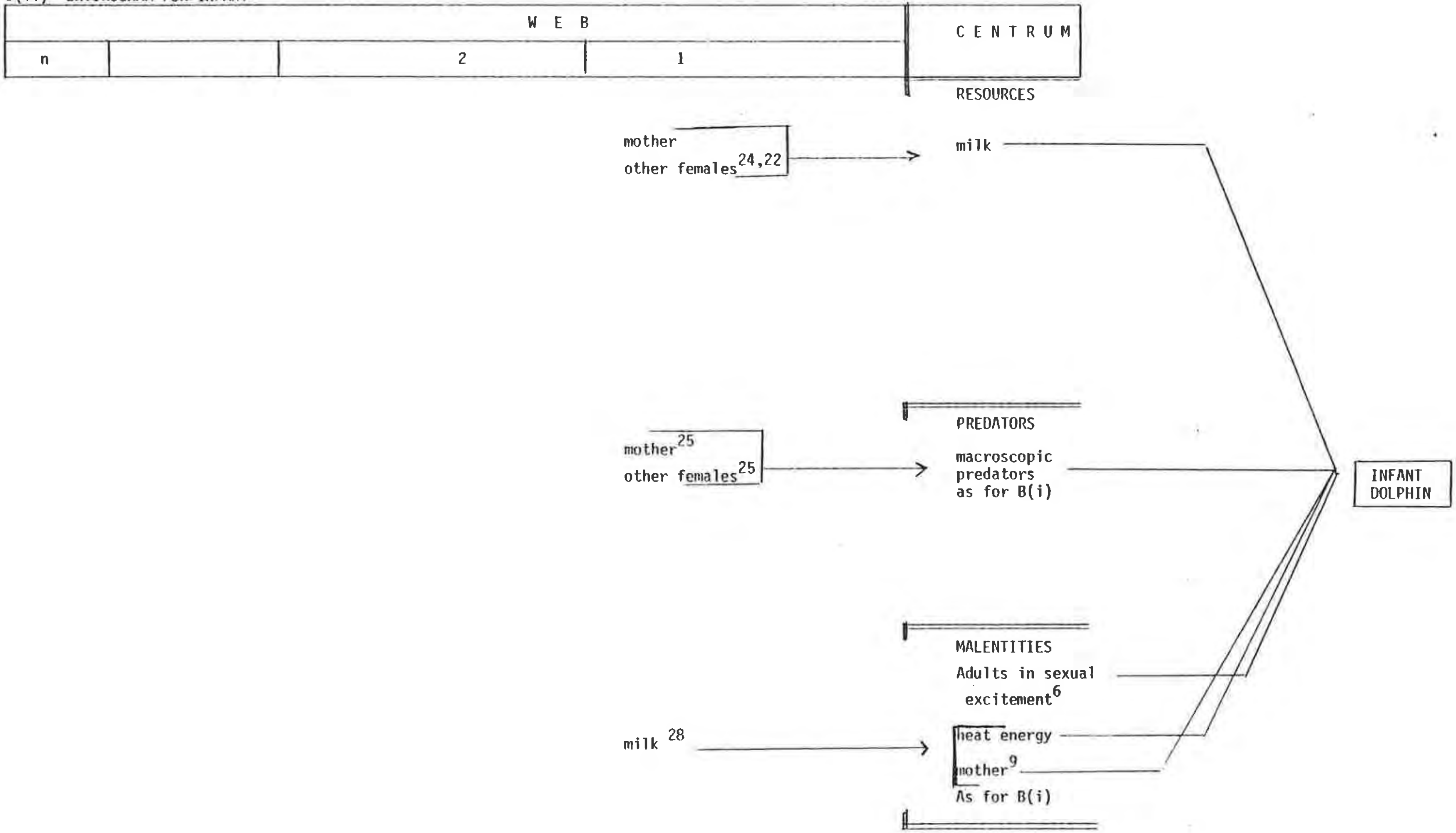
> *"The American cetologist Tavolga, who made the careful observations on the captive dolphins at Marine Studios, has given a necessary warning about the interpretation of cetacean behaviour (200).*
>
> *One of the most deceptive, and therefore one of the most dangerous, pitfalls awaiting the observer of dolphins is reliance on anthropomorphism. The bottlenose dolphin in particular, and many other dolphins in general, have built-in smiles, and exhibit types of behaviour which endear them to the observer. Thus the observer is led to describe the behaviour of the animal in human terms, and ascribe to the animal motives that he cannot be sure are actually there, as he is incapable of seeing inside the mind of the animal to determine its purposes. Some descriptions of dolphin behaviour abound in statements of purpose that can properly be ascribed only to humans. It is sincerely to be hoped that such accounts, most of which are misleading and probably inaccurate, will not gain credence in the literature to the extent that they are believed implicitly by other workers in the field".*

The map is from Marcuzzi and Pilleri (1971). We are indebted to Dr M.M. Bryden for many helpful remarks and for lending us his collection of reprints.

B(i) ENVIROGRAM FOR ADULT



B(ii) ENVIROGRAM FOR INFANT



C. NOTES ON THE ENVIROGRAMS

1. A dolphin disappeared from the vicinity of the Isle of Man after several months in which explosives were used for harbour works (Lockyer, 1978). Construction and dredging are believed to have driven *Tursiops truncatus* completely away from San Diego Bay (Lear and Bryden, 1980).

2. There is circumstantial evidence that a wound observed on one dolphin was caused by gunshot, without any suggestion that the local people might want to shoot the animal for food (Lockyer, 1978).

3. The whole boat is not necessarily a malentity; a dolphin reported by Lockyer (1978) apparently enjoyed "playing" round the boat. This difficult point, suggesting that a dolphin might play for pleasure, seems very similar to the problem of dealing precisely with objects of aesthetic interest in a human's environment; this problem will not be dealt with in these studies, which are restricted to non-human animals (see also section A). Lockyer also reported a dolphin seen to play with a guillemot for half an hour; the bird was unharmed. The surfing by dolphins in front of boats is also often reported as playing behaviour. However the dolphins are able to ride such bow-waves by setting their flukes at 28° to the upthrust water, thus moving without expending energy (Mathews, 1978); this may be an alternative explanation.

4. Dolphins are frequently caught in fishing nets and shark nets and drowned. It ias been observed that particular dolphins (with distinctive markings) learn to avoid fishing nets after being caught once. A dolphin can be safely submerged for at least five minutes.

5. Dolphins are known to inhabit waters with a wide temperature range - at least 8°C to 30°C. We do not know of any studies which have determined the beneficial range, however clearly there will be temperatures in which the animal cannot survive. Normal dolphin body temperature is approximately 38°C.

6. Widely collected data indicate a 1:1 ratio between the sexes. Sergeant *et al* (1973) reported that males attained an asymptotic length of 270cm, becoming sexually mature at 245cm, at a little over twelve years of age. Females attained an asymptotic length of 250cm and were sexually mature at just twelve years, slightly younger than males.

We are unsure of the meaning of 'asymptotic length' here and we do not know if these measurements are consistent with Gunter (1946) who reported a maximum length of twelve feet. An exception to the ages given above for sexual maturity was a captive female who produced her first infant at seven years; it was suggested that this was due to improved nutrition. This young dolphin was, however, a poor mother. (See note 11)

Compared to most mammals *Tursiops truncatus* has low rates of reproduction. The gestation period is usually 12-13 months. These is a marked summer calving season off Argentina (Wursig, 1978). The reason is not known, but the late summer peak for his study group corresponded with the highest water temperature. Wursig also observed high sexual activity during this period. Many others report bimodal calving, eg. McBride and Kritzler (1951) report peaks in autumn (September - December) and spring (March - May) in an acquarium in Florida. Gunter (1946) reported a peak in March off North Carolina.

It is considered likely that females will have one calf a year, or possibly one every two years. However it is often recorded that infant dolphins are weaned between twelve and eighteen months and that mothers lose interest in their yearling infants once their pregnancies are well advanced. This would seem to suggest that a bimodal calving is more likely, with females calving every eighteen months. Where only a single peak is recorded (eg. Wursig, 1978) an individual female may calve only biennually.

In any particular wild population the percentage of calves is usually given as about ten, however Lear and Bryden (1980) reported that calves make up only 1.2% of the population in Moreton Bay, (Queensland), although of those herds that contained calves the average was about 10%.

7. Recurrent bouts of dolphin pox in captivity have been induced by sudden temperature drops and badly filtered water. Dolphin skin has an extremely high turnover of epidermal cells, causing rapid disappearance of superficial scratches or marks - clean superficial wounds often heal within seven days. This property may contribute to the relatively non-contagious nature of dolphin pox.

8. The source of the infection is not known for certain. It has been observed, however, that a close relation exists between *Cryptococcus neoformans* and old pigeon nests and droppings and further that many seagulls roosted near the dolphin's compound. (No tests were done.)

9. Mothers have been known to 'punish' infants slow to respond to their calls, either by holding them down in or out of the water (Lockley, 1979). Since it is not absolutely clear that this is for the good of the infant (eg. safety from sharks) we have classified this behaviour as that of a malentity.

10. Lear and Bryden (1980) suggest that these two habitat types are used by dolphins to shelter from heavy seas. Their study was conducted in Morton Bay (Queensland) which contains three habitat types:

    (i) Rocky shore : reefs, islets and embayments - deep water close to shore.

    (ii) Ocean beach : often heavy surf.

    (iii) Bay shore : sand banks and ridges with occasional deeper channels.

    The density of dolphins was greatest in the Rocky shore habitats, particularly if the area provided protection from the prevailing weather. However, these areas are small and the majority of dolphins were more widely scattered and in the ocean beach habitats, especially the ocean bean habitats near rocky areas.

    Bay shore habitats did not harbour high densities and the dolphins were observed most frequently in shallow water adjacent to deeper channels.

    A second reason suggested for the preference for Rocky shore habitats was their proximity to good feeding areas in deeper water.

11. Collectors for zoos are classified here as malentitives because of the initial shock to the animal. However McBride and Kritzler (1951) comment that animals well-cared for in captivity are almost always heavier than their wild counterparts. Presumably because of better feeding one particular female was observed to mature and bear an infant at an earlier age than is usual in the wild (see note 6).

The selective capture of juveniles and prime breeding animals for use in zoos has an adverse effect on wild populations. This observation is, however, at the population level rather than the individual level.

12. Several authors have claimed that there are social structures analagous to those of the chimpanzees. As in the case of the chimpanzee there seem to be independent dominance heirarchies for males and females but the dominant animal in any one group will be a male. A dominant male or female will show aggression on occasion either over food or during mating behaviour. On these occasions captive dolphins inflict toothmarks, scratches and bruises using either the head to butt or the tail to slap, also there are many skeletons of wild dolphins showing healed rib fractures and broken jaws, the inference being these are the results of similar behaviour in the wild. (Broken jaws could also result from butting sharks.) Swimming formations tend to be layered in ascending order with dominant animals at the top.

13. Pollution is a serious problem for small whales. All the following areas show declining numbers of dolphins : Baltic, Bay of Fundy, European coasts, Mediterranean Sea, Azov Sea, Gulf of Mexico. Sewage, construction and dredging are believed to have eliminated *Tursiops truncatus* from San Diego bay.

14. Man is a predator of dolphins for various reasons :

    (a) for anatomical and biological research etc;
    (b) in Spain and Japan the animal is eaten;
    (c) Gunter (1951) records that farmers on the Gulf coast of the United States have been known to use harnesses made of dolphin leather in farm work. Because the leather is very oily it tends not to stiffen during the hot rainy season.

15. Dolphins can tolerate water with high vegetation and low oxygen contents as in Texas back bays. They can also tolerate a broad range of salinities, from brackish water to the high salinity of the Red Sea. As with heat energy (see note 5) there will be a range of salinities outside of which dolphins cannot survive.

16. Fishing, especially commercial fishing, tends to deplete food supplies and consequently reduce the size of the dolphin population. This has been recorded specifically for the Texas coast.

17. Gunter (1946) reported that dolphins in captivity fight; scars which could have been caused by fighting other dolphins have been observed in wild populations.

18. Gunter (1946) concluded, on the basis of examination of stomach contents (see Section D) that *Tursiops truncatus* is predominantly a benthic rather than a pelagic feeder. Tooth wear is consistent with taking animals directly from the substrate. Lear and Bryden (1980) suggest that dolphins also dig in the substrate. Support for this suggestion comes from Leatherwood *et al* (1978) who found sand and small rocks included in stomach contents. In addition fish are nearly always swallowed whole.

    The stomach of a fully grown animal weighs about 18kg when fully packed. In captivity an adult will eat approximately 36kg of food per day. Hotta *et al* (1970) reported that the weight of stomach contents for wild dolphins was well below that of captive dolphins; their estimate of the average consumption of food by a wild dolphin was 11.857kg/day.

    Fish are nearly always swallowed whole, there being no teeth-marks, indicating that teeth are not worn in the course of normal eating. This seems to hold irrespective of the size of the fish; Gunter recorded a case of a dolphin dying from the effects of trying to swallow a four-foot shark whole. They swallow shrimps whole and are known to tear shrimp nets in the Gulf of Mexico to reach the catch.

