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COMPETITION BETWEEN THE DASYURID MARSUPIALS, *ANTECHINUS STUARTII* AND *ANTECHINUS SWAINSONII*

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A thesis submitted for the degree of Doctor of Philosophy

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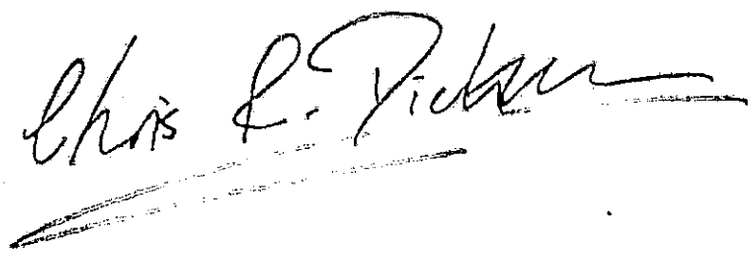
STATEMENT OF RESPONSIBILITY

This thesis is my own work, except where specifically acknowledged.



(Christopher R. Dickman)

The Brown Antechinus, Antechinus stuartii.

The Dusky Antechinus, Antechinus swainsonii.

Antechinus, my hero, small furred friend,
I come to bury, not praise you, in your house.
The sclerophyll forest - yet, if I commend
Your brief fierce life, intrepid marsupial mouse,
It is that your image, mirrored in my mind,
Strangely reflects features of my own kind.

First to rehearse your scarcely credible tale:
Born in September, reared two months in the pouch,
You live life as a solitary male;
By day in hollow trees or logs you crouch;
By night hunt worms and insects in the dew,
While owl and snake and native cat hunt you.

And, if you should survive till next July,
The time is ripe for you to find a mate;
Then, knowing that, having mated, you will die,
Your small, wild heart grows grim with rage and hate,
To hunt and savage all members of your race,
Even the female clutched in your embrace.

That copulation, charged with love and death,
May last ten hours and even more, they say;
And, though it trips the trap that stops your breath,
Does that supreme delirium repay
The solitude, the darkness, the blind strife
Of this short, savage irony, your life?

"Antechinus", A.D. Hope 1981.

SUMMARY

This thesis describes an experimental investigation of competition between the dasyurid marsupials, Antechinus stuartii and A. swainsonii. Most of the research was conducted in the Brindabella Range, Australian Capital Territory, between May 1978 and November 1981.

Initial experiments, conducted between May 1978 and December 1979, were designed to establish whether competition occurred. Five natural, semi-isolated enclosures (four experimental, one control) were established in tall open-forest; each contained populations of both species. Removal of the larger species, A. swainsonii, resulted in many shifts in the population parameters and resource use of the smaller A. stuartii. These included increased numbers, enhanced survival of newly weaned young, increases in movements, home range areas, home range overlaps, the use of complex terrestrial habitat, and the proportion of large, terrestrial invertebrate prey in the diet and decreased arboreal activity. The reintroduction of A. swainsonii produced reciprocal shifts in most of these parameters. In contrast, the removal and reintroduction of A. stuartii had little evident effect on A. swainsonii. It was concluded that competition occurred between the two species but that the effects of A. swainsonii on A. stuartii were more marked than the converse situation.

Subsequent manipulation experiments, conducted between January 1980 and November 1981, were designed to investigate the effects on A. stuartii of reducing and enhancing the numbers of A. swainsonii. When the numbers of A. swainsonii were reduced, the numbers of A. stuartii increased, and movements and arboreal activity decreased.

individuals also used more complex terrestrial habitat, and ate proportionately more terrestrial invertebrate prey. Enhancement of the numbers of A. swainsonii produced less marked, but reciprocal, responses in most of these parameters. It was concluded that the intensity of competition on A. stuartii depended, in part, on the relative abundance of A. swainsonii.

Throughout the manipulation experiments, samples of invertebrates were obtained in the enclosures by pitfall trapping, litter sampling and sticky trapping. These samples, totalling over 120,000 specimens, showed that whereas sessile invertebrates in the forest litter were abundant all year round, freely-moving invertebrates on the litter surface and tree trunks disappeared in winter. Since A. swainsonii forages principally in the litter, but A. stuartii takes freely-moving invertebrates, it appeared that the latter species could face a seasonal shortage of food. In accordance with the shifts in diet exhibited by A. stuartii when the numbers of A. swainsonii were manipulated, these findings strongly suggested that food was the object of competition.

To test the food competition hypothesis, a further experiment was conducted in 1981. Supplementary food was provided to two populations of A. stuartii, but not to a third, control population. The additional food resulted in increases in the survival, arboreal activity and body weights of A. stuartii, but a decrease in its movements. Reciprocal changes were observed when supplementary feeding was discontinued in one of the study areas. The findings demonstrated that A. stuartii was food limited, and also that competition occurred for this scarce resource.

Interference was shown to be the mechanism of competition. Antechinus stuartii probably detects A. swainsonii by smell and possibly by sound, and it responds, on a moment to moment basis, by climbing into the trees. Direct harrassment of A. stuartii by A. swainsonii has probably resulted in selection for specific competitor recognition and avoidance in the smaller species.

Transferrin allele frequencies were similar in all populations of A. stuartii, whether they were allopatric and sympatric with A. swainsonii, suggesting that gene flow occurred between them. It was proposed that gene flow between these populations could impede directional selection for divergence in sympatric A. stuartii, and so prolong competition in evolutionary time. However, some reduction in competition may be achieved by divergence in body size and possibly tail length: small body size and long tail length allow A. stuartii access to arboreal prey, whereas large body size allows A. swainsonii access to invertebrates buried in the forest litter.

In general, competition strongly influenced the population parameters and resources used by Antechinus, especially A. stuartii. This research shows that competition, in addition to habitat and climate, is probably important in determining the patterns of distribution and abundance of these marsupials.

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substitute the word "agilis" (my wife's suggestion) for "stuartii" on many thousands of specimen labels. My visit to the National Museum in Victoria was made possible by the hospitality of Dr. Mike Fleming, Ms. Rosemary Hook, and Mr. and Mrs. J. Barton.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. GENERAL INTRODUCTION ON COMPETITION AND NICHE THEORY

A simple definition of an ecological community is that it is an assemblage of organisms living together in the same area. These organisms may coexist passively, or they may interact in several ways. If only pairs of species are considered, four kinds of interactions may be distinguished: 1) the interaction is beneficial to both species (mutualism), 2) the interaction is beneficial to one species, but neither beneficial nor detrimental to the other (commensalism), 3) the interaction is beneficial to one species, but detrimental to the other (predation, parasitism), 4) the interaction is detrimental to both species (competition).

A considerable amount of research has attempted to elucidate the nature and importance of these interactions in conferring structure on both model (May 1976) and natural communities (Cody and Diamond 1975), but perhaps most controversy surrounds the importance of competition. On the one hand Bock (1972), Diamond (1978,1979), Dobzhansky (1950) and others argue that interspecific competition is of paramount importance in shaping community structure, while on the other Andrewartha and Birch (1954), Wiens (1977) and others suggest that its effects are small or negligible. In addition, recent studies of cooperation among organisms (Axelrod and Hamilton 1981) and of epigenetic selection (Steele 1979, Rosen and Buth 1980) undermine discussions of competition, and hence fuel the controversy. In asking why such a deep and divisive dichotomy has arisen between

the advocates and detractors of the concept of interspecific competition, it is instructive to review the approaches that have been used to study this phenomenon. Such a review has two further purposes. First, it serves as an introduction to the voluminous literature on competition, and second it provides background information useful in designing a research project on mammals.

In this chapter, "competition" and "niche" are introduced and defined. The theory of interspecific competition and niche is briefly discussed, and some of the approaches used to study competition, particularly among mammals, are reviewed. Studies of competition between small marsupial mammals are reviewed and finally a hypothesis is advanced that two species, Antechinus stuartii Macleay, 1841 and A. swainsonii (Waterhouse, 1840) may compete in the field.

1.1.1. Definition of "competition" and "niche"

The term "competition" is used widely in the ecological literature but often lacks precise definition. MacArthur (1972a) believed that a precise definition of competition could not be obtained, but several have nevertheless been advanced (Crombie 1947, Hartley 1948, Weatherley 1963, Williamson 1957, Birch 1957, see also Milne 1961 for a review). A definition proposed by Birch (1957) has perhaps received widest acceptance in the literature (Klomp 1961, Krebs 1972, Schoener 1977, but cf. Van Valen 1976), and is used in this thesis: "Competition occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or other in the process".

Schoener (1977) noted that this definition could apply either to populations or to individual organisms, and suggested that both applications could be used in ecological and evolutionary studies. It is important to emphasize here that only individuals can compete (Ehrlich and Holm 1962). Population responses to competition reflect the collective responses of individuals comprising that population. Competition is termed intraspecific if it occurs between individuals of the same species, and interspecific if it occurs between individuals of different species. Unless otherwise stated, the term competition is taken to imply interspecific competition throughout this thesis.

Competition, whether intra- or interspecific, is generally considered to be of two kinds (Park 1954, Miller 1967). Interference competition "....refers to any activity, which either directly or indirectly limits a competitors access to a necessary resource or requirement", whereas exploitation competition "is the utilization of a resource once access to it has been achieved" (Miller 1967). Miller (1969) described further characteristics of both kinds of competition.

Nicholson (1954) introduced the additional terms "contest" and "scramble" but these are less widely used and are considered by Miller (1967) to be broadly synonymous, respectively, with interference and exploitation. However, Ayala (1970) noted that contest and scramble can have different effects on the outcomes of competition, and discussed some possible examples among Drosophila. Interference and exploitation are used in this thesis in the sense of Miller (1967).

Central to an understanding of competition phenomena is the concept of the ecological niche. The term "niche" was used by Elton (1927) to connote the "role" of a species, especially its energy

relations, in a community, and by Grinnell (1917) to connote the habitat used by a species, together with all the essential components of that habitat. As Ayala (1970) notes, "It has become a commonplace to say that for Grinnell the niche is the "address" of the species, while for Elton the niche is the "function" or role of the organism." The niche remained a static and rather nebulous concept (see for example Linsdale 1957) until it was formally defined by Hutchinson (1958) in terms of set theory. Hutchinson proceeded by considering two independent environmental variables which can be measured along ordinary rectangular coordinates. The ranges of values of these variables within which a species can survive and reproduce are determined, and an area is thus defined. The addition of a third variable produces a volume, and when all variables relative to the species are considered an "n-dimensional hypervolume" is formed. Since this hypervolume describes the whole range of environmental conditions in which an organism or species is able to survive and reproduce, it was termed by Hutchinson the "fundamental niche". In contrast, Hutchinson (1958) defined the "realised niche" as the actual range of conditions in which an organism or species lives, and pointed out that this is almost always a subset of the fundamental niche. This dichotomy explicitly recognises that, in nature, factors such as competition may restrict the occupied region of the fundamental niche.

Although Hutchinson's original definition retains heuristic value, "niche" has since been expanded to include behavioural, structural and physiological characteristics of organisms (Odum 1959, Hutchinson 1965) or restricted to refer only to "... the nutritional role of an animal in its ecosystem....." (Weatherley 1963, see also Cohen 1978). Niche is used in this thesis in a broad sense as

defined by Pianka (1978) "the sum total of the adaptations of an organismic unit," where an organismic unit is an individual, population or species.

1.1.2. The mathematical theory of competition

The population growth of some organisms follows a simple logistic curve (Verhulst 1838; cited in Krebs 1972) which is described by the equation:

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right) \qquad \text{...equation 1}$$

where N = population size
t = time
r = intrinsic rate of natural increase (Malthusian parameter)
K = carrying capacity or maximal value of N.

This equation states that the rate of change (increase) in population size depends on the intrinsic rate of natural increase x population size x the unused opportunity for population growth (after Krebs 1972). By definition, the inhibitory effect of each individual on population growth is 1/K.

The population growth of species may be affected by several factors, among them competition for food or space from other species. Lotka (1925) and Volterra (1931) modified equation 1 to describe the population growth of two species in competition:

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1-N_1-\alpha_{12}N_2}{K_1}\right) \qquad \text{...equation 2}$$

which is the population growth of Species 1, in competition and

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2-N_2-\alpha_{21}N_1}{K_2}\right) \qquad \text{...equation 3}$$

which is the population growth of Species 2 in competition.

α is a coefficient of competition and varies usually between 0 and 1. α_{12} measures the competitive inhibition (per individual) of Species 2 on the population growth of Species 1, and α_{21} the reciprocal effect of Species 1 on the population growth of Species 2. The inhibitory effect of each N_2 individual on the N_1 population is α_{12}/K_1, and the reciprocal effect of each N_1 individual on the N_2 population is α_{21}/K_2. If interspecific competition does not occur (if α_{12} or $N_2 = 0$ in equation 2 or if α_{21} or $N_1 = 0$ in equation 3) the equations reduce to the logistic form and population growth asymptotes at K. The four possible outcomes of competition between Species 1 and Species 2 are well known and depend on the relative values of α_{12}, α_{21}, K_1 and K_2:

	Relative values	Outcomes
Case 1:	$\alpha_{12} > K_1/K_2$, $\alpha_{21} > K_2/K_1$	Species initially commonest survives,
Case 2:	$\alpha_{12} < K_1/K_2$, $\alpha_{21} > K_2/K_1$	Only Species 1 survives,
Case 3:	$\alpha_{12} > K_1/K_2$, $\alpha_{21} < K_2/K_1$	Only Species 2 survives,
Case 4:	$\alpha_{12} < K_1/K_2$, $\alpha_{21} < K_2/K_1$	Both species survive.

These results are shown graphically in Krebs (1972), Fenchel and Christiansen (1976) and Hutchinson (1978).

The logistic equation (and hence equations 2 and 3) is based on several assumptions (Krebs 1972) and has been criticised extensively for its apparent lack of relevance to nature (Andrewartha and Birch 1953 and 1954, Smith 1952, Slobodkin 1961, Wiegert 1979, Ayala 1970 and references therein). Such criticism has been addressed by incorporating qualifying terms into equations 1-3, which take account of density independent mortality (Shorrocks and Begon 1975),

genetical heterogeneity (Levin 1971, Leon 1974), immigration/ emigration (Langhaar 1972, Levins and Culver 1971), time lags (Wangersky and Cunningham 1956, MacDonald 1978), threshold effects (Wiegert 1974), non-linear effects (Gilpin and Ayala 1973) and resource renewal and availability (Wiegert 1974, Shorrocks et al. 1979). Many other modifications of the logistic and Lotka-Volterra competition equations are documented in Wangersky (1978) and Schoener (1977).

The logistic equation adequately describes the growth of some invertebrate organisms such as protozoa (Gause 1934, Vandermeer 1969, cf. Feller 1940) and some insects (Chapman 1928, Crombie 1945) in the laboratory, but it is less successful in describing the population growth of vertebrates in the field (Sewertzoff 1933, cited in D'Ancona 1954, Krebs 1972 and references therein). Despite problems with the logistic and Lotka-Volterra equations, they have been of great heuristic value in the development of concepts of limiting resources, competition coefficients and diffuse competition, which are introduced in section 1.1.3.

Alternative mathematical treatments of competition are provided by Schoener (1973,1974a), Kerner (1957,1959), Levins (1975,1979), Wilbert (1971), Brown (1981) and others. Some treatments, such as that of Herbert et al. (1956), are mathematically related to the Lotka-Volterra equations (Waldon 1975); others, such as that of Turelli (1981), are structurally analogous. These treatments have not yet received wide currency in the literature.

1.1.3. The theory of niche

In situations where two species compete for a common and finite resource, the Lotka-Volterra equations (section 1.1.2.) predict that

either one species or both species will survive indefinitely. To introduce niche theory it is convenient to examine some of the theoretical consequences of these predictions.

1.1.3.1. Ecological exclusion and coexistence

Exclusion is the elimination of one species by another species in a competitive situation (cases 1-3, section 1.1.2.), whereas coexistence (case 4, section 1.1.2.) occurs when each population inhibits its own population more than that of the other species. In this section, I consider ecological exclusion and coexistence that arise from present-day competitive interactions. The evolutionary consequences of past competitive interactions are considered largely under the heading "evolutionary coexistence" (section 1.1.3.2.), although some overlap between sections is inevitable.

Originally attributed to Gause (1934), the concept, or principle, of competitive exclusion has been stated concisely by Hardin (1960) as "complete competitors cannot coexist". Although circular (Cole 1960, Slobodkin, 1961, Peters 1976), the principle has been interpreted to mean that two coexisting species must differ in their use of the environment, and hence that each exploits a different resource (MacArthur and Levins 1964, Rescigno and Richardson 1965). The principle has received its strongest support from experiments in which populations of microorganisms have been forced to interact to extinction or equilibrium in simplified laboratory environments (see reviews by Crombie 1947, Hassell 1976, Hutchinson 1978). However, Ayala (1969) has challenged the findings of such studies by documenting coexistence in fruit flies competing for limited food and space (see replies by Gause 1970, Ito 1971, Gilpin and Justice 1972),

and additional cogent criticism of field evidence for exclusion has been provided by Birch (1979) and Den Boer (1980).

Several questions arise from the principle and from attempts to interpret it:

How different must species be before they can coexist?

How are such differences measured?

How do similar species divide the environment among themselves?