    The fact that certain small fish, eg. the Puffer and the Needle-Gar, were eaten (see Table M Section D) is surprising and indicates the dolphin's catholic taste in fish.

19. Every dolphin captured by Gunter (1946) was infested with parasitic round worms of this genus, which is also found in other mammals and in fish-eating birds.

20. Sharks and dolphins attack each other, however Wood *et al* (1970) suggest that sharks are usually the aggressors. Many dolphins bear the appropriate crescent-shaped bite scars. Most recorded instances have been in shallow water; two reasons are suggested:

    (i) shallows do not allow dolphins to use all of their superior manoevreability

    (ii) accidental clashes occur in the shallows when both species are feeding on the same schools of fish, because of the murkiness of the water

21. Dolphins have been known to kill sharks in the wild by repeated butting with their hard beaks. The sharks are invariably not eaten so it seems that this is a protection against predation. Wood *et al* (1970) record a case of a group of obviously tired *Delphinus delphinus* forming a protective circle (under a boat) with the young in the centre. They repeatedly repulsed shark attacks although many were badly wounded. Similar well-substantiated cases have been recorded for *Tursiops truncatus*.

    There are also, however, many recorded cases of mutual toleration, both in acquaria and in the wild. There are also cases in which cetaceans of different species, though usually of the same size, form mixed herds (see note 27). This may be associated with some of the factors mentioned above.

22. There is a considerable body of evidence showing that a dolphin will aid and distressed dolphin by pushing it to the surface and supporting it so that it can breathe. The following quotation is from Chapter 8 in the book by L. Harrison Mathews (1978):

    > *"Apart from the care given by female cetaceans to the welfare of their young, which was for long exploited by whalers through killing a calf in order the more easily to kill the mother who lingered near it, and the solicitous behaviour seen among captive dolphins, there is another type of care-behaviour shown by the odontocetes. The former, known as nurturant behaviour, is almost universal among the mammals, but the latter,*

or succorant behaviour, in which help is given to an adult in distress, is extremely rare. The American cetologists M.C. and D.K. Caldwell have classified this kind of behaviour in the odontocetes into three types (30). The first, which they call'standing by' - the old whalers called it 'heaving to' and similar nautical names - is shown by a school remaining near or approaching the neighbourhood of a distressed or wounded companion but without giving any assistance. This occurs under conditions that would be expected to lead to alarm and flight; it is sometimes seen also in land mammals, particularly in gregarious species. The second, 'excitement', consists of approaching a comrade in distress and showing evidence of unusual excitement and of distress in the succorant animals. The succorants may even attempt a rescue of the animal in trouble, and this has been particularly noticed in Sperm whales which have been known to attack whale boats that have harpooned a companion, or to push an injured animal away from the source of danger.

The most remarkable is the third, 'supporting behaviour', in which one or more companions support the distressed animal at the surface. This type of behaviour can only occur among cetaceans, which must come to the surface at comparatively short intervals to breathe; in contrast land mammals do not drown however badly they may be injured. The supporting of a distressed odontocete by its companions must surely be an extension of the maternal behaviour of a mother towards its young at birth. The mother pushes the newborn young up to the surface so that it can draw its first breaths, and is often assisted by her companions who appear to be solicitous to help in this early care of the infant animal. It is evidently a strong instinct, or 'innate behaviour pattern', as instinct is now called for short, that causes a cetacean to help another that appears to have difficulty in breaking surface to breathe. It is extraordinary that this kind of behaviour is sometimes given to creatures other than cetaceans.

Many instances have been recorded in which a human swimmer in distress has been helped by dolphins to reach the surface and avoid being drowned. Some at least of these occurrences

> *are properly authenticated and are not merely the legends of folklore. To a dolphin a man struggling in the sea must appear to be the most helpless and inefficient swimmer, so that the instinct to help a companion in need of succour is easily transferred to the distressed human being. This phenomenon has been cited as confirming the alleged intelligence of cetaceans; but were they intelligent they would not aid man, who for the greater part has been a ruthless destroyer of dolphins for centuries. They should rather pull a human swimmer in difficulties down to death by drowning instead of helping him up to life.*
>
> *There are no grounds, however, for imputing any use of intelligence in such acts, nor even for supposing that the animals know what they are doing. There is no proof that any intention to achieve a specific end is involved and the actions can be regarded as no more than instinctive reactions released by the right stimulus of seeing an object not behaving normally for a dolphin. This view is supported by the behaviour of a captive dolphin that spent many hours pushing a dead shark to the surface."*

23. The Marine Mammal Protection Act 1972 (USA) is in part aimed at reducing the large numbers of dolphins drowned during fishing operations in United States waters.

24. A foundling infant, introduced into a tank of captive dolphins, attempted to feed from and was accepted by a pregnant female. She showed the slowed swimming-stroke characteristic of nursing mothers, but was unable to supply milk, so that the infant died. This raises the possibility that a foundling in the wild may be fortunate enough to be accepted by an already nursing mother. Infant dolphins achieve high growth-rates because of the high protein content of dolphin milk.

The table below is from Arvey (1973-74)

Table 12. Comparison of milk from *Tursiops, Stenella and Homo* (in g/L)

Species	Water	Proteins	Lipids	Sugar
Tursiops truncatus	713.7	96.4	167	7.73
Tursiops truncatus	674.2	-	148	-
Tursiops truncatus (at end of lactation)	755.5	111.1	108	3.88
Stenella pernettyi	689.8	94.2	180	6.30
Human	874.1	22.8	37.6	62.9

Young dolphins are not fully weaned until 18 months.

25. Infant dolphins always follow their mothers in a protected position just above and just behind the dorsal fin. If another mature female is in the group she will often swim beside the mother, with the infant between them. Mothers with or without protecting females usually swim in the centre of any group (see also note 22).

26. Biocides and heavy metals are especially dangerous in enclosed waters because of the long turnover time (of the water) so that concentrations tend to be maintained. The Mediterranean Sea, the Black Sea and Morton Bay (Queensland) are examples of such areas.

27. Particularly at sea schools of one species of cetacea may contain one or more individuals of another species; the two species will usually be of similar size. Frazer (1976) suggests that this behaviour is due to both a need for companionship and the fear of larger species. Mixed herds often occur after the different species have been feeding on the same prey. Kraus and Gihr (1971) record a particular case in which a dolphin was present in a school of Northern Pilot Whales *(Globicephala melaena)*; the dolphin had scars around its head clearly caused by cephalopods (presumably when being eaten), a standard diet of the Pilot Whale, although the normal diet of the dolphin is almost exclusively fish. The implication is that the intruder, in this case the dolphin, will modify its diet because of the presence of the other species.

28. Cetacean milk is highly calorigenic:
Calories/100gms of milk are:

for cows - 60
for humans - 65
for whales (*Balenoptera physalus*) 300-350

This heat production is essential because cetacean infants are born without blubber and without extra heat they would die (Arvey, 1973-74).

29. Several authors are of the opinion that dolphins cooperate in feeding eg. Saayman *et al* (1972) record large schools of dolphins (up to 500) apparently feeding cooperatively by herding pelagic fish from the open sea into shoals. Such activity had peaks in the early morning and late afternoon.

The study by Lear and Bryden (1980) indicated that the size of groups of dolphins tends to get progressively larger out to sea and it is suggested that cooperative feeding may be the reason.

L. Harrison Mathews (1978) records the following unusual case of cooperation:

> *"One might think that it would be impossible for a cetacean to leave the water and catch its food on the land, yet such a happening has indeed been recorded. In 1964 and 1966 H.D. Hoese found Bottle-nosed dolphins inhabiting a tidal creek draining a salt marsh near Boboy Sound, Georgia, where there are plenty of small fish during the summer months. The dolphins entered the creek at every low tide to feed, presumably finding the fish in the muddy water by echolocation. In the autumn and spring the fish were fewer, so the dolphins hunted in pairs apparently to round up the small shoals and drive them to the edge of the water, whereupon they suddenly rushed up the bank together, usually both on the right side and pushing a large bow wave ahead that broke on the bank immediately before them. At each rush the wave carried with it several fishes 3-4 inches long, which were stranded and eaten by the dolphins when the wave*

> *broke. Usually the whole body of the dolphins came out of the water, sometimes with the tail flukes as well, and the animals quickly picked the fish off the mud and then slid back down the slippery bank. Hoese noted the remarkable mobility of the neck of the dolphins when they caught the fish 'with several surprisingly agile biting movements of the head' and added 'it is difficult to understand why such an apparently agile animal cannot capture fish in the water once the prey is congregated in a school'. This manoeuvre that the dolphins had invented was possible only for a short time each tide when enough of the banks was exposed to allow the fish to be stranded and the dolphins to slide back. It was no isolated instance, but a regular habit often seen during two years, and perhaps a local 'tradition' learned by younger ones imitating the older ones."*

30. Hearing is the dolphin's most important sense; this includes its ability to hear ultrasonic sounds, including self-generated signals while ecolocating. The mechanism for transmitting and receiving is not yet completely understood. It has been suggested that cetaceans may be able to hear sounds made as far away as 330km.

Dolphins characteristically exhibit behaviour described as 'auditory glancing', i.e. producing short bursts of ultrasonic sounds at approximately 20-second intervals without any immediate stimulus. A splash, whether or not accompanied by an object, will trigger ecolocation among captive dolphins. They can detect an object only 4 1/3mm in diameter and experiments seem to indicate that they can accurately detect the size and shape of fish. Ecolocation is extremely accurate for position, prey and potential hazards. It has so far proved impossible to block or jam the dolphin's ecolocation sounds, even by playing back recordings made by the same dolphin.

While the causes of cetacean strandings are not always apparent at least three conditions which may produce disorientation or incoordination have been noticed; each has a significant effect on auditory response and ecolocation:

(i) Sinuses of stranded cetaceans are frequently infested with nematodes.

(ii) Cerebral and cerebellar abscesses are observed to contain trematode ova. Also reported is one cerebral abscess due to *Staphylococcus aureus*.

(iii) Trematodes are attracted to the round window of the ear, eg. a fluke of the family Nasitrematidae Yamaguti 1951.

D. DETAIL

Food Resources

The following table is from Lear and Bryden (1980); the study area was Morton Bay in Queensland.

Table 5

Stomach contents of *Tursiops truncatus* accidentally drowned in the Specific Study Area

Species	Frequency in stomach	Habitat
(a) BONY FISH		
Tailor (*Pomatomus saltatrix*) (Pomatomidae)	uncommon	surface and midwater
Sand Mullet (*Myxus elongatus*)	common	surface and shallows
Diamond-scaled Mullet (*Mugil vaigensis*) (Mugilidae)	common	surface and shallows
Sea-pike *Sphyraena* sp. (Sphraenidae)	uncommon	surface and midwater
Scorpaenid (Scorpaenidae)	uncommon	bottom-dwelling
(b) CEPHALOPODS		
* Squid 2 species?	common	midwater
* Octopus	uncommon	bottom-dwelling

* awaiting identification

The following table is from Gunter (1946). The study area was off the coast of Texas.

Table 2. The numbers and species of the fishes taken from the stomachs of twenty-nine bottlenose dolphins taken in Texas waters.

NUMBER	SPECIES	COMMON NAME
423	*Mugil cephalus* Linnaeus	Striped Mullet
40	*Dorosoma cepedianum* Le Sueur	Gizzard Shad
3	*Sphoeroides marmoratus* (Ranzani)	Puffer
2	*Archosargus probatocephalus* (Walbaum)	Sheephead
1	*Strongylura marina* (Walbaum)	Needle-gar
1	*Pogonias cromis* (Linnaeus)	Black Drum
1	*Cynoscion nebulosus* (Cuvier & Valenciennes)	Spotted Trout
1	*Cynoscion arenarius* Ginsburg	Sand Trout
1	*Paralichthys lethostigmus* Jordan & Gilbert	Flounder
(12?	*Leiostomus xanthurus* Lacépède	Spot
* (12?	*Micropogon undulatus* (Linnaeus)	Croaker
(12?	*C. arenarius*	Sand Trout
1	*Penaeus setiferus* (Linnaeus)	Shrimp

The last thirty-six fish were all taken from one animal. There were 17.6 fish to a stomach (range 3 to 52) and 83.1 percent of the number devoured were mullet. Some of the mullet may have been *Mugil curema* Cuvier and Valenciennes, but all those distinguished were *M. cephalus*.

* These 36? fish were all taken from the stomach of the one dolphin in the sample that was captured in deep water.

In addition, the dolphin has been recorded by various authors as eating:

Spanish mackeral (*Scomberomorus maculatus*)
King Fish (*S. regalis*)
Tarpon (*Tarpon atlanticus*)
Sailfish (*Istiophorus americanus*)
Hammerhead shark (*Sphyrna zygaena*), caught on a handline and decapitated by *Tursiops truncatus* when being hauled in.

Pike or Roballo (*Centropomus undecimalis*)

Spotted eagle ray (*Stoasodon narinari*)

Sea catfish (*Galeichthys felis*) - bodies anterior of dorsal fin only; heads left floating in the water.