Levins (1968) states that measurements of some niche parameters (sensu Hutchinson 1958) suffice to address such questions. These parameters are niche breadth, niche overlap, niche dimension and community diversity. Although the niche has an infinite number (n) of dimensions, for practical purposes niche parameters are usually calculated from three dimensions only: place, food and time (Pianka 1978). Each dimension may, however, be subdivided (see Schoener 1974b).

Niche Breadth. Niche breadth (B) is the "distance through" the niche along a particular resource coordinate (Levins 1968). It may be measured by:

$$\log B = -\Sigma pi \log pi$$

or

$$1/B = \Sigma\, pi^2$$

where pi is the proportion of the species which is found in, or selects, environment i (Levins 1968, Colwell and Futuyma 1971). Measurements of niche breadth allow comparisons to be made of specialist (narrow B) versus generalist (broad B) species, and may lead to conclusions about patterns of exclusion.

Levins (1968) notes that species with broad niches are often more abundant than species that occupy narrow niches, and are more

likely to occur in "uncertain" environments. Niche breadth may also increase when resource availability decreases (Schoener 1971, Charnov 1976). When resource units are in short supply, it may be advantageous for consumers to accept each item that is encountered, since the expectation of encountering other, superior items, is low (Charnov 1976). In terms of competitive exclusion, specialist species are more likely to eliminate generalist species from the relatively narrow part of the niche axis that they occupy, but generalists may predominate elsewhere (Pianka 1978, cf. MacArthur and Levins 1964, 1967). Pianka (1978) discusses other effects of interspecific competition on niche breadth, and Van Valen (1965) and Roughgarden (1974) discuss consequences of differences in niche breadth of individuals comprising a single population.

Niche Overlap. Niche overlap (O) is the joint use of a resource or environmental variable by two organismic units, and is directly relevant to considerations of interspecific competition and exclusion. If the niches of two species do not overlap, perforce they cannot be in competition. Conversely, if the niches of two species do overlap, competition may occur but its intensity may be influenced by:

1) The degree of environmental fluctuation (Hutchinson 1958, May and MacArthur 1972, cf. Ågren and Fagerström 1980)
2) The temporal stability of the place of competition (Hutchinson 1953,1961)
3) The operation of density independent factors (Andrewartha and Birch 1954, Pianka 1972, cf. Abrams 1977)
4) The vagility of the competitors (Ross 1957 and summary in Hutchinson 1965)

5) Predation (Paine 1966, Parrish and Saila 1970, cf. Cramer and May 1971)

6) Parasitism (Utida 1953)

7) Intraspecific regulation of numbers below environmental carrying capacity (Marshall 1960)

8) Hybridisation (Alerstam et al. 1978)

9) Agressive neglect (Ripley 1961, Brown 1971), and other factors.

Hence, the relationship of niche overlap to interspecific competition and exclusion may be complex.

Despite the complex relationship between niche overlap and interspecific competition, several studies nevertheless suggest that coexistence is unlikely if overlap is high (MacArthur and Levins 1967, May 1974). If only one resource dimension is considered, coexisting species are often found to assort evenly along it and exhibit regular niche dispersion. Well known examples are the sizes of seeds eaten by desert rodents (Brown 1975), altitudinal zonation of birds (Diamond 1973) and body sizes of mammals (Coe 1975, Fox 1982a). May and MacArthur (1972) suggest that the formal limit to similarity of such competitors corresponds (in a varying environment) to a pattern in which the means of the resource utilisation curves of adjacent species are separated by a distance of about one standard deviation of the curves. This model has been generalised by May (1974) to consider multidimensional niche space.

For habitat, a commonly-used measure of overlap is:

$$O_{ik} = \frac{\sum_j p_{ij}\, p_{kj}}{\sum_j p_{ij}^2}$$

where p_{ij} refers to the proportion of resource type j used by consumer i (MacArthur and Levins 1967). This measure may be related to the competition coefficient α in the Lotka-Volterra equations (MacArthur 1968,1972b). MacArthur (1972b) argued that to infer competition was reasonable if the resources consumed by two species were similar, and further, if there was a close correspondence between habitat overlap and total resource overlap. The use of overlap measures as approximations of competition coefficients has, however, been criticised (Colwell and Futuyma 1971, Schoener 1974a, Abrams 1975,1980), and has led to alternative methods of estimating α (Schoener 1974a, Hallett and Pimm 1979). Lawlor (1980) argued further that measures of niche overlap reflect only consumer-environment interactions, and suggested that measures of species similarities are more appropriate in detecting past (and possibly present) responses to competition.

A second approach to the question of niche overlap involves the concept of coevolution (Lawlor and Maynard Smith 1976, Slatkin and Maynard Smith 1979, Roughgarden 1976). Instead of asking how much overlap is tolerable along a resource dimension, these studies consider how species partition resources to maximise the fitness of the individuals. Roughgarden (1976) assumed that niche breadth was fixed, but niche position was free to shift under selection. Under these conditions, the fitness of individuals of two or more species was maximised at a particular niche position that represented a trade-off between mutual avoidance of interspecific competition (coevolution), and tolerance of resources that supported a lower carrying capacity (K). Further studies of coevolution have proposed theoretical models for two species and two resources (Pimm and Rosenzweig 1981), n

genotypes and one resource (Matessi and Jayakar 1976), n species and one resource (Matessi and Jayakar 1980,1981) and variable niche breadth (Case 1981). A particularly lucid discussion of the coevolution of competing species is provided by Connell (1980).

Niche Dimension. Most niche theory considers only a single niche dimension at a time. In contrast, "niche dimensionality" refers to the "number of factors which serve to separate species" (Levins 1968), and emphasises that competition may be spread among several species that overlap in their use of several niche dimensions.

The theory of niche dimensionality appears to have been approached in two ways. First, in a direct extension of Gause's (1934) contention that two species cannot occupy the same niche (coexist on a common resource), several studies have attempted to model the coexistence of n species on n or < n resources (Armstrong and McGehee 1976, Haussman 1973). Such models fall into two groups according to whether the regeneration of resources is described by (1) an algebraic relationship or (2) differential equations (Armstrong and McGehee 1980). Group 1 models (Waldon 1975) assume that the specific growth rates of competitors are linear functions of resource densities, and resources, such as space or nutrients, are abiotic. Group 2 models (Koch 1974, Hsu et al. 1978) allow the specific growth rates of competitors to be non-linear functions of resource densities. The resources, such as prey, are assumed to be biotic and hence have their own dynamical properties. These models conclude that n competing species cannot coexist on < n resources if their densities are fixed and the specific growth rates vary linearly with resource density, but coexistence is possible if both constraints are relaxed (Armstrong and McGehee 1980).

The second approach to investigating the theory of niche dimensionality introduces the concept of "maximum tolerable niche overlap" (Pianka 1972). Pianka proposed that maximum tolerable niche overlap should be lower in communities where interspecific competition is intense than in communities where it is weak. This proposal assumes that when the demand for resources is low relative to supply, competitors may tolerate some overlap in resource use. Conversely, when the demand/supply ratio is high, overlap in resource use may not be tolerated. The extent of niche overlap may be closely related to the total competitive effects of several interspecific competitors in a community (Pianka 1974); this situation has been termed "diffuse competition" (MacArthur 1972b). MacArthur (1972b) noted that the numbers of potential "neighbours" (specific overlaps in resource use) in niche space increase roughly geometrically with the numbers of niche dimensions added. Hence, as more niche dimensions are subdivided by species, the potential for diffuse competition increases (Pianka 1974). Diffuse competition may also be most evident among closely related species, and so lead to a negative correlation between the mean population densities of species and their taxonomic distance (Hebert et al. 1974, cf. Taylor and Woiwod 1975, Den Boer 1980). Methods of measuring niche overlap along two or more dimensions have received comparatively little attention (see also section below on the community matrix), but have been discussed by Pianka (1974), Cody (1974) and May (1975).

The Community Matrix. Proceeding from the Lotka-Volterra equations (equations 2 and 3), Levins (1968) introduced the concept of the community matrix. For a community composed of n species, an n x n

matrix may be constructed that shows the coefficient of competition (α) for each pair of species. Because competition results in the mutual inhibition of population levels, pairs of competing species have positive α's; the magnitudes of these values, which may not be symmetrical, indicate the intensity of competition. In communities where diffuse competition is intense, relatively more cells of the matrix will contain positive α's, and the variance of the matrix will fall. This property led Pianka (1974) to propose "mean nonzero niche overlap" as an inverse measure of the intensity of diffuse competition, after substituting a measure of overlap (Pianka 1973) for competition coefficients in the community matrix. Pianka (1978) and Pianka et al. (1979) discuss further aspects of the community matrix concept.

1.1.3.2. Evolutionary coexistence

The Lotka-Volterra competition equations assume, among other things, that intrinsic rates of natural increase (r), competition coefficients (α) and carrying capacities (K) are constant among all individuals and populations. Further, two competing species are not allowed to diverge (they are genetically immutable), and the environment where competition occurs is usually assumed to be homogenous (cf. Levins and Culver 1971, Slatkin 1974).

In natural populations, however, these assumptions are rarely justified: natural selection may favour niche separation (reduction of niche overlap), and hence lead to a reduction over evolutionary time of the mutually depressing effects of interspecific competition. Some aspects of the evolution of competing species have been modelled (Leon 1974, Fenchel and Christiansen 1977, Roughgarden 1976,1979 and other references above), but the evolutionary consequences of interspecific competition on the patterns of resource use of organismic

units are nevertheless controversial (e.g. compare Dobzhansky 1950, Pianka 1978 with Birch and Ehrlich 1967). I outline below three observations that have been interpreted as evidence for the past action of competition in facilitating niche separation, and hence, coexistence: character displacement, niche dimension complementarity and body size stepping.

Character Displacement. Character displacement is "the process by which a morphological character state of a species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively" (Grant 1972a, see also Brown and Wilson 1956). Changes in the ecological, behavioural or physiological attributes of a species are considered to be analogous to morphological changes (Grant 1972a) and may reduce the intensity of interspecific competition. These changes may be convergent or divergent (Grant 1972a), and may involve unknown proportions of genetical and phenotypical components.

MacArthur and Wilson (1967) point out that character displacement may arise during the process of island colonisation. An invading species may change (narrow) the range of habitats it occupies, but not the range of foods that it eats (MacArthur and Pianka 1966, Schoener et al. 1979). Such change may at first be phenotypical and reflect the species behavioural plasticity, but later be translated into genetical differences by natural selection (MacArthur and Wilson 1967). Sequential invasions of species may hasten this process in the older residents of islands (MacArthur and Wilson 1967, see also Nørrevang 1959). Ecological character displacement has been modelled by Slatkin (1980), and an interesting

possible example of character displacement in the fossil record is discussed by Eldredge (1974).

The converse situation to character displacement has been termed character release (MacArthur and Wilson 1967), and it may be defined in the same way as character displacement above, except that the word absence is substituted for the word presence (Grant 1972a). Character release does not facilitate niche separation: it reflects instead a tendency for a species to occupy a greater range of habitats and show greater variability in some morphological characteristics (Van Valen 1965, cf. Beever 1979) when competition from other species is reduced or absent.

Niche Dimension Complementarity. If the patterns of resource use of two species are considered, niche dimension complementarity is the tendency for high overlap along one niche dimension to be associated with low overlap along other niche dimensions (Schoener 1974b, Huey 1979). This pattern is presumed to reflect the past action of interspecific competition, and it is expected to reduce the overall, or multidimensional, niche overlap between the two species. Schoener (1974b) suggests that separation along the habitat dimension is often more important than separation along the food-type dimension, which is often more important than separation along the temporal dimension. Separation may, however, be very fine and difficult to detect (Broadhead and Wapshere 1966).

Body Size Stepping. Hutchinson (1959), Schoener (1965) and others have reported that a constant ratio exists in the body sizes, or sizes of the trophic apparatuses, of two or more coexisting, related species. Such "body size stepping" may allow consumers access to foods of different sizes or types; this may reduce dietary overlap,

and hence reduce interspecific competition. Body size stepping may not be advantageous if the populations concerned diverge in other ways, and in this respect, the phenomenon may be a special case of niche dimension complementarity. The biological importance of body size stepping has been questioned by Horn and May (1977) and Simberloff and Boecklen (1981) on the grounds that actual size ratios differ little from randomly generated ratios.

Past competitive interactions must be inferred from their present day results, and this usually necessitates comparison of allopatric with sympatric populations of species, or detailed knowledge of their past distributions. As Birch and Ehrlich (1967), Grant (1972a) and Paterson (1978) point out, such knowledge may be difficult to obtain, and inferences concerning the past action of competition should be used with caution.

1.2 CRITERIA FOR RECOGNISING INTERSPECIFIC COMPETITION IN NATURAL COMMUNITIES

The above introduction provides a brief and simplified view of some aspects of competition and niche theory. In general, the theory seems to be far in advance of what is known about many natural communities of organisms (see Colwell and Fuentes 1975), and much theory can be expected to be irrelevant for organisms of a particular community. For example, interspecific competition is more likely to contribute to the structure and diversity of mammalian communities than to communities of bivalve molluscs (Stanley 1974, see also Menge and Sutherland 1976), and mechanisms of competition may differ between individuals competing for space (a non-renewable resource) or for food (a renewable resource) (Yodzis 1978). Such differences may contribute to the dichotomy of opinion about the importance of

interspecific competition in shaping community structure (section 1.1); they also make it difficult to apply criteria for recognising competitive phenomena in nature. Before considering competition between species of small mammals, I consider what criteria are necessary to provide unequivocal evidence for interspecific competition from field data.

There appear to have been three broad approaches, where observations are made of species populations 1) in sympatry only, 2) in sympatry and allopatry, and 3) following the manipulation of abundances of resources or competitor species. The first approach compares the relative abundances, and/or the relative spatial distributions, and/or the niche associations of populations of two or more species that occur together. Competition may be occurring if the populations show an inverse numerical or spatial association. Parapatry, whether stable as in altitudinal zonation, or unstable as in invasions, may represent the most extreme form of inverse association. In contrast, observations of niche dimension complementarity and body size stepping between the species (section 1.1.3.2) may suggest that competition has occurred in the past. Competition coefficients are sometimes calculated to increase confidence in inferences of competition, but other, biologically intractable methods of estimating competition have also been advocated (e.g. Emlen 1981). This first, observational approach, is widely used to infer the existence of competitive interactions between organisms (Schoener 1974b), although the results may also be interpreted in other ways, such as predation (Eadie 1952), or interspecific differences in habitat selection (Schroder and Rosenzweig 1975, Rosenzweig 1977).

The second approach compares populations of one species which occur in allopatry and in sympatry with other species. Present day competition may be inferred if the size, distribution or resource use of a population is depressed in the presence of, but not in the absence of, populations of one or more competitor species, whereas past competition may be inferred if character displacement or character release are observed (section 1.1.3.2). As with the first approach, however, allopatric/sympatric comparisons provide equivocal evidence for competition, since the results may reflect responses to geographical differences in resource levels rather than responses to competitors.

The third approach is the experimental manipulation of resources or population sizes of competitor species; this provides the most convincing evidence for present-day interspecific competition, although it fails to reveal mechanisms of competition (Schoener 1974b) and may often be impractical and time-consuming (Pianka 1978). Grant (1972b) graphically illustrated three steps required to unequivocally demonstrate competitive interactions in a two species, two habitat system. If the investigator wishes to examine the effect of Species 1 on Species 2, three similar enclosed study areas are required, each containing similar proportions (50%) of the habitat preferred by each species. In the first step, Species 2 is placed into each of the three enclosures, but Species 1 is placed into one enclosure only. Competitive interactions may then be inferred if Species 2 occurs in the habitat preferred by Species 1 more frequently in the absence than in the presence of that species. This inference may not be valid, however, if the two-species enclosure differs in certain ways from the single species enclosures, or if the

population parameters of Species 2 differ between the enclosures. In the second step, all individuals of Species 1 are removed from the first enclosure and placed into a second enclosure formerly housing only Species 2. Competitive interactions may again be inferred if Species 2 occurs in the habitat preferred by Species 1 more frequently in the absence than in the presence of that species, but confidence is gained in the knowledge that other factors (enclosure differences or differences in the population parameters of Species 2 between enclosures) are now less likely to be important. The inference of competitive interaction is critically tested in the third step when, following the reintroduction of Species 1 back into the enclosure from which it was removed in the first step, Species 2 again exhibits the pattern of habitat use observed previously in two-species conditions. A discussion of the advantages and disadvantages of such manipulations is given by Grant (1972b). Two further points should be mentioned that pertain to uncertainty, or indeterminism, in the outcome of competition between species in the enclosures. Indeterminism may occur first, if the genetical constitutions of individuals of each species differ between enclosures (Lerner and Dempster 1962, King and Dawson 1972 and references therein), and second, if species that are superfluous to the investigations are present, whether as competitors, or as predators (e.g., Morin 1981). Indeterminism may be reduced if organisms of known genetical constitutions are used, and if superfluous species are removed.

Reynoldson and Bellamy (1971) discuss five criteria that constitute evidence for interspecific competition in the field. Although these are essentially an expansion of the three approaches outlined above, these authors emphasise the additional need to show

that competing species use a common resource. The observational and the experimental approaches listed above may both be necessary to answer evolutionary questions of community structure and function that implicate interspecific competition (Grant 1978), but the experimental approach alone may suffice to address questions concerning present-day, competitive interactions.