Squeteague (*Cynoscian regalis*)

Mummichog (*Fundulus heteroclitus*)

Hake (*Urophycis* spp.)

Silver perch (*Bairdiella chrysura*)

Atlantic menhaden (*Brevoortia tyrannus*)

Mojarra (*Eucinostomus* spp.)

Molluscs

Squid (*Loligo pealei*)

Unidentified shell fragments

Hermit crabs

Algae

Inverterbrate larvae

Jelly fish

* * * * * * *

PREDATORS

Pox virus

Cryptococcus neoformans

Erysipelothrix rhusiopathiae)
Streptococcus spp.) - cutaneous lesions

Escherichia coli - lungs

Staphylococcus from blowhole, also *S. aureus* reported as causing a cerebral abscess. (Lice of the genus *Syncyamus* have been found; we are not certain as to whether they should properly be classified as predators.) Fluke of the family Nasitrematidae Yamaguti attached to round window of the ear.

Blubberhelminths (cutaneous parasites)
Digestive tube parasites including *Pholeter* which causes gastric trematodiasis. Larvae of Phyllobothriadae : *Monorygme* inhabits the mesentary and peritoneum, while *Phyllobothrium physeteris* and *P. delphini* cysts are found all over the body.

Crassicaudata crassicaudata in kidneys and penis
(*Xenobalanus globicipitis* Steenst up has been observed on
Tursiops truncatus; their function is unknown.)

The following tables are from Murray and Brownell (1976)

Tursiops truncatus (Bottlenosed Dolphin)

Trematoda

Braunina cordiformis, (Wolf, 1903); Delyamure, 1955
- *Nasitrema sp.*, *Neiland, et al.* (1970)
Synthesium tursionis, (Marchi, 1873); Baylis, 1932
Zalophotrema hepaticum, (Stunkard and Alvey, 1929); Brown,*et al*, 1960

Cestoda

Diphyllobothrium sp;, Delyamure, 1955
Monorygma delphini, (Gervais, 1847); Baylis, 1932
Monorygma grimaldii, (Moniez, 1889); Delyamure, 1955
Phyllobothrium delphini, (Bose, 1802); Baylis, 1932

Nematoda

Anisakis simplex, Delyamure, 1955 (some as *Anisakis tursionis*, Crusz 1946)
Halocercus lagenorhynchus (Baylis and Daubney, 1925); Delyamure,1955
Stenurus ovatus (Linstow, 1910); Baylis, 1932
Crassicauda crassicauda (Creplin, 1829); Baylis, 1932.

Acanthocephala

Corynoroma cetaceum (Johnston and Best, 1942) - Delyamure, 1955

ECTOPARASITES AND EPIZOITES ON CETACEANS

A wide variety of organisms are found attached to cetaceans, ranging from diatoms to lampreys and whalesuckers. No summarised host records are given, but the following groups and genera are reported from cetaceans:

Diatoms

Cocconeis ceticola and species of *Gyrosigma, Licmophora, Navicula Plumosigma, and Stauroneis* (Hart, 1935; Nemoto, 1956 and 1958)

Sessile Barnacles

Coronula, Cryptolepas, Tubicinella, and *Xenobalanus*
(Thoracica: Balanidae)
(Dollfus, 1968; Ross and Newman, 1967)

Stalked Barnacles

Conchoderma auritum and *Conchoderma virgatum*
(Thoracica: Lepadidae)
(Clarke, 1966; Perrin, 1969)

Copepod

Balaenophilus, Penalla, and *Harpacticus*
(Caligoida: Lernaeoceridae)
(Humes, 1964; Rice, 1963)

Whalelice

Cyamus, Isocyamus, Neocyamus, Platycyamus, and *Syncyamus*
(Amphipoda: Cyamidae)
(Leung, 1965 and 1967)

Lampreys

Lampetra and Petromyzon
(Hyperoartii: Petromyzontidae)
(Nemoto, 1955; Pike, 1951; Utrecht, 1959)

Whalesucker or Remora

Remora australis
(Discocephali: Echineididae)
(Follett and Dempster, 1960; Rice and Caldwell, 1961; Radford and Klawne, 1965)

CETACEA

Trematoda	Locality in Hosts
Family Fasciolidae	
Fasciola	Liver
Family Campulidae	
Campula	Liver

Lecithodesmus	Liver
syn. *Hadwenius*	Intestine
Leveasiella	Intestine
Odhneriella	Liver
Orthosplanchus	Liver
Oschmarinella	Liver
Zalophotrema	Liver
Synthesium	Intestine
Hunterotrema	Lung
Family Ratziidae	
Cychlorchis	Liver
Family Troglotrematidae	
Pholeter	Stomach
Family Opisthorchidae	
Nasitrema	Air sinuses
Opisthorchis	Bile ducts
Amphimerus	Not indicated, bile ducts (?)
Delphinicola	Bile ducts
Family Echinostomatidae	
Echinochasmus	Intestine
Family Herterophyidae	
Galactosomum	Intestine
Family Notocotylidae	
Ogmogaster	Intestine
Family Brauninidae	
Braunina	Stomach and intestine

Cestoda	Locality in Hosts
Family Tetrabothriidae	
Tetrabothrius	Intestine
Anophryocephalus	Intestine
Priapocephalus	Intestine
Strobilocephalus	Intestine (rectum)
Trigonocotyle	Intestine

Family Diphyllobothriidae	
Diphyllobothrium	Stomach and intestine
Diplogonoporus	Intestine and liver
Hexagonoporus	Intestine
Family Phyllobothriidae	
Phyllobothrium	Blubber
Monorygma	Abdominal cavity

Nematoda	Locality in Hosts
Family Pseudaliidae	
Pseudalius	Lungs, heart
Delamurella	Lungs (trachea)
Halocercus	Lungs
Otophocaenurus	Air sinus
Pharurus syn. *Torynurus*	Lungs, heart, air sinus
Pseudostenurus	"Accessory nasal cavity"
Skrijabinacius	Lungs
Stenurus	Air sinus, lungs, heart
Family Heterocheilidae	
Anisakis	Stomach, intestine
Contracaecum	Stomach, intestine
Pseudoterranova	Stomach
Phocanema	Stomach
Porrocaecum	Stomach
Family Crassicaudidae	
Crassicauda	Kidneys, muscle, urogenital system
Placentonemma	Placenta, mammary gland, subdermis

Acanthacephala	Locality in Hosts
Family Polymorphidae	
Corynosoma	Intestine, stomach
Bolbosoma	Intestine

The following sharks have been recorded as having *T. truncatus* remains in the stomach (Wood *et al.*, 1970):

Tiger shark *(Galeocerdo cuvieri)*
Dusky shark *(Carchartinus obscurus)*

Bull shark *(C. leucas)*
Greenland shark *(Somniosus microcephalus)*

Also various Australian sharks.

The killer whale *Orcinus orca* has also been recorded as a predator.

E. REFERENCES

A useful bibliography is that of D. Truitt: *Dolphins and porpoises: a compreshensive, annoted bibliography of the smaller cetacea.* (Gale Research Co., Detroit, 1974).

Arvy, L. (1973-4). Mammary glands, milk and lactation in cetaceans. In Pilleri (Ed.), Vol. 5, 157-202.

Arvy, Lucie (1973-4). The kidney, renal parasites and renal secretions in cetaceans. In Pilleri (Ed.), Vol. 5, 231-310.

Caldwell, D.K. (1955). Evidence of home range of an Atlantic bottlenose dolphin. *J. Mammaology* 36 (2), 304-305.

Colgrove, G.S. and G. Migaki (1976). Cerebral abscess associated with stranding in a dolphin. *J. Wildl. Dis.* 12 (2), 271-274.

Contos, S.M. (1973). The porpoise and the tuna - tale of two species. *M.T.S. Journal* 7 (5), 3-7.

Dailey, M.D. and S.H. Ridgway (1976). A trematode from the round window of an Atlantic bottlenosed dolphin's ear. *J. Wildl. Dis.* 12 (1), 45-47.

Flom, J.O. and E.J. Houk (1979). Morphologic evidence of pox virus in tattoo lesions from captive bottlenose dolphins *(Tursiops truncatus). J. Wildl. Dis.* 15 (4), 593-596.

Frazer, J.F.D. (1976). Herd structure and behaviour in cetaceans. *Mammal Rev*, 6 (1), 55-59.

Geraci, J.R., B.D. Hicks, D.J. St. Aubin (1979). Dolphin pox: a skin disease of cetaceans. *Can. J. Comp. Med.* 43 (4), 399-404.

Gunter, G. (1946). Contributions to the natural history of the bottle-nose dolphin *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits.

Gunter, G. (1951). Consumption of shrimp by the bottle-nosed dolphin. *J. Mammalogy* 32 (4), 465-466.

Hall, N.R., R.D. Schimpff, J.C. Woodard, C.C. Carleton and R.T. Goldston (1977). Intracerebral hemorrhage in a bottle nosed dolphin *(Tursiops truncatus). J. Wildl. Dis.* 13 (4), 341-345.

Hotta, H., H. Mako, K. Okada, and U. Yamada (1970). On the stomach contents of dolphins and porpoises off Kyushu. *Bull. Seikai Reg. Fish. Res. Lab.*, 37, 71-85.

Kellogg, W.N. (1961). *Porpoises and sonar.* (University of Chicago Press).

Kraus, C. and M. Gihr (1971). On the presence of *Tursiops truncatus* in schools of *Globicephala melaena* off the Faeroe islands. In Pilleri (Ed.), Vol. 3, 180-183.

Lear, R.J. and M.M. Bryden (1980). A study of the bottlenose dolphin *Tursiops truncatus* in eastern Australian waters. *Aust. National Parks and Wildlife Service,* Occasional Paper No. 4.

Leatherwood, S., M.W. Deerman and C.W. Potter (1978). Food and reproductive status of nine *Tursiops truncatus* from the northeastern United States coast. *Cetology* 28 (April).

Lockley, R.M. (1979). *Whales, dolphins and porpoises.* (Methuen).

Lockyer, C. (1978). The history and behaviour of a solitary, wild, but sociable bottlenose dolphin *(Tursiops truncatus)* on the west coast of England and Wales. *J. Nat. Hist.* 12 (5), 513-528.

McBride, A.F. and H. Kritzler (1951). Observations on pregnancy, parturition and post-natal behaviour in the bottlenose dolphin. *J. Mammalogy* 32 (3), 251-266.

Marcuzzi, G. and G. Pilleri (1971). On the zoogeography of cetacea. In Pilleri (Ed.), Vol. 3, 101-170.

Mathews, L. Harrison (1978). *The Natural History of the Whale.* (Columbia University Press, New York).

Migaki, G., R.D. Gunnels and H.W. Casey (1978). Pulmonary crypotcoccosis in an Alantic bottlenosed dolphin *(Tursiops truncatus). Lab. Anim. Sci.* 28 (5), 603-606.

Migaki, G., J.C. Woodard and R.T. Goldston (1978). Renal adenoma in an Atlantic bottlenosed dolphin *(Tursiops truncatus). Am. J. Vet. Res.* 39 (12), 1920-1921.

Murray, D.D. and R.L. Brownell (1976). A checklist of marine mammal parasites. In S.H. Ridgway (Ed.), *Mammals of the sea: biology and medicine.* (Charles C. Thomas).

Pilleri, G. (Ed.) (1969---1978). *Investigations on Cetacea*, Vols, 1, 2, ---9. (Berne, Switzerland).

Pilleri, G. (1970). *Xenobalanus globicipitis* Steenstrup on *Delphinus delphis, Stenella styx* and *Tursiops truncatus* of the western Mediterranean. In Pilleri (Ed.) Vol. 2, 248-249.

Puente, A.E. and D.A. Dewsbury, (1976). Courtship and copulatory behaviour of bottlenosed dolphins *(Tursiops truncatus). Cetology* 2, 1-19.

Saayman, G.S., D. Bower and C.K. Tayler (1972). Observations on inshore and pelagic dolphins on the Southeastern Cape Coast of South Africa. *Koedoe* 15, 1-24.

Sergeant, D.E., D.K. Caldwell and M.C. Caldwell (1973). Age, growth and maturity of bottlenosed dolphin *(Tursiops truncatus)* from northeast Florida. *J. Fisheries Research Board of Canada,* 30 (7), 1009-1011.

Sergeant, D.E. and I. Stirling (1976). Comments on objectives of marine mammal management. *Advisory Committee on Marine Resources Research. Scientific Consultation on Marine Mammals* ACMRR/MM/Cmt 1, July 1976. (F.A.O. of the U.N.)

Streitfeld, M.M. and C.G. Chapman (1976). Staphylococcus aureus infections of captive dolphins *(Tursiops truncatus)* and oceanarium personnel. *Am. J. Vet. Res.* 37 (3), 303-305.

Wood, F.G., D.K. Caldwell and M.C. Caldwell (1970). Behavioural interactions between porpoises and sharks. In Pilleri (Ed.), Vol. 2, 264-277.