1.3 INTERSPECIFIC COMPETITION AMONG SMALL MAMMALS

Studies of small mammals reflect the dichotomy that exists in the larger scientific literature concerning the importance of interspecific competition in shaping community structure. Van Valen (1978) and French (1978) suggest that competition is a major organising force in (eutherian) mammal communities, but the subject is given scant mention in several recent works (for example, Stoddart 1979, Hendrichs 1978, Golley et al. 1975). Few long term studies of mammals have been conducted (Keith 1973), and this may have hampered application of classical Lotka-Volterra theory (cf. de Bruyn 1980).

1.3.1 Interspecific competition among small eutherian mammals

Grant (1972b, 1978) concluded that most of the evidence for interspecific competition among small eutherian mammals (especially rodents) was derived from observations of two or more sympatric species that exhibit either an inverse numerical or an inverse spatial relationship. Subsequent studies have generally supported this conclusion. In field studies, Drickamer (1978), Henttonen et al., (1977), Montgomery (1978), Blaustein (1980) and Glass and Slade (1980) have inferred competition from inverse numerical associations

between sympatric species, whereas Myllymäki (1977), Randall (1978), Mehlhop and Lynch (1978), Lackey (1978), Dienske (1979) and de Jonge and Dienske (1979), have inferred or discussed competition from inverse spatial associations between sympatric species. Krebs (1977) inferred competition from an inverse numerical association between the voles Microtus pennsylvanicus and M. ochrogaster in high density field enclosures, and similar inferences have also been drawn from inverse spatial associations between species in confined laboratory conditioins (Blaustein and Risser 1974, Petersen and Helland 1978, Petersen 1979).

Further inferences about competition have been derived from other kinds of observations. Thus stable parapatry, presumably due to competition between two species, has been recorded by McPhee (1976), Meredith (1977) and Weigl (1978); unstable parapatry (invasions) by MacKinnon (1978) and Taylor (1978); character release by Patterson (1981) and Lawlor (1982); possible examples of character displacement by Erdakov et al. (1978) and Niethammer (1978); and diffuse competition by M'Closky (1978) and Glazier (1980). All examples except one (Niethammer 1978) concern species of rodents; evidence of competition between species in other mammalian Orders is very weak (Fargher 1977, Hawes 1977, Andersen 1978, Fleming 1979) or disputed (compare Grainger and Fairley 1978 with Ellenbroek 1980).

All the above studies provide observations suggestive of competition, but they do not prove it (see Section 1.2). Stronger, less inferential evidence for interspecific competition, has been obtained in several studies in which resources or the population densities of competing species were manipulated (Table 1.1). Most of

these studies were published after the reviews of Grant (1972b, 1978) and Brown (1978), and all concern species of rodents. Of the 13 studies listed, only two conducted all the steps necessary to demonstrate competitive interactions (section 1.2), and some dealt with the more complicated situations of three or more species. Most studies discussed other, corroborative, evidence for competition however, so that objections to the interpretation of competition may as Diamond (1978) puts it, "strain one's credulity". Hence these experiments and those of Grant (1969, 1970, 1971) and others (reviewed in Grant 1972b, 1978) provide the strongest available evidence for interspecific competition among small mammals. Other manipulative experiments, such as those of Schroder and Rosenzweig (1975), have shown that present-day competitive interactions do not always occur, although they may have occurred in the past.

In general, mechanisms of competition among species of small mammals are poorly known, although Brown (1978) has suggested that interference interactions are characteristic of rodents inhabiting grassland and mesic forest, whereas exploitation interactions characterise those inhabiting desert and arid grassland. Laboratory observations of interspecific intolerant (aggressive) behaviour sometimes conflict with expectations derived from fieldwork (see Baenninger 1973). The outcomes of interspecific encounters may depend on the prior intraspecific experience of the combatants (McElman and Morris 1977) or prior experience of elements such as shelters in the test arenas (Banks et al. 1979). The intensity of such encounters may depend also on the reproductive status of one or both of the interacting species (Rowley and Christian 1977).

Further generalisations about competition between species of small mammals and introductions to the extensive literature on this topic are provided by Grant (1972b, 1978) and Brown (1978).

1.3.2 Interspecific competition among small marsupial mammals

Evidence for competition among small marsupials is almost wholly observational, and only one study (Serventy 1951) has been explicitly concerned with competition. Marsupials have traditionally been considered as second-class, inferior mammals, able to flourish only because of the lack of early eutherians to compete with them (Lillegraven 1974, 1975). Although this view is disputed (Kean 1961, Kirsch 1977, Low 1978), until recently very few studies have attempted to examine the possible importance of competition in shaping community structure (but cf. Fox 1981, 1982a,b; Main 1978). Laboratory studies of competitive interactions are even more sparse, although some preliminary and unpublished encounters have been conducted by Kenner (1972), Braithwaite (1973) and Biggins (1979). This situation stands in sharp contrast to the large number of competition studies conducted on small eutherians (section 1.3.1), and suggests either that small marsupials rarely compete, or that the interpretation of competition is seldom applied.

In view of the paucity of direct evidence for interspecific competition, much of the literature on the geographical distributions, ecology, behaviour, taxonomy, biogeography and reproduction of Australasian small marsupials has been reviewed for inferences suggestive of competition (Dickman in press,a). The inferences were adduced from a review of 356 published and unpublished studies (Appendix 1), and were based largely on observations of differences

in patterns of niche use by two or more species. The inferences led to three preliminary generalisations (Dickman in press,a). First, differences in the patterns of niche exploitation between guilds (sensu Root 1967) of small marsupials lead to differences in the patterns of competition among member species. Second, interference competition is probably most prevalent among arboreal marsupials (Biggins 1979), whereas exploitation competition may occur among some of the smaller, terrestrial species. Third, competition between small marsupials occurs only in the peripheral, forested areas of Australia and possibly in New Guinea.

Apparently nothing is known of competitive interactions between species of Neotropical small marsupials (Hunsaker 1977, Streilein 1982), although interesting patterns of niche separation among sympatric species of Mouse Oppossums (Marmosa spp.) are discussed by O'Connell (1979).

McNab (1980) concluded that marsupials are competitively inferior to eutherians because (other things, such as body weights, being equal) their basal metabolic rates and intrinsic rates of natural increase (r) are relatively low. This conclusion ignores the success of invasions of marsupials such as Cuscuses (Phalanger spp.) into faunas already rich in eutherians (Hooijer 1950, 1958; Groves 1976), but it should also serve to stimulate research on the actual competitive abilities of species of marsupials, and on the importance, prevalence and nature of interactions that occur between these species.

1.4 A HYPOTHESIS: COMPETITION BETWEEN TWO SPECIES OF SMALL MARSUPIALS, ANTECHINUS STUARTII[1] AND A. SWAINSONII.

The foregoing sections have attempted to introduce some of the mathematical and conceptual approaches to the study of interspecific competition, and to show further how some of these approaches have been used in studies of small mammals. This section introduces two species of small dasyurid marsupials, Antechinus stuartii Macleay, 1841 and Antechinus swainsonii (Waterhouse, 1840), and proposes a hypothesis that these species compete with each other in natural conditions.

Antechinus stuartii and A. swainsonii occur sympatrically throughout much of their geographical ranges, although the smaller species, A. stuartii, occurs in a wider range of habitats than its larger congenor (Appendices 2a and 2b). The two species are similar in several aspects of their biology (compare Appendices 2a and 2b), but additional evidence on which to propose a hypothesis of competition is provided by the following observations.

1) The arboreal activity of A. stuartii increases when the activity of A. swainsonii increases on the ground (Hall and Lee 1982).

2) Correlations of the numbers of captures of each species at a trapsite are sometimes negative (Hall and Lee 1982).

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[1] Preliminary genetical evidence suggests that the form of A. stuartii encountered in this study differs at least subspecifically from populations of the nominate subspecies A. s. stuartii of coastal New South Wales. There are, however, no evident genetical differences among any of the populations sampled in this thesis; hence until definitive taxonomic evidence is obtained, it is convenient to refer to them as A. stuartii. The taxonomic status of A. stuartii is currently under review (P.R. Baverstock and D.H. King, personal communications; unpublished findings).

3) A negative correlation of percentage capture rates of the two species over several trapping sessions has been recorded (Reed and Wallis 1975). (Note: this correlation was not discussed by these authors, but a correlation coefficient r of -0.89, $P < 0.001$ was calculated from Table 1 of their paper. This value excludes data from their area "X" where no animals were captured).

4) The absence of A. stuartii from apparently suitable forest may be attributable to the "unusual abundance" of A. swainsonii (Emison et al. 1975).

5) The two species show an inverse spatial association at certain times of the year (D.P. Woodside, personal communication).

Although tenuous, these observations suggest that the distributions of the two species may at times vary inversely in space, or their numbers may vary inversely. As Grant (1978) notes, such observations are consistent with the interpretation of competition, but they do not prove it. From May to August 1978, a pilot study was conducted in the Brindabella Range near Canberra to investigate whether the hypothesis of competition was indeed sufficient to account for shifts in the population parameters or resource use of the two species. It was. Consequently, a series of manipulative experiments was designed and carried out to test more fully the hypothesis of interspecific competition, and to investigate in more detail the extent and kinds of changes that were attributable to such competition. These experiments are described in Chapter 2.

Table 1.1. Studies of interspecific competition among small eutherian mammals in which population (or resource) manipulations have been conducted. Underlining shows which parameters (population or resource) were measured but did not change; ticks indicate those parameters that changed, after manipulations, in one or more of the species investigated. Parameter changes were in the direction expected if competition was occurring, except where stated below.

Source	Steps conducted *	Manipulations conducted on one or more spp? **	Effects of manipulations: Population parameters: Numbers	Survival	Sex ratio	Breeding	Movements	Body Wt.	Resource use: Habitat	Micro-habitat	Activity
Joule and Jameson (1972)	1,2	2/3	_____		√			√			
Cameron (1977, Cameron et al. 1979)	1,2	2/2	a√	_____	_____	a√		a√			_____
Redfield et al. (1977)	1,2,3	1/2	b√	_____		√					
Price (1978)	1,2,3	3/4								√	
Mann and Bindra (1978)	1,2	1/3		?	√						
Chappel (1978)	1,2	2/3					_____		√		
Terman (1978)	1,2	2/2	√	√	√		√	_____	√	√	
Wondolleck (1978)	1,2	1/2								√	
Abramsky et al. (1979)	1,2	3/5	√								
Pitcher and Keller (1979)	1,2	1/2	_____	?√	√	_____	_____				
Holbrook (1979)	1,2	3/3	_____						√	c√	
Gliwicz (1981)	1,2	1/3	√	√		a√	√				
Montgomery (1981)	1,2	2/2	√	_____		√		_____	√	_____	

* Step 1 refers to observations of two or more species in sympatry; step 2 refers to observations of one species after one or more competitor species have been removed; step 3 refers to observations of the same species after the competitor species have been reintroduced. These steps are a simplification of the procedure described in section 1.2.

** The first figure (numerator) shows how many species were manipulated, the second figure (denominator) shows the total number of species used in the study.

Notes: [a]Changes in these parameters were in the opposite direction to those expected if competition was occurring. [b]Trappability also changed. [c]Arboreal activity changed.

CHAPTER 2

COMPETITION BETWEEN A. STUARTII AND A. SWAINSONII: THE EFFECTS OF COMPETITOR REMOVAL AND REINTRODUCTION

2.1 INTRODUCTION

Experimental manipulations of resources or the population sizes of sympatric species provide the best test of the hypothesis that these species are currently competing (section 1.2). What kinds of experiments are most appropriate? At the beginning of this study, competitive interactions between A. stuartii and A. swainsonii were only suspected, and the demonstration of such interactions, or the lack of them, was the most important initial aim. Appropriate experiments to demonstrate the existence of current competitive interactions are those in which one species is observed in the presence of a second species, and again when the second species has been removed. Hence this chapter describes only the effects of complete removal of one species of Antechinus on population parameters and patterns of resource use of the other species. These experiments were conducted between May 1978 and December 1979.

The success of experimental manipulations depends largely on where and when they are conducted, and on a basic knowledge of the species that are to be manipulated. These considerations are discussed briefly before the experimental design used in this chapter is presented.

Where should experimental manipulations of Antechinus populations be conducted? Grant (1972b) noted that species manipulation experiments can be conducted more easily on enclosed populations than on unrestrained ones, and in his experiments, actual fenced-in enclosures were used. Although such enclosures may give

the investigator control over the interacting species and their predators (Grant 1972b), they suffer two disadvantages. First, enclosures are expensive and laborious to construct, and second, they artificially restrict movements and may lead to unu ually high population densities (Krebs et al. 1973). In contrast, unenclosed populations are more "natural", but the investigator usually has little control over the numbers of animals present or their population structure.

In the present study, artificially enclosed populations of Antechinus were not available, but a population that was naturally enclosed had been identified by Stewart (1979a, b) in the Brindabella Range, near Canberra, Australian Capital Territory. Stewart (1979a, b) found that populations of A. swainsonii, and to a lesser extent A. stuartii, were restricted to dense habitat along the bottom of a valley; few captures of either species occurred in more open habitat or in an exotic pine plantation on the surrounding slopes. The use of such a "natural enclosure" would, it was hoped, overcome the disadvantages of studying artificially enclosed populations and unrestrained ones, and hence was considered potentially suitable for conducting manipulation experiments. Other "natural enclosures" were found near the one trapped by Stewart (1979a, b), and these are described in section 2.3. Henceforth, "natural enclosures" are referred to simply as "enclosures".

When should experimental manipulations of Antechinus populations be conducted? Both species of Antechinus live in relatively predictable, seasonal environments, and, within any population, reproductive and population events usually occur at the same time each year (Lee et al. 1977, 1982). As far as possible, it was felt

desirable to time population manipulations to coincide with times of natural population upheaval or movement, since this would involve less trauma for displaced animals and also allow subsequent observations to begin when populations were "settling down" again. Studies of A. stuartii in Queensland suggested that two such times would be appropriate. The first would be in May-June when juveniles disperse from their maternal home ranges and nest alone (Braithwaite 1979). The second would be when male movements increase prior to mating in late September (Wood 1970). Near Canberra, A. stuartii mates at least a month earlier than in Queensland (Moore 1974), so corresponding increases in movements were also expected to occur earlier. Antechinus swainsonii mates even earlier (July) than A. stuartii in the Canberra area (Moore 1974); hence appropriate times to conduct manipulations for both species were considered to be in March-April and July.

What are the likely responses to competition in the two species of Antechinus? In rodents, interspecific competition may influence a wide range of population phenomena and patterns of resource use (section 1.3.1), and it is reasonable to expect that competition, if it occurs, may also influence populations of Antechinus in similar ways. Hence, to investigate the kinds of responses to competition in Antechinus, observations were made of several population parameters, and also of the resources used by these populations. These are listed below.

Population parameters	Resources
Numbers	Habitat (terrestrial)
Composition	Habitat (arboreal)
Survival	Food (type and size)
Trappability	Time (periodicity of activity).
Reproduction	
Movements	
Home range (size and overlap)	
Body size (weight and length).	

Some population parameters, such as trappability and body size, have little relevance for understanding population structure and dynamics, but are included because they may nevertheless be affected by competition. The terms "population parameters" and "patterns of resource use" are used throughout this thesis to refer either collectively or specifically to the population parameters and resources listed above.

2.2 EXPERIMENTAL DESIGN

A series of simple experiments designed to investigate competition between A. stuartii and A. swainsonii is shown in Fig. 2.1. Each of the rectangles (EXPT. 1 - EXPT. 4 and CONTROL, Fig 2.1) represents an enclosure containing the two species. In the first step, conducted between May and early July 1978 (July I), population parameters and patterns of resource use of the two species were monitored in all enclosures. In the second step conducted between late July 1978 (July II) and early April 1979 (April I) A. swainsonii was removed from two enclosures (EXPT. 1 and EXPT. 2), A. stuartii was removed from two other enclosures (EXPT. 3 and EXPT. 4), and the fifth enclosure was left intact as a two species control. If one species exhibited an expansive shift[1] in population parameters or patterns of resource use in the enclosures from which its congenor

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[1] "Expansive" here refers to an increase in population size and associated parameters such as survival, as well as to an increase in the kinds and amounts of resources used. Conversely, a decrease in such parameters in the absence but not in the presence of a congenor would indicate not competition, but mutualism.

had been removed, but not in the control enclosure where its congenor remained, it would be reasonable to infer that competition occurred. In the third step, conducted between late April 1979 (April II) and December 1979, this inference would be critically tested by reintroducing the species which was formerly removed from two enclosures back into one of these enclosures (A. swainsonii into EXPT. 1, A. stuartii into EXPT. 3, Fig. 2.1); a reciprocal shift in population parameters or patterns of resource use of the other species would confirm that competition occurred.

This experimental design has several advantages and a disadvantage. On the positive side, the enclosures are natural and semi-isolated, and the effects of A. swainsonii on A. stuartii, and of A. stuartii on A. swainsonii, are clearly separable. In addition, the entire experiment was designed to last 1½ years, so that a further replication of the entire design would be possible within the three year duration of a Ph.D. scholarship. (This design was not, after all, repeated in 1980-81, due to unforeseen events that are described in later sections.) On the negative side, a superfluous and abundant third species, the Bush Rat Rattus fuscipes (Waterhouse, 1839), was also present. This disadvantage is discussed in section 2.6.