Wursig, B. (1978). Occurrence and group organization of Atlantic bottlenose porpoises *(Tursiops truncatus)* in an Argentine Bay. *Biol. Bull (Woods Hole),* 154 (2), 348-359.

Wursig, B. and M. Wursig (1979). Behaviour and ecology of the bottlenosed dolphin, *Tursiops truncatus*, in the South Atlantic. *U.S. Natl. Mar. Fish. Serv. Fish. Bull.* 77 (2), 399-412.

Anon. (1976). Mammals in the seas. Advisory Committee on Marine Resources Research *ad hoc* Group II - Small Cetaceans and Sirenians. Report, Supp. 1. ACMRR/NM/SC/3 Suppl. 1 June 1976. Food and Agricultural Organization of the United Nations.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS
III THE MOUNTAIN GORILLA *(Gorilla gorilla beringei)*

by

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ABSTRACT

The precise environment of the mountain gorilla *(Gorilla gorilla beringei)* is given, using as a basis for the classification the defining equations of Niven (*Erkenntnis*, 1982). A diagram developed by H.G. Andrewartha called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

CONTENTS

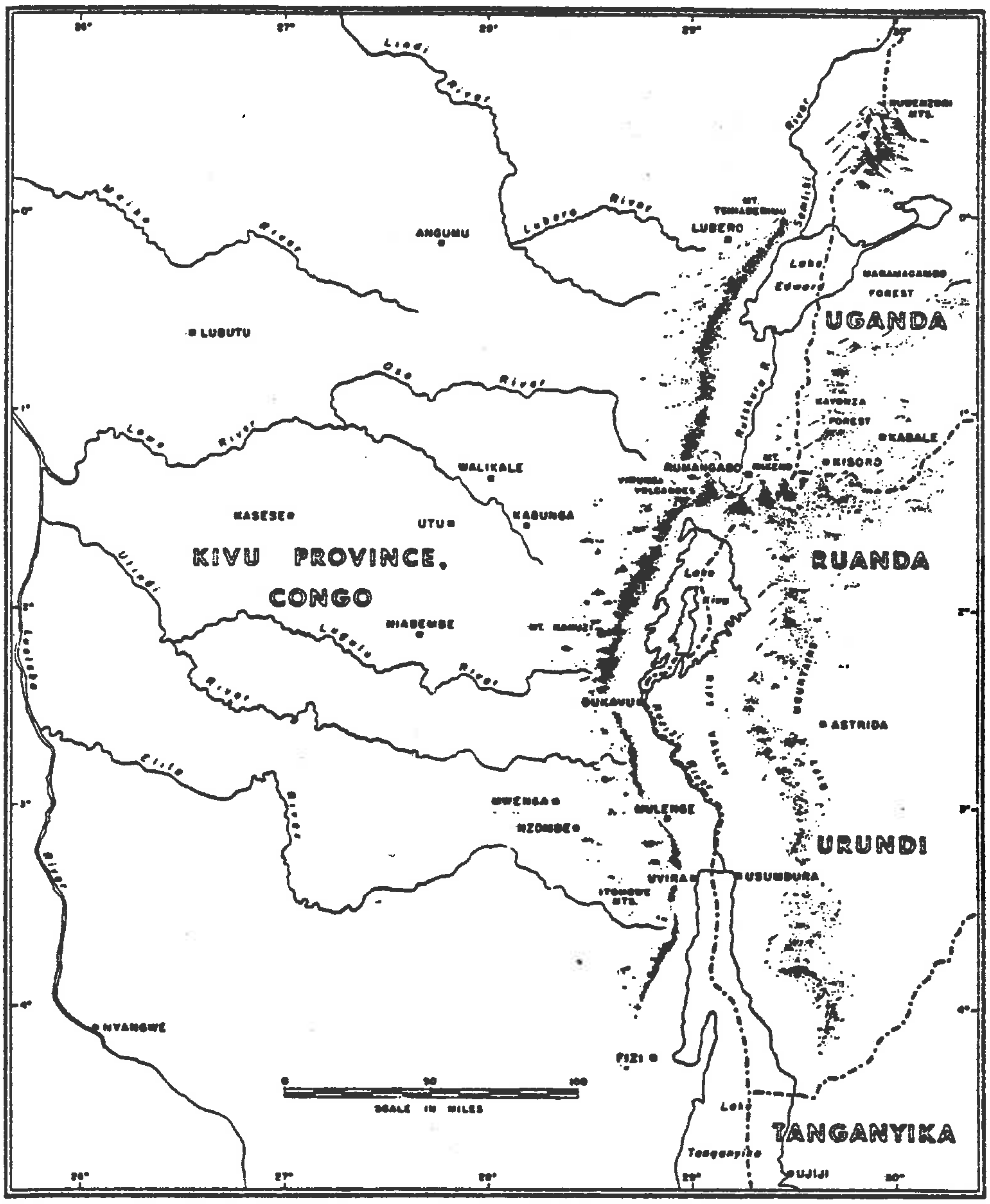


FIG. 1.—Regional map of the eastern Congo, western Uganda, and western Ruanda-Urundi, showing the major physical features in the range of the mountain gorilla.

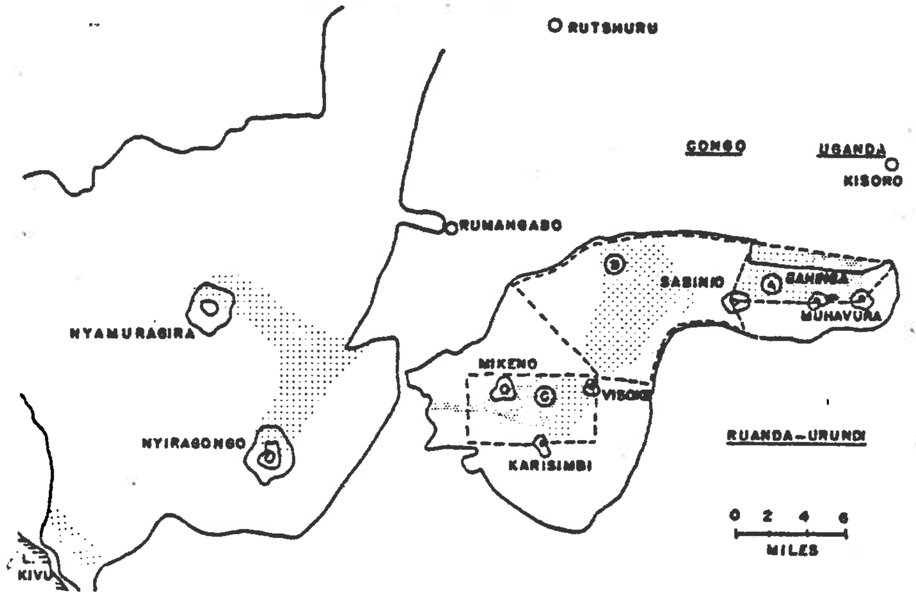


FIG. 6.—The southern sector of Albert National Park, Congo, which comprises the Virunga Volcanoes.

——— Albert National Park boundary

▭ Areas of intensive study

(From G.B. Shaller: *The Mountain Gorilla. Ecology and Behaviour*).

A INTRODUCTORY NOTE

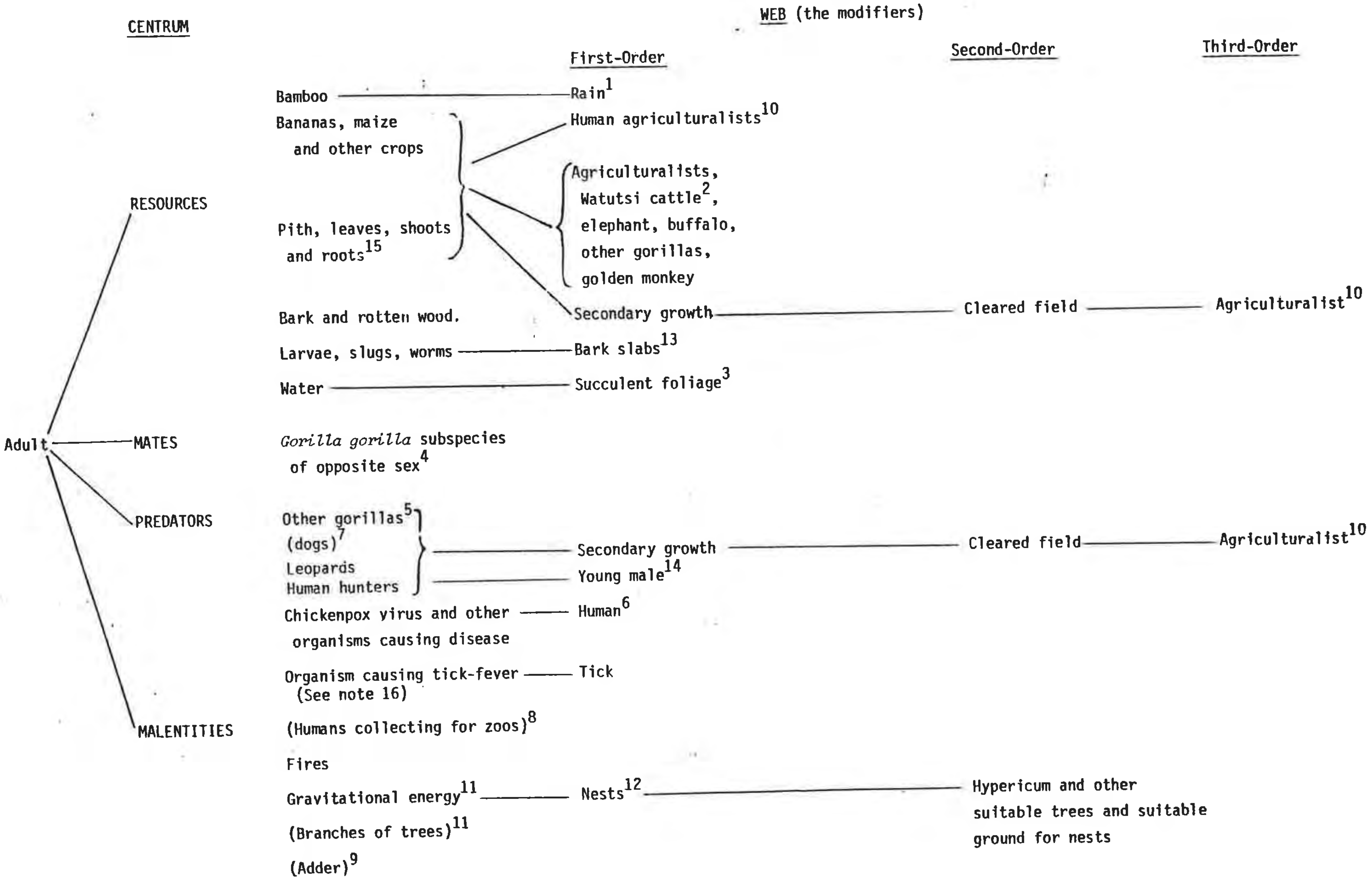
The envirogram for the gorilla has been constructed for female or male adults.

The maps are from Schaller (1963). Information has been obtained very largely from studies carried out in the Albert National Park. The diagram of the floral zones is from Spinage (1972). Gorillas are not found above 4,500 m.

Most studies on the gorilla recognise two species; *Gorilla gorilla gorilla*, the Lowland Gorilla, and *G. gorilla beringei*, the Mountain Gorilla. However, debate on taxonomy continues.

The methodology used in the construction of the envirogram is explained in detail in the general introduction to the series (AES Working Paper 9/81). The defining equations for the environment of an animal are also given in the general introduction, together with some indications as to the place of the present study within the development of a mathematical theory of ecology.

B ENVIROGRAM



C NOTES ON THE ENVIROGRAM

1. There are two wet seasons: (i) March-April, (ii) October- November. The wet season promotes new growth of bamboo. During these periods the gorillas, which eat only the new shoots, are found almost exclusively in the bamboo forest. At other times of the year they are not found there.

2. Food sources are often trampled (or eaten) by cattle, humans, other gorillas and other large animals. The golden monkey *(Cercopithecus mitis Kandti)* competes significantly with the gorillas for bamboo shoots.

3. Gorillas have never been seen to drink from rivers, lakes or pools. They do drink, using their hands or directly, in captivity.

4. Dixson (1981) recognises three subspecies.

5. A fight between the chief gorillas of two troops resulted in the death of one; he was strangled. It has been suggested that strangling is one of the gorilla's fighting tactics. They also bite; some adults have been observed with bites and an infant died in one incident.

   Although troop ranges overlap the population density is low (2/sq mile) and very few inter-group fights occur. Many peaceful interactions have been observed.

6. An eight-month old gorilla was infected with chicken-pox *(Varicella-zoester)* by contact with a human.

7. No attacks by dogs have been recorded, but gorillas have been reported as strongly fearful of dogs.

8. The initial capture probably acts against the welfare of the animal, so a zoo-collector is best thought of as a malentity.