2.3 THE ENCLOSURES

Preliminary trapping in May 1978 revealed three enclosures, including the one trapped originally by Stewart (1979a,b), that appeared to be suitable for manipulation experiments. The enclosures occur along Lees Creek and Blundell Creek in the Cotter Catchment, Brindabella Range, Australian Capital Territory (35°21'S, 148°50'E). The enclosures may be thought of as "islands" of relatively dense,

wet vegetation that occur along the banks of the creeks. They are surrounded by extensive areas of drier, more open vegetation or pine plantations that occur on the valley sides and ridges. The zone of contact between the dense valley vegetation and the vegetation of the slopes is usually clearly defined, but transition zones of mixed vegetation (<20 m wide) also occur.

For the purposes of the present study, the perimeters of the enclosures were defined to extend 10-30 m beyond the edges of the dense valley vegetation or transitional vegetation onto the open slopes. Preliminary trapping results, and the findings of Stewart (1979a), suggested that relatively dense populations of both species of Antechinus occurred within the enclosures, and, moreover, that movements into and out of the enclosures occurred infrequently. So defined, the enclosures were actually only semi-enclosed, but immigration to and emigration from them appeared limited. Movement of Antechinus in relation to the enclosures is discussed further below (see also Tables 2.1 and 2.2).

Before proceding further, it will be remembered that five enclosures, not three, were called for in the design described in section 2.2. Unfortunately, two further enclosures could not be found, and it was decided to subdivide the two larger enclosures to obtain the required number. Splitting these enclosures by the erection of a fence would have introduced an undesirable, artificial barrier to the movements of Antechinus. However, extensive trapping in these areas in May 1978 suggested that the creeks themselves already formed a partial barrier to movements, and moreover, that they split the two larger of the three enclosures into roughly equal parts.

The possibility of using the creeks as barriers was attractive for several reasons: they already formed partial barriers, they are continuous, at least 1 m wide throughout their lengths and, since Antechinus appear to be extremely reluctant to enter water or to wet their fur (personal observations), they were a potentially very effective means of dividing the two largest enclosures. In addition, unusually heavy rainfall in 1978 (Fig. 2.2) increased the speed and volume of water flow in the creeks (D. Platts, personal communication), and the only obvious crossing points for small mammals were fallen logs and overhanging shrubs. To increase the effectiveness of the creeks as barriers to the movements of Antechinus, small fallen logs and debris were removed throughout the lengths of the creeks in the enclosures, and overhanging shrubs were cut back. Large logs were difficult to remove and were left in place. To render them less attractive as creek crossing points, however, they were wrapped with a sheet of black polythene. It was hoped that this material, 1m wide, shiny and durable, would act as a deterrent in itself and also provide a slippery substrate for animals attempting to cross it. The effects of these efforts are described in section 2.5.1.

The habitat of the five enclosures is tall open-forest (sensu Specht 1970), dominated by Ribbon Gum Eucalyptus viminalis, Brown Barrel E. fastigata and Narrow-leaved Peppermint E. radiata. The understorey vegetation is dense and dominated by Water Fern Blechnum nudum with patches of Bracken Pteridium esculentum, Tree Fern Dicksonia antarctica and Blackberry Rubus fruticosus. Leaf litter up to 20 cm deep occurs under B. nudum; elsewhere the litter is 1-10 cm deep and composed of leaves, bark and decaying logs.

The proportional abundances of plant species appeared, subjectively, to differ little between the five enclosures.

The habitat of the slopes and ridges surrounding the enclosures is mostly tall open-forest with some open-forest (sensu Specht 1970), but in marked contrast to the enclosures, the understorey vegetation and ground litter are far less dense. No ferns or Blackberry occur on the slopes, but species that are characteristic of drier sites, such as Cassinia aculeatum, Coprosma hirtella and Lomatia myrcoides are relatively abundant. On some slopes exotic pines (Pinus radiata) have been planted; these areas are largely devoid of understory vegetation and ground litter. The vegetation of the enclosures and the surrounding slopes is compared in Figs. 2.3a and 2.3b; more detailed information and plant species lists are provided by Florence (1973) and Stewart (1979b).

All five enclosures are linear and follow the shapes of the valley floors (Figs. 2.4a-2.4c). The control enclosure (C1) encompasses both sides of the creek (Fig. 2.4a), since no attempt was made here to clear the creek of bridging points. The experimental enclosures EXPT. 1 and EXPT. 2 (abbreviated henceforth as E1 and E2), in contrast, are separated from each other on either side of the creek (Fig. 2.4b), as are experimental enclosures EXPT. 3 and EXPT. 4 (E3 and E4, Fig. 2.4c). The maximum distance separating the enclosures is 2.3 km (from C1 to E1 and E2), and the minimum distances are the widths of the creeks that separate E1 from E2 and E3 from E4.

The enclosures differ slightly in mean altitude above sea level: C1 is 825 m a.s.l., E1 and E2 are 740 m a.s.l., and E3 and E4 are 835 m a.s.l. The areas of each enclosure are also slightly different:

C1 is 1.75 ha, E1 is 1.73 ha, E2 is 1.72 ha, E3 is 1.73 ha and E4 is 1.75 ha. The rainfall and temperature regimes of the enclosures are almost identical, although mean minimum winter temperatures are 1-2°C less at E3 and E4 than at E1 and E2 (Fig. 2.2).

In summary, the enclosures may be thought of as islands of relatively dense vegetation that occur along the floors of wet river valleys. These enclosures are surrounded and separated from each other by relatively large areas of drier, more open forest or pine plantation. Four enclosures (E1-E4) are bounded along one side by a creek, whereas the fifth enclosure (C1) encompasses the creek. The enclosures are similar in size, shape, climate and vegetation. Relatively dense populations of both species of Antechinus occur within the enclosures, and immigration to and emigration from them appear to be limited. In short, the enclosures appear to conform very well to the requirements discussed earlier for an experimental study of competition.

2.4 METHODS

Antechinus populations were usually sampled once or twice a month to assess population parameters and patterns of resource use. In months when two sampling sessions were conducted, the first session is denoted by the name of the month followed by the numeral I (in the text and tables), or by the initial of the month (in the figures). The second session is denoted by the name of the month followed by the numeral II (in the text and tables), or by the initial of that month followed by an asterisk (in the figures). For example, two sampling sessions were conducted in each of July 1978 and April 1979, one immediately before Antechinus were manipulated, and the

other immediately afterwards. These are denoted July I 1978 (prior to removal), July II 1978 (after removal), April I 1979 (prior to reintroduction) and April II 1979 (after reintroduction).

The methods used to assess population parameters and resource use are described below.

2.4.1. Field methods for assessment of population parameters.

Live trapping was used to assess the effects of population manipulations of one species of Antechinus on the population parameters of the other species. Two kinds of live traps were used. The first kind of trap, the Elliott type B folding metal trap (33x10x10 cm), was used for most trapping. These traps were baited with a mixture of rolled oats, honey, peanut butter and bacon pieces, and provided with non-absorbent cotton wool for bedding. In wet or cold weather traps were placed in plastic bags and covered with bark or other debris; in very cold weather extra bedding was provided in a polystyrene cup. Elliott traps were used in grid trapping (section 2.4.1.1), line trapping (section 2.4.1.2) and source area trapping (section 2.4.1.3). The second kind of trap used was the pitfall trap. These traps were constructed from two commercial fruit cans that were bolted one on another to form a cylinder 50 cm deep and 23 cm diameter. Traps were sunk flush to ground level under ferns and covered when not in use. A polystyrene egg carton containing bait and cotton wool bedding was placed at the bottom of each pitfall to provide a warm, relatively waterproof "nest" for captured animals, as well as a place to hide if two or more individuals were captured. The use of pitfall trapping is described in section 2.4.1.4.

2.4.1.1 Grid trapping

Grid trapping was conducted entirely within each enclosure to obtain information on all of the population parameters listed in section 2.1. Trap stations were located at 10m intervals (± 2m) on a grid that extended to the perimeter of each enclosure (Figs. 2.4a-2.4c). Except for months when manipulations were conducted (July 1978 and April 1979) and when matings and births in Antechinus occurred (July-September in both years), grid traps were set for four days a month. In other months, traps were set either for eight days (4 days immediately before and 4 days immediately after manipulations had been conducted) or for up to 12 days, at irregular intervals, to obtain precise information on the timing of reproductive events. Traps were set at the trap stations on every fourth line of the grids and moved daily to the next line along; hence each trapping session of four days resulted in each trap station being trapped once. This procedure was a compromise between the toil of setting traps at each trap station each day, and the need to maintain adequate capture loci to assess movements (see Flowerdew 1976a). Traps were set for four consecutive days at a time except in the winter months (June-August) when animals were susceptible to hypothermia. In these months, traps were set for two consecutive days, closed for one to two days, and then re-opened for the final two days of the session. In May 1978 one trap was placed at each trap station, but subsequently, to reduce competition for traps, two were placed at most stations that were located in very dense vegetation near creeks.