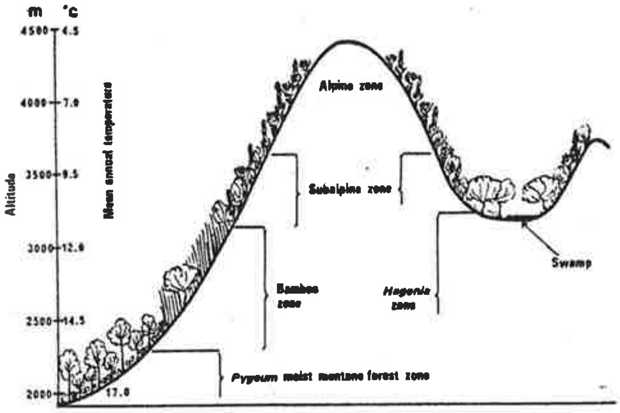


Fig. 6. Schematic representation of the floral zones.

(From Spinage, 1972)

9. Mentioned by Kawai and Mizuhara (1959); unidentified, deadly poisonous, no record of an attack.

10. Schaller (1963) reported that the animals occasionally raid fields still under cultivation. Native agriculturalists clear the forest, plant crops then move on after a couple of years. Gorillas generally prefer dense undergrowth to primary forest. The secondary growth in the abandoned areas is not only dense but also provides succulent young plants, some of which arise from the human cultivation. It has also been suggested that dense undergrowth will provide shelter against large predators (note 14).

11. Schaller (1965) observed fourteen injuries, most minor. All were consistent with collisions with branches or falls from trees, notably a female blinded in one eye and another female with a broken jaw.

12. Gorillas build both day and night nests; in trees and on the ground.

    (i) Day nests. More likely to be on the ground. Used for resting in the heat of the day and for eating gathered food.

    (ii) Night nests. More likely to be in trees. However, not all biotypes have trees sufficiently large, particularly Hagenia woodland. The table below is from Schaller, 1965.

HEIGHT OF GORILLA NESTS ABOVE GROUND

Location	*Hagenia Woodland Kabara, Virunga Volcanoes 2488 Nests (percent)*	*Mountain Woodland and Bamboo Uganda Side, Virunga Volcanoes 106 Nests (percent)*	*Mountain Rain Forest. Kayonza Forest, Uganda 179 Nests (percent)*	*Lowland Rain Forest Near Utu., Congo 110 Nests (percent)*
On ground	97.1	45.3	53.5	21.8
2-10 feet above ground	2.3	50.0	35.4	13.6
11-20 feet above ground	0.3	4.7	8.9	26.4
21+ feet above ground	0.3	0	2.2	38.2

13. Gorillas peel off bark slabs in order to obtain larvae, slugs, and worms; apart from these they are not known to eat meat.

14. It has been suggested that characteristically young males act as decoys while the silverback male leads the females and young to safety. Human hunters are considered to be the chief predator; even so, a gorilla hunt is rare.

15. Gorillas usually eat only one type of plant at a time; the animal will pick a bunch then go away to eat it in a day nest (Note 12) or shady spot.

16. The occurrence of testicular atrophy is frequently reported; this may relate to the low fertility of the Mountain Gorilla. The disease has not been included in the envirogram since the cause is unknown.

D DETAIL

The following tables are from (i) Fossey (1974): Table III. Records of Gorilla Feeding on Various Food Items in Different Months of the Year; (ii) Kawai and Mizuhara (1959): Table I. Foods of Mountain Gorillas at Bufunvira range (1959.5 - 1959.8); (iii) Donisthorpe (1958): 1-Staple Foods: Plants eaten frequently; (iv) Schaller (1963): Tables 27, 28, 29, 30, 31, 32, 33, giving food plants eaten by the animal in various areas.

TABLE III. Records of Gorilla Feeding on Various Food Items in Different Months of the Year

Food	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec
Nettles*	7	10	5	12	13	12	4	2	3	15	14	6
Galium*↑†	29	21	24	30	15	30	25	20	15	12	3	12
Hagenia↑				3	7		2			1		
Polypodium↑	12	20	4					1		1	5	17
Misc. Herb Plants↑†	2	3	10	10	7	10	9	10	3	15	5	12
Thistle↑†	19	10	19	15	15	32	20	22	12	29	28	12
Celery↑†	2	3	7	10	7	4	9	8	21	12	13	3
Hypericum↑†	4	1		2				3		4		3
Rotten Wood↑†§	2	2	12	6	13	3	5	2				
Blackberries§	2	7	1	3	5		5	8	3	1	6	6
Pygeum§			4				4	7				
Vernonia¶	2	6	4	4	14	8	13	11	36	15	11	31
Helichrysum‖	12	1	2		2		5	2	6	3	5	
Kerstenii‖		3	2					2	3		2	
G. Senecio‖		1	2	1						3		3
Slugs, larvae, worms			2		1			1		1	5	
Dung		1	2	6	6						5	
Total records	41	99	86	159	144	40	101	106	34	79	64	36

Zones: nettles=*; saddle=↑; berbaceous=†; ridge=§; vernonia=¶; sub-alpine=‖

The figures are expressed as percentages of the records for the month in question. The totals on which the percentages are based are given at the bottom.

Nettles:	*Laportea alatipes* (Urticaceae) *Urtica massaica* (Urticaceae)
Galium:	*Galum spurium* (Rubiaceae)
Hagenia:	*Hagenia abyssinica* (Rosaceae)
Polypodium:	*Polypodium sp.* (Polypodiaceae)
Misc. Herbaceous Plants	*Lobelia giberroa* (Lobeliaceae) *Senecio trichopterygius* (Compositae) *Leucas deflexa* (Labiatae) *Carex petitiana* (Cyperaceae) *Cynoglossum geometricum* (Boraginaceae) *Cynoglossum amplifolium* (Boraginaceae) *Rumex ruwensoriensis* (Polygonaceae) *Solanum nigrum* (Solanaceae)
Thistle:	*Carduus afromontans* (Compositea)
Celery:	*Peucedanum linderi* (Umbelliferae)
Hypericum:	*Hypericum revolutum* (Hypericaceae)
Rotten Wood:	Decaying wood primarily from Hypericum and Hagenia trees. Bracket fungus *(Ganoderma applanatum)*
Blackberries:	*Rubus runssorensis* (Rosaceae) *Rubus apetalus* (Rosaceae)
Pygeum:	*Pygeum africanum* (Rosaceae)
Vernonia:	*Vernonia adolphi-frederici* (Compositae)
Helichrysum:	*Helichrysum formosissimum* (Compositae) *Helichrysum guilelmii* (Compositae)
Kerstenii:	*Peucedanum kerstenii* (Umbelliferae)
Gt. Senecio:	*Senecio evici-rosenii* (Compositae) *Senecio alticola* (Compositae)

This is not meant to be a complete food list but only lists those species most commonly observed to have been consumed within a particular vegetation zone.

Name			Native's name	Description	How part eaten	Taste
No.	Fam.	Ge. & Sp.				
	Staple Foods					
1	Umbelliferae	*Peucedanum* spp. (Giant Celery)		(D)	(D) stem, leaf	slightly bitter
2	Gramineae	*Arundinaria alpina* sp. (Bamboo)	Umuto	(D)	(D) bamboo shoot	slightly bitter
3	Compositae	*Veronia* spp.	Iriherehere	(D) *V. issiopus* & *V. syringiforia*	(D) stem, leaf a little	leaf very bitter, ste dry
4	Labiatae	*Plectranthus or Colenus* sp.	Umtindikwa		(D) stem, leaf a little	leaf very bitter, ste dry
		(Prychnostachys goetzenii)	Sindikwa	name Donisthorpe's description		
5	Boraginaceae	*Cynoglossum amplifolium*	Igifashi	(D)	(D) root only	dry
	Supplementary Foods					
6	Umbelliferae	*Peucedanum runssoricum* Engl.	Kisengasengo	(D)	(D) stem, root	leaf a little, root dry
		(Anthriscus sylvestris)		name Donisthorpe's description		
7	Campanulaceae	*Loberia* (Giant loberia)		(D)	(D) stem, leaf a little	leaf very bitter, ste dry
8		*Kniphofia* sp. (Red hot poker)	Umrenbehra	(D)	(D)	stem dry
9	Piperaceae	*Piper capense* Linn. F.	Ichunge	(D)	(D) stem	slightly bitter
10	Polygonaceae	*Rumex usambarensis* Dammer	Umhunba		stem	sour
11	Compositae	*Senecio* (Giant groundsel)		(D)	(D) leaf base, stem	leaf and it base bitter
12	Euphorobiceae	*Acalypha bipartia* Muell.Arg.	Umnyanung		leaf, stem	grassy flavour
13	Labiatae ?	?	Munbuliza		leaf, stem	
14	Cucurbitaceae	*Momordica foetida* Schum. et Thom	Umhanba		leaf, stem	grassy flavour
15	Papilionaceae	?	Umranrashi		leaf, stem	grassy flavour

Name		Native's Name	Description	How part eaten	Taste
16 Rosaceae	*Rubus pinnatus* Willd(Bramble)	Mkehre		leaf, fruit	sour
17 Hypericaceae	*Hypericum lanceolatum* Lam.	Umshunguru	(D)	bark of stem	
18 Basellaceae	*Basella alba*		(D)	(D) leaf, stem a little	
19 Compositae	*Sonehus oleraceus* L.	Ulubunange		leaf, stem	bitter
20	? (Thistle)	Ikirongorela		leaf, stem	grassy flavour
21	?	Umhurura	(D) ?	leaf, stem	
22	?	Igitamatama		root	
23	?	Umhanda	(D) ?	leaf, stem	
24	?	Umnanira		nut	
25	?	Ugundirizi	(D)	(D) a little eaten	

TABLE I. Staple Foods: Plants Eaten Frequently

NAME	DESCRIPTION	HOW EATEN
Peucedanum spp. Giant celery (Umbelliferae) Native name - Kisengosengo	Abundant in lower forest, often occurring in large patches. Like a much branched garden celery, average height 2-3 feet but sometimes 6-8 feet.	Collected. Outer fibrous portions of stem discarded and soft inner parts eaten (Figure 3).
Arundinaria alpina Bamboo	I tried to discover a season for the appearance of young shoots but could not. There seems to be some new shoots all the time, even during the dry season.	Collected and eaten in two ways:- i. The whole of the young shoot is eaten, the papery sheath being discarded. ii. Larger stems about an inch in diameter are broken across, then split and the white pith, which has the consistency of coconut, is eaten.
Vernonia spp. (Compositae) Native name - Ijiheriheri	Woody shrub found from 7,000 feet upwards but dominant on the saddle. It was at first thought to be *Erlangea tomentosa*, but the latter has smaller inflorescences and has never been recorded above 7,000 ft. Two species were found, possibly *V. lasiopus* and *V. syringifolia*, having mauvish-white heads, the former somewhat larger.	Collected, bark peeled off and inner portion of stems eaten. Mostly eaten on saddle and just above, where there is little choice.
Pychnostachys goetzenii (Labiatne) Native name - Sindikwa	Woody shrub with purplish spikes. Leaves and growth similar to above.	As above.

NAME	DESCRIPTION	HOW EATEN
Basella alba (Basellaceae)	Climber with light green, heart-shaped leaves and small white flowers, found in lower forest.	Leaves are eaten, possibly on the spot, for the plant is often found with a number of leaf stalks about an inch long remaining. Sometimes the plant is hauled down from a tree and in this case a resting place is often found at the base of the tree, showing that a meal has taken place.
Cynoglossum amplifolium (Boraginaceae)	Herb about 2 feet tall with flowers like a forget-me-not but very much larger and broader leaves. Found in lower forest.	The root is eaten and the rest of the plant discarded. It is scooped out of the ground leaving a characteristic round hole which helps to identify a gorilla trail. Discarded plants are found by each hole, indicating that the the roots are eaten on the move (Figure 4).

TABLE II - Supplementary Foods: Plants eaten as tit-bits, or only during certain seasons

NAME	DESCRIPTION	HOW EATEN
Anthriscus sylvestris (Umbolliferae)	Plant 12-18 inches tall with feathery leaves, like a cross between a fern and garden parsley. The stalk bearing the inflorescence is much taller (2-2½ feet). The base of the leaves form a sheath like that of celery and the flavour is more like celery than is *Peucedanum*. Found on upper slopes and in sub-alpine zone.	The sheath-like leaf bases are eaten. They are not pulled off separately but the whole plant is pulled up and the "heart" bitten. Probably eaten on the move.
Bramble (Rosaceae)	Similar to British type though restricted to a few branches, not a large bush.	Young leaves, and very likely fruits also, are eaten leaving the whole branch bate. A favourite tit-bit.
Droquetii iners (Urticaceae)	Creeper with toothed, nettle-like leaves, but no sting.	Stems eaten.
Stephania abyssinica var tomentella (Menisparmaceae)	Climber with roundish leaves. No flowers were found.	Leaves eaten.
Piper capense	Climber with large dark green roundish leaves with palmate venation and a greenish-white spike.	Young stems are eaten, also the bark of older stems.
Kniphofia Red hot poker	The same plant which is cultivated in gardens grows wild on the mountains, in clearings in bamboo forest, or *Hypericum* woodland.	The succulent, almost fibreless stems are eaten during the flowering season from February to April. The heads are found scattered about, indicating that the stems are eaten on the spot.
Giant lobelia	Grows mainly in the alpine and sub-alpine zones, but also on the saddle swamp with a few isolated plants on the lower slopes. The narrow leaves form a rosette with the flowering spike growing 6-9 ft tall from the centre. The old, hollow spikes contain water which gorilla are said to drink, though no evidence of this was seen.	The bases of the leaves which have a bitter, peppery flavour like a chili are eaten.

NAME	DESCRIPTION	HOW EATEN
Senecio Giant groundsel (Compositae)	Found in alpine and sub-alpine zones only. Has a soft pulpy stem with clusters of large floppy leaves and yellow inflorescences which bloom during the dry season.	Leaf bases on low plants are eaten.
Carex petitiana	A rush which grows on the saddle swamp and is much eaten by buffalo.	The soft white bases of the leaves are eaten and the tough upper parts are laid in piles indicating a sit-down meal (Figure 5).

TABLE III - Plants eaten only occasionally.

NAME	DESCRIPTION	HOW EATEN
Laportea alatapes Nettle	Large and virulent type of stinging nettle found at all levels up to the tree line.	Tops eaten. Lower parts of stem and root seen eaten once.
Rumex nepalensis Giant doek	Perennial with large leaves growing 4-5 feet tall, mainly in lower forest.	Stem and leaf base eaten.
Rumex usambarensis	A type of bushy dock with thin pointed leaves and fruits a small red siliqua. Occurs as secondary growth in neglected cultivations.	Thick part of stem eaten.
Thistle	A very tall variety growing 7-8 feet high often in large patches in clearings in lower forest.	Stem and leaf eaten.
Bracken	Found in clearings in lower forest.	On two occasions the stem was seen bitten but not broken off, as if the animal had sucked the juice and fibres.
Lactuca paradoxa (Compositae)	Scrambler with narrow indented leaves and yellow inflorescences found 7-8,000 feet.	Where these plants occur, numerous resting places are usually found and wide areas are beaten down, but no piles of remains are to be seen.
Crassocephalum mannii (Compositae)	Herb with yellow head found in lower forest.	
???	Climber with deeply indented vine-like leaves and a red cucumber-like fruit.	Fruit was once found partly eaten on a gorilla track, but it cannot be definitely established that it was eaten by gorillas.
???	Orange coloured fungus about the size of a grapefruit which grows on bamboo.	Often found broken up on gorilla trails, but no proof that it is actually eaten.

TABLE 27: Food Plants Utilized by Gorillas at Kabara

Name	Relative Degree of Utilization*	Part Eaten
Grass-Sedge		
Arundinaria alpina	xx	Young stem, shoot
Carex petitiana	x	Base of leaves
Fern		
Polypodium sp.	xx	Whole plant
Herb		
Lobelia wollastonii	xx	Root, base of leaf cluster
Lobelia giberroa	x	Stem
Peucedanum linderi	xxx	Inside of stem
Peucedanum kerstenii	xx	Lower part of stem
Chaerofolium silvestre	xx	Root, lower part of stem
Cynoglossum geometricum	xx	Root, lower part of stem
Cynoglossum amplifolium	xx	Root
Rumex ruwenzoriensis	xx	Root, lower part of stem
Laportea alatipes	xxx	Bark, stem, leaves
Carduus afromontanus	xxx	Leaf, flower, stem
Helichrysum (probably *H. formosissimum*)	xx	Leaves, stem
Vine		
Droquetia iners	x	Whole plant
Clematis sp.	x	Bark
Galium simense	xxx	Whole plant
Stephania abyssinica	x	Fruit
Urera hypselendron	x	Bark
Shrub		
Rubus runssorensis	xx	Fruit, leaves, small branches
Pycnostachys goetzenii	x	Bark
Vernonia adolfi-frederici	xxx	Flower, pith
Tree		
Pygeum africanum	xx	Bark, fruit
Rapanea pulchra	x	Bark
Erica arborea	x	Bark
Hagenia abyssinica	x	Pith, bark, root
Hypericum lanceolatum	x	Bark, root, rotten wood
Senecio erici-rosenii	xx	Pith, base of leaf cluster
Senecio alticola	xx	Pith, base of leaf cluster

xxx: heavily used
xx : moderately used
x : infrequently used

TABLE 28: Food Plants Utilized by Gorillas in the Kayonza Forest

Name	Part Eaten	Relative Degree of Utilization†	Source‡
Sedge			
Cyperus sp.	Base of leaves	?	*
Fern			
Cyathea deckenii	Shoot, pith of front	xxx	
Conchitis sp.	Inside of stem	xx	
Dryopteris sp.	Inside of stem	xx	
Herb			
Aframomum milbraedii	Fruit	xx	
Rumex usambarense	Stem	xx	
Pilea bambuseli	Leaves	x	
Brillantaisia nyanzanrum	Bark	x	
Vine			
Senecio syringifolius	Leaves	x	
Culcasia scandens	Bark	x	
Momordica foetida	Leaves	xxx	
Urera hypselendron	Bark	xxx	
Fleurva ovalifolia	Stem	xx	
Crassocephalum bojeri	Bark	xx	
Piper capense	Bark	xxx	
Basella alba	Leaves	xxx	
Kigelia sp.	Fruit	?	*
Mikania cordata	Leaves	xxx	
Shrub			
Rubus pinnatus	Leaves	xx	
Mimulopsis arborescens	Bark	x	
Pycnostachys goetzenii	Bark	x	
Acalypha sp.		?	***
Tree			
Xymalos monospora	Bark	x	
Myrica kandtiana	Bark	x	
Ensete sp.	Pith of stem	?	**
Myrianthus arboreus	Leaves, bark, fruit	xx	
Cultivated			
Musa sp. (banana)	Pith of stem	x	

†xxx: heavily used
xx: moderately used
x: infrequently used

‡ x: Batwa guide
xx: Bantu assistant
xxx: Pitman (1942)

TABLE 29: Food Plants Utilized by Gorillas at Kisoro

Name	Part Eaten	Relative Degree of Utilization†	Source ‡
Grass Sedge			
Arundinaria alpina	Young stem, shoot	xxx	
Carex petitiana	Base of leaves	x	
Cyperus sp.	Base of leaves	?	**
Herb			
Lobelia wollastonii	Base of leaves, root	xx	
Peucedanum linderi	Inside of stem	xxx	
Peucedanum kerstenii	Lower part of stem	xx	
Chaerefolium silvestre	Lower part of stem	xx	
Cynoglossum geometricum	Root	xxx	
Cynoglossum amplifolium	Root	xxx	
Rumex nepalensis	Stem and leaf base	?	*
Rumex usambarensis	Stem	?	
Carduus afromontanus	Stem and leaf	xx	
Senecio trichopteryglus	Inner part of stem	?	**
Laportea alatipes	Leaves, stem	xx	
Kniphofia grantii	Stem	x	
Vine			
Crassocephalum bojeri	Bark	xx	
Stephania abyssinica	Fruit	x	
Droquetia iners	Leaves, stem	?	*
Basella alba	Leaves	?	*
Piper capense	Bark, stem	?	*
Shrub			
Vernonia adolfi-frederici	Pith	xxx	
Pycnostachys goetzenii	Bark	x	
Rubus runssorensis	Fruit, leaves	x	
Tree			
Hypericum lanceolatum	Bark	x	
Xymalos monospora	Fruit, bark	x	
Senecio erici-rosenii	Pith, base of leaves	xx	
Senecio alticola	Pith, base of leaves	xx	

†xxx: heavily used
xx: moderately used
x: infrequently used

‡ x: Donisthorpe (1958)
xx: Bolwig (pers. comm.)

TABLE 30: Food Plants Utilized by Gorillas at Mt. Tshiaberimu and Vicinity

Name	Part Eaten	Relative Degree of Utilization†	Source‡
Grass			
Arundinaria alpina	Young stem, shoots	xxx	
Pennisetum purpureum	Stem	?	*, **
Herb			
Rumex bequaertii	Stem	xx	
Rumex ruwenzoriensis	Stem	xx	
Peucedanum linderi	Stem	?	*
Sonchus schweinfurthii	Leaves	?	***
Gunnera perpensa	Leaves	?	***
Vine			
Smilax kraussiana	Leaves	xx	
Urera hypselendron	Bark	xx	
Shrub			
Rubus runssorensis (?)	Leaves, bark, small branches	xx	
Pycnostachys goetzenii	Bark	x	
Mimulopsis arborescens	Bark	x	
Tree			
Pygeum africanum	Bark	xx	
Macaranga kilimandscharica	Bark	x	
Maesa lanceolata	Bark	xx	
Galiniera coffeoides	Pith	x	
Grumilia megistosticta	Bark	x	
Cultivated			
Zea sp. (maize)	Fruit	?	*, ***
Pisum sp. (peas)	Fruit	?	*

†xxx: heavily used
xx: moderately used
x: infrequently used

‡ *: Bantu assistant
**: White settler
***: J.T. Emlen

TABLE 31: Food Plants Utilized by Gorillas in the Mt. Kahuzi Region West of Lake Kivu

NAME	PART EATEN	SOURCE
Grass		
Pennisetum purpureum	Stem	Rahm (pers. comm.)
Arundinaria alpina	Young stem, shoot	This study
Herb		
Brillantaisia nyanzarum	Bark	Christiaensen (pers. comm.)
Aframomum sp.	Pith	Agricultural official (pers. comm.)
Vine		
Urera hypselendron	Bark	Agricultural official (pers. comm.)
Gynura scandens	Bark	Christiaensen (pers. comm.)
Ficus thonningii	Bark	Christiaensen (pers. comm.)
Shrub		
Mimulopsis arborescens	Bark	Christiaensen (pers. comm.)
Vernonia kirungae	Pith	This study
Tree		
Galiniera coffeoides	Pith	This study
Cohopharyngia holstii	Bark	This study
Cultivated		
Daucus sp. (carrot)	Root	White planter

TABLE 32: Food Plants Utilized by Gorillas in the Mwenga-Fizi Region

Name	Part Eaten	Collecting Station†	Source‡
Grass			
Arundinaria alpina	Shoot, stem	F, M	*
Pennisetum purpureum	Stem	F	*
Fern			
Cyathea deckenii	Inside of frond	N	*
Dryopteris sp.	Stem	N	
Marattia fraxinea	Inside of stem	N	
Herb			
Aframomum sanguineum	Pith	F, N	
Brillantaisia cicatricosa	Bark	N, M	
Triumfetta annua	Leaves	M	*
Hypoestes verticillaris	?	M	*
Palisota ambigua	Leaf base	N	
Vine			
Urera hypselendron	Bark	F, N, M	
Piper capense	Bark	F	
Adenia cissampeloides	Bark	M	
Lasianthus kilimandscharica	Bark	N	
Oncinotis glabrata	Bark	N	
Cissus petiolafa	Leaves	N	
Shrub			
Triumfetta macrophylla	Bark	F	*
Alangium chinense	Bark	M	
Tree			
Xymalos monospora	Bark	M	
Galiniera coffeoides	Pith	M	
Maytenus acuminata	Bark	M	
Trema guineensis	Bark	M	*
Polyscias fulva	Bark	N	*
Myrianthus arboreus	Fruit	N	*
Cultivated			
Musa sp. (banana)	Pith of stem	near N	**

†F: Fizi
M: Mulenge
N: Nzombe

‡ *: Bantu guide
**: J.T. Emlen

TABLE 33: Food Plants Utilized by Gorillas in the Utu Region

Name	Part Eaten	Relative Degree of Utilization†	Source‡
Fern			
Dryopteris sp.	Base of stem	x	
Marattia fraxinea	Inside of stem	xx	
Herb			
Marantochloa leucantha	Young shoots	xx	
Megaphynium macrostachyum	Fruit	?	*
Palisota sp.	Base of main stem	xx	
Aframomum sp.	Pith, fruit	xxx	
Costus affer	Pith	xx	
Tree			
Musanga cecropioides	Fruit, leaf	?	*
Ficus exasperata	Leaf	xx	
Ficus vallis-choudee	Leaf	?	
Raphia sp.	Base of frond	?	*
Pycnanthus angolensis	Leaves	x	
Myrianthus arboreus	Fruit	xx	
Uapaca sp.	Pith	x	
Culivated			
Musa sp. (banana)	Pith of stem	xxx	
Manihot sp. (manioc)	Tuber, bark of stem	xx	
Colocasia esculenta (taro)	Root	?	*

†xxx: heavily used
xx: moderately used
x: infrequently used

‡ *: Bantu guide

E REFERENCES

Antonius, J.I.; Ferrier, S.A. and Dillingham, L.A. (1971). Pulmonary embolus and testicular atrophy in a gorilla. *Folia Primatol.* 15, 277-292.

Bingham, H.C. (1932). *Gorillas in a Native Habitat.* (Carnegie Institute of Washington).

Caro, T.M. (1976). Observations on the ranging behaviour and daily activity of lone silverback Mountain Gorillas. *(Gorilla gorilla beringei).* *Anim. Behav.* 24, 889-897.

Casimir, M.J. and E. Butenandt (1973). Migration and core area shifting in relation to some ecological factors in a mountain gorilla group (Mt. Kahuze region, Zaire). *Z. tier psycol.* 33, 514-522.

Dixson, A.F. (1981). *The Natural History of the Gorilla.* (Wiedenfeld and Nicolson).

Donisthorpe, J.H. (1958). A pilot study of the Mountain Gorilla *(Gorilla gorilla beringei)* in south-west Uganda, February-September, 1957. *S. Africa J. Sci.* 54, 195-217.

Elliot, R.C. (1979). Observations on a small group of Mountain Gorillas *(Gorilla gorilla beringei).* *Folia primatol.* 25, 12-24.

Fossey, Dian (1974). Observations on the home range of one group of Mountain Gorillas *(Gorilla gorilla beringei).* *Anim. Behav.* 22: 568-581.

Harcourt, H.A. (1978). Strategies of emigration and transfer by primates with particular reference to gorillas. *Z. tierpsychol.* 48, 401-420.

Kawai, Masao and Hiroki Mizuhara (1959). An ecological study on the wild Mountain Gorilla *(Gorilla gorilla beringei).* *Primates* 2, 1-42.

Napier, J.R. and Napier, P.H. (1967). *A Handbook of Living Primates.* (Academic Press).

Schaller, George B. (1963). *The Mountain Gorilla. Ecology and Behavior.* (University of Chicago).

Schaller, George B. (1965). The behaviour of the Mountain Gorilla. In: De Vore, I. (Ed.) *Primate Behaviour: field studies of monkeys and apes.* Chapter 10, 324-367. (Holt Rinehart and Winston).

Spinage, C.A. (1972). The ecology and problems of the Volcano National Park, Rwanda. *Biol. Conserv.* 4, 194-204.

White, R.J. (1972). Chickenpox in young anthropoid apes: clinical and laboratory findings. *J. Am. Vet. Med. Assoc.* 161, 690-692.

THE PRECISE ENVIRONMENT OF SOME WELL-KNOWN ANIMALS,
II THE CHIMPANZEE *(Pan troglodytes)*

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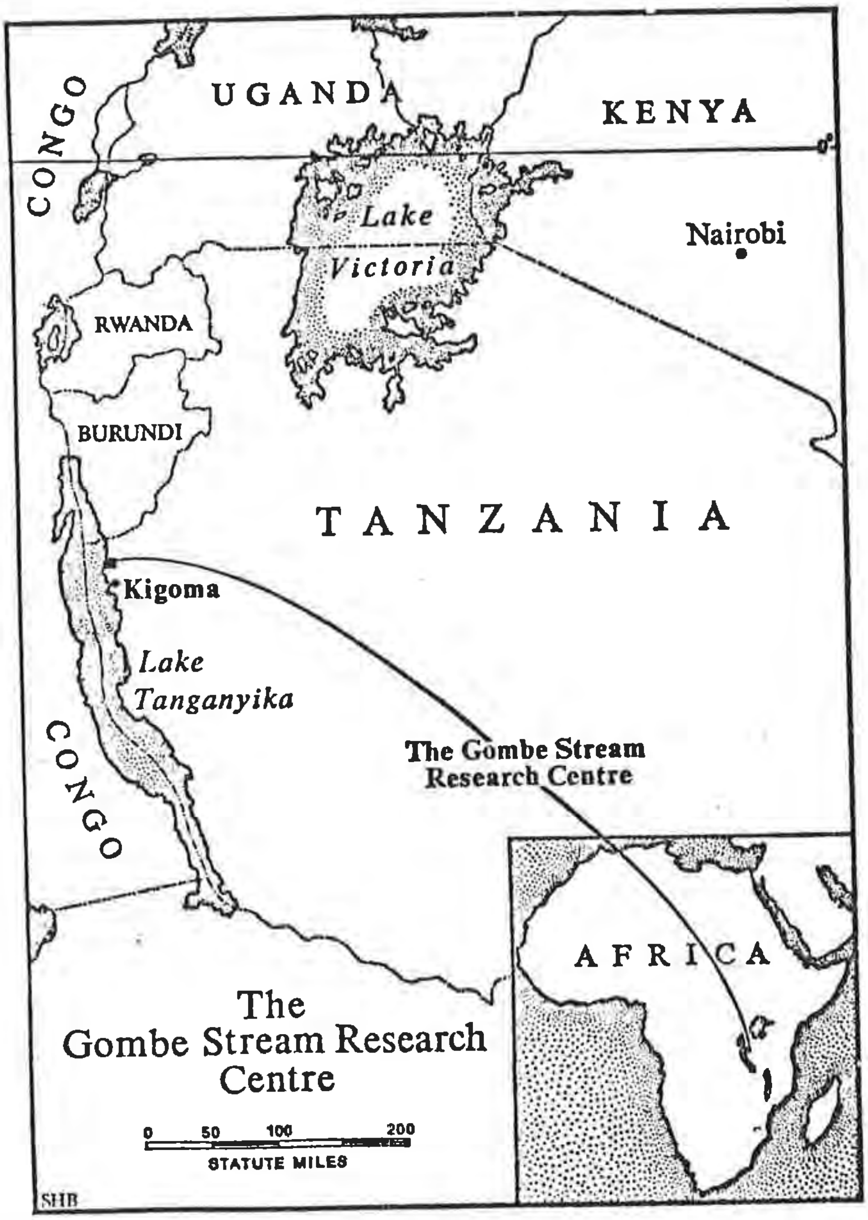
ABSTRACT

The precise environment of the chimpanzee *(Pan troglodytes)* is given, using as a basis for the classification the defining equations of Niven (*Erkemtnis*, 1982). A diagram developed by H.G. Andrewartha called an 'envirogram', is used for displaying the objects in the environment. Details of the environment not included in the envirogram are listed separately.

* * * * *

A general introduction to the whole series of reports on the precise environment of the various animals is available as AES Working Paper 9/81. This paper contains (a) the defining equations for the precise environment; (b) the interpretation of the four primitive (undefined) terms which are used in the definitions; (c) a detailed discussion of the method of using the defining equations, with the chimpanzee and the three-spined stickleback as examples; (d) indications of the way in which the work is being used in the formalization and development of the mathematical theory of animal ecology.

CONTENTS



(From J. van Lawick-Goodall: *In the Shadow of Man.*)

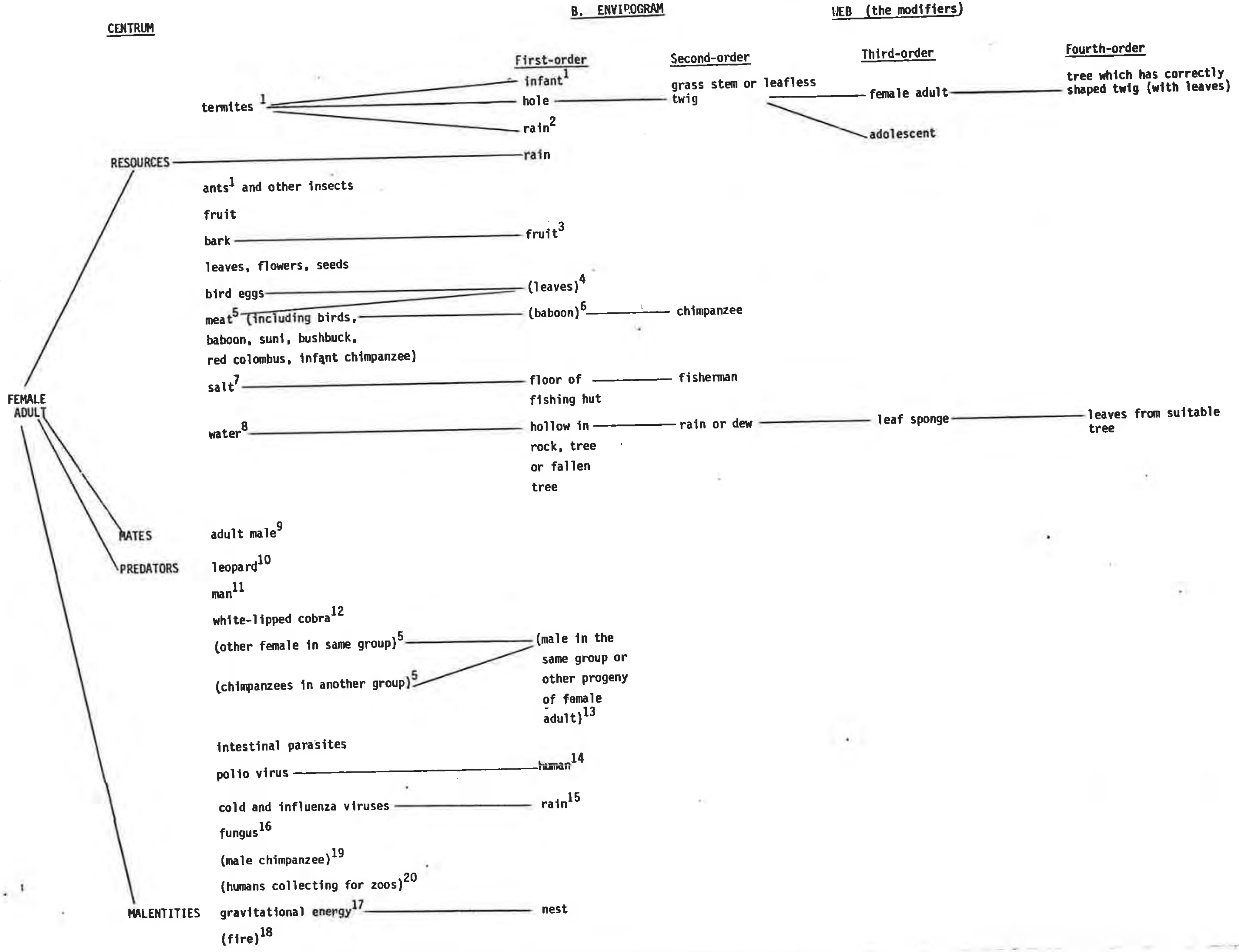
A INTRODUCTORY NOTE

The envirogram for the chimpanzee has been constructed specifically for a female adult in oestrus with an infant of about four years which has been partially weaned and an adolescent of about seven years i.e. near puberty.

Information has been obtained largely from studies in the Gombe National Park in Tanzania. The map has been taken from Lawick-Goodall (1971).

The envirogram should be looked at concurrently with the notes. In particular the environment of the young or the adult males is referred to in the notes; this device has been used in preference to drawing up a number of separate envirograms.

The methodology used in the construction of the envirogram is explained in detail in the general introduction to the series (AES Working Paper 9/81). The defining equations for the environment of an animal are also given in the general introduction, together with some indications as to the place of the present study within the development of a mathematical theory of ecology.


B. ENVIROGRAM
WEB (the modifiers)
CENTRUM
First-order
Second-order
Third-order
Fourth-order
termites [1]
infant[1]
hole
rain[2]
grass stem or leafless twig
female adult
tree which has correctly shaped twig (with leaves)
adolescent
RESOURCES
rain
ants[1] and other insects
fruit
bark
fruit[3]
leaves, flowers, seeds
bird eggs
(leaves)[4]
meat[5] (including birds, baboon, suni, bushbuck, red colombus, infant chimpanzee)
(baboon)[6]
chimpanzee
salt[7]
floor of fishing hut
fisherman
FEMALE ADULT
water[8]
hollow in rock, tree or fallen tree
rain or dew
leaf sponge
leaves from suitable tree
MATES
adult male[9]
PREDATORS
leopard[10]
man[11]
white-lipped cobra[12]
(other female in same group)[5]
(male in the same group or other progeny of female adult)[13]
(chimpanzees in another group)[5]
intestinal parasites
polio virus
human[14]
cold and influenza viruses
rain[15]
fungus[16]
(male chimpanzee)[19]
(humans collecting for zoos)[20]
MALENTITIES
gravitational energy[17]
nest
(fire)[18]

C NOTES ON THE ENVIROGRAM

1. Termites are eaten from October to January. The soldier termites are readily available after rain, when they are near the surface. The female adult chimpanzee will choose a grass-stem or a twig of a suitable shape, from one of a number of different species of tree or bush. She strips the leaves from it, thus acting as a modifier of the tool which she then pokes into the hole to collect the termites, which are then eaten. They may be given to her infant to eat. An infant cannot use the tool but an adolescent may make use of one, although unable to manufacture it. Thus the adolescent (offspring of the female adult) appears in the envirogram as a modifier, since he or she may be given the tool by the mother. A tool is also used for ants, presumably at least partly because the ants may bite.

2. Rain acts as a modifier for all food resources, since chimpanzees very rarely eat when it is raining. Males sometimes perform a "ritual dance" in the rain.

3. Bark is eaten only if no fruit is present; thus fruit is a first-order modifier of bark which is a resource. Formally, if w represents a piece of fruit, y and a both represent the animal, and x a piece of bark we have:

$$w \ \mathrm{Mod}_t^1 \ a =_{\mathrm{Df}} (\exists x)\left[(\sim \xi_t \ wy \supset x \ \mathrm{Mod}_t^0 \ a) \ \& \ (\xi_t \ wy \supset \sim x \ \mathrm{Mod}_t^0 \ a)\right].$$

   In this particular case only the second part of the definition is used. The modifier of order zero is a resource.

4. Leaves are always seen to be eaten with the eggs, however it is not known whether a chimpanzee would sometimes eat an egg without leaves. Leaves are also sometimes eaten with meat. In both cases these need not be the kind of leaves normally eaten for food (see Section D, Food: edible plants, leaves marked "(R)").

5. The hunting of bushbuck and other animals tends to occur in cycles; the chimpanzee, mainly the male, will hunt for two months, say, and then not at all for the following month. Hunts are usually more successful when the chimpanzees cooperate. All chimpanzees, adolescent or adult, female or male, occasionally beg meat from

successful hunters. There is one recorded case of a chimpanzee building a tree-nest and eating his meat in it.

Nishida *et al* (1979) remark that although in the Gombe National Park baboons are often attacked this does not occur in the Mahali Mountains forty miles away; they suggest that the artificial feeding at Gombe brings chimpanzees into contact with baboons more often. In the Mahali area much less meat is eaten and hunting is invariably opportunistic rather than co-operative.

There are two varieties of cannibalism:

(i) Inter-group. When a mother with an infant is attacked the mother often escapes but the infant is captured and eaten, often with accompanying ritual. The suggestion has been made that such infant killings are related to tensions arising because of overlapping ranges. A female who has lost her infant changes her status within the group from "mother" to "female" and may be expected to go into oestrus within two months. One female who lost her infant was groomed for a long period by three males without, however, reciprocating.

(ii) Intra-group. A higher-ranking female will (very seldom) steal and eat another female's infant.

6. Chimpanzees often steal meat from a baboon; in this case the baboon "supplies" the resource and so is acting as a first-order modifier. The chimpanzee, usually a male, acts as a second-order modifier in his own environment by catching the baboon. See note 5.

7. The floor of the fishing-huts are a mixture of soil and salt. The chimpanzee eats the mixture.

8. There is no evidence that the animals obtain their water directly from nearby streams or lakes. However, they have been observed drinking from water-filled tree-holes. The envirogram shows the case in which the tree-hole is out of lip-reach. The chimpanzee chews a wad of leaves into a "sponge"; the sponge is then used

to sop up water thus the animal acts as a fifth-order modifier, analogous to its role in note 1.

9. A female will copulate with all mature males although copulation between siblings is very rare, and mother-son true copulation has never been observed. In any one period of sexual activity the males present will copulate in sequence according to their social rank. Occasionally, a female will have a consort (a male who accompanies her; these associations are relatively brief, never more than six months). The consort is not preferred for copulation but simply because of his proximity he is likely to copulate with her more often than other males. Thus the α-male and the consort are most likely to sire any offspring. In the course of the usual social training she will also "copulate" (in a non-adult sense) with juveniles and infants, including her own if sufficiently young.

10. There are no recorded kills by a leopard, but Lawick-Goodall (1971) makes it clear that in her opinion leopards are potential killers.

11. Some African people consider that chimpanzee flesh is a delicacy.

12. It is not clear from the literature whether the cobra should be classified as a predator or a malentity.

13. This refers to the case of infant cannibalism. A male in the same group or other offspring of the mother may act as protector.

14. Fifteen chimpanzees were affected and six of them died at Gombe in one epidemic which followed an outbreak of poliomyelitis in neighbouring villages. The suggestion has been made that many diseases of humans also affect chimpanzees.

15. Every rainy season at least some chimpanzees catch cold.

16. An unknown fungal disease was reported as affecting one female.

17. Chimpanzees occasionally fall or are pushed out of trees without damage, however in one recorded instance the animal fell partially on to a rock, broke his neck and died. Day-nests always built in

trees, helps the animal to avoid falling. It is made by weaving branches together; a few branches are broken off in the process. Several different species of tree are used. D-nests are often built during rain, though almost never during dry periods.

18. No cases of a chimpanzee being damaged by fire have been recorded. However fires do occur in their habitats.

19. This refers to the envirogram for an adult male chimpanzee. The males come to blows to establish dominance. An attacking male could be classified as either a predator or a malentity since its H would be inflated in the case that its status was increased, via the probability of reproduction. In the case that the attacking male lost its H would either be reduced or, more probably, remain unchanged; in this case the animal is acting as a malentity.

20. The initial capture probably acts against the welfare of the animal, so a zoo-collector is best thought of as a malentity.

D DETAIL

Food

An asterisk indicates a major food of its type.

EDIBLE PLANTS

Over 90 identified species supply fruit, flowers, seeds, barks, leaves, resin and/or dead wood fibre, including over 50 types of fruit and over 30 types of leaf.
Crosses in the right hand columns indicate the part(s) eaten. In the 'bark' column 'I' and 'O' indicate inner and outer bark respectively. '(R)' indicates that the leaf is rarely eaten (c.f. note C4).

NAME	TYPE	FRUIT	LEAF	FLOWER	BARK	SEED	PITH
Adenia spp.	Vine		x				
Afzelia africana	Tree				I+O		
Albizia glaberrima	Tree				I+O		
Ampelocissus spp.		x					
Annona senegalensis	Tree		x		I		
Asystasi gangetica		x					
Azanza garckeana	Tree				I		
Baphia capparidifolia			x				
Brachystegia bussei	Tree				*I		
B. spiciformis	Tree				I		
Canthium hispidium	Vine				I+O		
Cissus petiolata	Vine		x				
Clorophora excelsa			x				
Combretum mollee	Tree		x				
Diplorhynchus condylocarpon	Tree		x		I	*x	
Dracaena usambarensis	Tree				I+O		
Dalbergia spp.		x					
Elaesis guneensis	Tree	*x	x				
Erythrophleum suaveolens	Tree		x(R)				
Ficus capensis	Tree	x			I+O		
Ficus spp.	Tree	x					
Ficus vallis-choudae	Tree	x					
Grewia platyclada		x					

NAME	TYPE	FRUIT	LEAF	FLOWER	BARK	SEED	PITH
Harungana madagascariensis							
Landolphia spp.	Vine	x			I+0		
Maytenus senegalensis	Tree				I+0		
Merremia pterygocampus		x					
Monanthotaxis poggei		*x					
Monotes elegans	Tree			x	I+0		
Mucuna gigantea	Vine		x(R)				
Mussaenda spp.	Vine				I+0		
Oxyanthus spp.	Shrub				I+0		
Paranari curatellifolia		*x					
Phragmites mauritanus							x
Phyllanthus muellerianus		x					
Psuedospondias microcarpa	Tree	x			I+0		
Pterocarpus tinctorius				x			
Pycnanthus angolensis	Tree				I+0		
Saba florida	Vine	x	x(R)				
Sterculia quinqueloba	Tree				*I		
S. tragacantha	Tree				I		
Strychnos spp.		x					
Tinospora caffra			x				
Uapaca sansibarica	Tree				I+0		
Uvaria angolensis	Tree	x	x		I+0		
Vitex spp.		x					
TOTALS		18	13	2	21	1	1

The information on bark is virtually complete and bark is therefore over-represented as against the more commonly consumed fruit and leaves.

INSECT FOODS

4 genera of ant:	
	1. *Anomma spp.*
	2. *Crematogaster spp.*
	3. *Dorylus spp.* (Army ant)
	4. *Oecophylla spp.*

2 genera of termite: one with 3 sub-species

1. *Macrotermes bellicosus
   M. mülleri
   M. sjöstedt

2. *Pseudocanthotermes spp.*

1 species of caterpillar: (of an unidentified moth)

Many species of grub: larvae of beetles, wasps, gallflies etc.

Bee larvae and Honey: eaten together on hive raids.

BIRDS, FLEDGLINGS AND BIRD EGGS

Always hunted or gathered opportunistically. Eggs and fledglings of several species, including:

Melanopteryx nigerrimus (weaver birds)

Eggs always eaten with a wad of leaves.
Two recorded cases of attempted bird hunting:

Francolinus squamatus (scaly francolin), unsuccessful;
Guinea Fowl (successful).

ANIMAL MEAT

Cercopithecus aethiops centralis	(Vervet monkey)
C. ascanius schmidti	(Red-tailed monkey)
C. mitis doggetti	(Blue monkey)
* *Colobus badius tephrosceles*	(Red colobus)
Cricetomys eminii	(Giant rat)
Galago crassicaudatus crassicaudatus	(Greater galago)
Ichneumia albicauda	(White-tailed mongoose)
* *Nesotragus moschatus*	(Suni)
* *Papio anubis*	(Baboon)
Potamochoerus porcus	(Bush pig)
Protoxerus stangeri	(Giant forest squirrel)
* *Tragelaphus scriptus*	(Bush buck)
Pan troglodytes	

MINERALS

Sodium chloride
Water

MATES

For males - oestrus females of 3 sub-species

1. *Pan troglodytes schweinfurthii*
2. *P. troglodytes troglodytes*
3. *P. torglodytes verus*

For oestrus females - males of 1, 2 and 3.
For anoestrus females - nil.

PREDATORS

Homo sapiens
Panthera pardus (leopard)
Variety of snakes, including white-lipped cobra.
Pan troglodytes
Intestinal parasites including:

- *Probstmayria gombensis*
- *Strongyloides fuelleborni*
- *Necator spp.*
- *Oesophagostomum spp.*
- *Abbreviata causasica*
- *Trichuris spp.*
- *Troglodytella abrassarti*

Virus causing common cold.
Virus causing goitre
Virus causing poliomyelitis.
Fungus causing nose-swelling.
Many organisms responsible for human diseases are thought to affect chimpanzees also.

MALENTITIES

Gravitational energy.
Humans collecting for zoos.
Fire.

E REFERENCES

We examined fifty-eight articles on the chimpanzee and one book. We extracted the information for the envirogram from the seventeen articles and one book listed below. A useful bibliography is by L.A. Baldwin and G. Teleki; Field Researchon Chimpanzees and Gorillas: An Historical Geographical and Bibliographical Listing; *Primates* 14(2/3), 315-330, 1973. Another bibliography is "The Chimpanzee: a topical bibliography", Ed. F.H. Rohles (Uni. of Wash., Seattle, 2nd Edn., 1972).

de Waal, F. Explorative and familiarity dependent support strategies in a colony of semi-free living chimpanzees. *Behaviour* 66 (3/4), 268-312, 1978.

File, S.K. *Probstmayria gombensis* from the chimpanzee. *J. Parasitol.* 62, 256-258, 1976.

File, S.K., W.C. McGrew and C.E.G. Tutin. The intestinal parasites of a community of feral chimpanzees. *J. Parasitol.* 62, 259-261, 1976.

Goodall, J. Infant killing and cannibalism in free living chimpanzees. *Folia primatol.* 28, 259-282, 1977.

McGrew, W.C. Tool use by wild chimpanzees in feeding upon driver ants. *J. Hum. Evol.* 3, 501-508, 1974.

Morris, K. and J. Goodall. Competition for meat between chimpanzees and baboons of the Gombe National Park. *Folia Primatol.* 28, 109-121, 1977.

Myers, B.J. and R.E. Kuntz. A checklist of parasites and commensals reported for the chimpanzee. *Primates* 13, 433-471, 1972.

Nishida, Toshisada, Shigeo Uehara and Ramadhani Nyundo. Predatory behaviour among wild chimpanzees of the Mahale Mountains. *Primates* 20, 1-20, 1979.

Nishida, T. The bark-eating habits in primates, with special reference to their status in the diet of wild chimpanzees. *Folia Primatol.* 25, 277-287, 1976.

Riss, D.C. and C.C. Busse. Fifty-day observation of a free-ranging adult male chimpanzee *(Pan troglodytes schweinfurthii)*. *Folia Primatol.* 28, 283-287, 1977.

Riss, D.C. and J. Goodall. The recent rise to the alpha-rank in a population of free-living chimpanzees. *Folia Primatol.* 27, 134-151, 1977.

Silk, J.B. Patterns of food sharing among mother and infant chimpanzees *(Pan troglodytes schweinfurthii)* at Gombe National Park, Tanzania. *Folia Primatol.* 29, 129-141, 1978.

Suzuki, A. Carnivorality and cannibalism observed among forest-living chimpanzees. *J. Anthropol. Soc. Nippon* 79, 30-48, 1971.

Teleki, G. Notes on chimpanzee interactions with small carnivores in Gombe National Park, Tanzania. *Primates* 14, 407-411, 1974.

Teleki, G. Group response to the accidental death of a chimpanzee in Gombe National Park, Tanzania. *Folia Primatol.* 20, 81-94, 1973.

Tutin, C.E.G. and W.C. McGrew. Chimpanzee copulatory behaviour. *Folia Primatol.* 19, 237-256, 1973.

van Lawick-Goodall, J. *In the Shadow of Man.* (Houghton Mifflin, Boston, 1971).

van Wulffden Palthe, T. and J.A.R.A.M. van Hoopf. A case of the adoption of an infant chimpanzee by a suckling foster chimpanzee. *Primates* 16, 231-234, 1975.