2.4.1.2 Line trapping

Line trapping was conducted in areas immediately surrounding each enclosure for two reasons. It was hoped to provide, first, a yardstick for assessing movements of individuals into and out of the enclosures (it must be remembered that the enclosures were actually only semi-enclosed), and second, a buffer zone for picking up and removing any incoming individuals that were extraneous to the experimental design. (Extraneous individuals would be, for example, A. stuartii if this species had previously been removed from the enclosure). Line trap stations were located 25m apart (± 4m) on the valley slopes above the enclosures, as well as along the creeks beyond the ends of the enclosures (Figs. 2.4a-c). Line traps were always set singly. They were operated for 2-3 consecutive days each month concurrent with grid trapping, except in June 1978 and September 1979 when no line trapping was conducted.

2.4.1.3 Source area trapping

Source area trapping was conducted on an irregular basis between June 1978 and July 1979 at sites 3-11 km away from the enclosures. In June 1978, such trapping was undertaken to find suitable sites in which to place individuals that were to be removed from enclosures E1-E4 the following month. Although both species of Antechinus were found to occur already at most such sites, it was hoped that the individuals displaced from the enclosures would increase the densities of these populations, and so, after breeding, ensure large populations for the following year. These were then

used as source populations to restock enclosures E1 and E3 in April 1979 (see Fig. 2.1).[1]

Between November 1978 and April 1979, source area trapping was conducted for 3-4 days a month to obtain information on the spatial relationships of mothers and their young. Since young A. stuartii remain for some time within the maternal range (Wood 1970), it was hoped that family groups could be identified and transferred together to restock enclosures E1 and E3 in April 1979. Although the restocking of these enclosures was timed to coincide with a population upheaval (section 2.1), it was thought that related or familiar individuals would settle more easily then unfamiliar ones. After the initial restocking of enclosures E1 and E3 in April 1979, several reintroduced individuals disappeared. Between April and July 1979, source area trapping was conducted for 2-3 days a month to capture replacement individuals. Source area trapping procedures were similar to those used in line trapping, except that traps were placed irregularly in habitat where, by experience, I thought Antechinus would be captured.

2.4.1.4 Pitfall trapping

All trapping procedures outlined above depend on folding metal traps. At the beginning of the study, it was not known whether these traps would catch all individuals within the enclosures, although such knowledge was obviously important for conducting precise manipulations of population numbers and for measuring numerical

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[1]Because of the unusual life history of Antechinus, it was not possible to reintroduce the same individuals that were removed from enclosures E1-E4 in July 1978.

responses. As a check on the efficiency of the folding metal traps, a line of 28 pitfall traps was established in the E2 enclosure in June 1978. These traps were spaced 10-25m apart, and were operated for 2-4 days a month three days after grid trapping had finished.

Unfortunately, pitfall traps proved to be very inefficient at capturing Antechinus. No more than 69% of A. stuartii individuals known to be alive from grid trapping were captured in pitfalls in any month, and no unmarked individuals of either species of Antechinus were ever caught. Consequently, pitfall trapping was discontinued in February 1979.

2.4.2 Animal handling

Except when trapping to determine the periodicity of activity (sections 2.5.4.4 and 2.5.6.4), all traps were checked, cleared and reset as soon as possible after sunrise. (In practise, when many animals were captured, "as soon as possible" could mean up to nine hours later). Newly captured Antechinus spp. were given a unique toe clip. At each capture all animals were individually identified, sexed and weighed, and their general appearance and reproductive condition were noted.

Reproductive condition was assessed by the appearance of the pouch in females and the penis and scrotum in males (Woolley 1966). If young were present in the pouch they were counted, measured (see Lyne and Verhagen 1957) and, when possible, sexed. Sexing the pouch young was possible only in the last few days of pouch life. Males were identified by the presence of a minute, stalk-like scrotum (always translucent in the pouch young of A. stuartii, but translucent or blue-pigmented in those of A. swainsonii), females by

the presence of a translucent, triangular-shaped patch on the pink ventral surface where the pouch would later develop. Lactation in females could not be accurately assessed. In contrast to the findings of Wood (1970), I was unable to express milk from females of either species of Antechinus at any time. A rough assessment of the duration of lactation was therefore based soley on the appearance of the nipples and pouch (Woolley 1966).

In the course of a four day grid trapping session in each enclosure, head-body and tail measurements were taken from most individuals. Measurements were made by holding the animal against a measuring rule, usually after it had been lightly anaesthetised with ether. Such measurements were taken once only from any individual in a trapping session, and not from females with pouch or nestling young.

Weak or hypothermic animals were encountered occasionally, especially in winter. Every attempt was made to revive such animals by providing them with a mixture of honey and water, and by warming them in the investigator's shirt. Very weak, moribund animals were sometimes injected intraperitoneally with a solution of 10% glucose. These efforts substantially reduced trap mortality. Excluding males trapped at the time of mating and die-off, only 2% of A. stuartii and <1% of A. swainsonii individuals died in traps in the enclosures throughout the study.

2.4.3 Field methods for assessment of resource use

Live trapping and tracking methods were used to assess the effects of population manipulations of one species of Antechinus on the patterns of resource use of the other species.

To assess the types and sizes of food eaten, scat material was taken from the floors of occupied folding metal traps. Scats were collected only at the first apture of an individual in a trapping session, and were transferred within 18 hours to 70% ethanol for preservation.

To assess the periodicity of activity, a variation of grid trapping was used. Thirty-six to forty-one traps were set singly at trap stations on a section of each enclosure, and checked at three hourly intervals, beginning at 12.00h, for a continuous period of 24h. All individuals captured were identified and released immediately, so that none remained in traps for more than three hours. Such trapping was conducted for one 24h period a month, one day after ordinary grid trapping had finished.

To assess habitat use, live trapping and tracking methods were used. Tracking, using hair sampling tubes (Suckling 1978), was used to compare the relative use of terrestrial and arboreal habitat by Antechinus. In each enclosure, 25 tubes were attached to the bases of trees, and 25 more were attached to tree trunks 2½-4m above ground. All tubes were baited with rolled oats and honey, and lined with double-sided sticky tape (Suckling 1978). At the end of each monthly grid trapping session, bait was replaced and the sticky tape was examined for hairs left by visiting mammals. Hairs were later identified to species and used to provide an index of the extent to which Antechinus spp. used terrestrial and arboreal habitat.

Live trapping provided more detailed information on the use of terrestrial habitat by Antechinus spp., and followed a method described by Barnett et al. (1978) and Newsome and Catling (1979). These authors "split" habitat into its most obvious components, and

rated the quantity of each component around each trap station on a subjective numerical scale of 0-3. In the present study, the following habitat components were recognised: 1) Logs (> 8 cm diameter and > 100 cm long), 2) litter, 3) rocks, 4) vegetation < 1m high, and 5) vegetation > 1m high. The amount of each component 1m above and around each trap station was assessed visually and given a score of 0-3. A score of 0 denoted that the component was absent near the trap site, a score of 3 that it was relatively abundant.

To obtain an overall index of structural habitat complexity (S.H.C.), at each trap station, the scores for all the habitat components were summed. This yielded total scores that ranged from 0 (no S.H.C.) to 15 (maximum S.H.C.) per trap station. The proportional abundances of sites of different S.H.C. were similar in the five enclosures ($G_{(56\ d.f.)} = 55.33$, n.s.).

2.4.4 Analytical methods for assessment of population parameters

Population parameters of both species of Antechinus were estimated largely from grid trapping within each enclosure. Line trapping results were used only where stated specifically below.

Population numbers were expressed as the minimum number known to be alive (MNA) during each trapping session, and were calculated from the total number of animals captured during a trapping session plus those marked animals that were captured at a later date (Krebs 1966, Hilborn et al. 1976). Most individuals of both species of Antechinus were normally captured during grid trapping within each enclosure, but occasionally some individuals were captured also on one of the trapping lines (Fig. 2.5). Such individuals were counted as enclosure residents only if <10% of their total captures

occurred outside the enclosures (Fig. 2.5); other individuals were considered either as transients or as residents of open habitat outside the enclosures and were excluded from estimates of population numbers.

Minimum survival between trapping sessions was calculated as the percentage of those animals known to be alive in one trapping session that were recorded in subsequent trapping sessions. This method does not distinguish death from emigration (Flowerdew 1976a), but it has nevertheless been used successfully in many studies of small mammals (e.g. Watts 1969, Wood 1970, 1971).

Trappability was defined as the number of individuals captured in a trapping session divided by the MNA at that time (Krebs 1966).

Movements were calculated as the average distance moved between successive captures in a single trapping session (Av.D., after Brant 1962). This measure is correlated with home range size in Peromyscus leucopus (Wolfe 1968) and has been used as an index of movement in several studies of Antechinus spp. (Braithwaite 1973, Barnett et al. 1977, Wainer 1976).

Home range was calculated by the minimum area method, as modified by Jennrich and Turner (1969). This method defines an area (the smallest convex polygon containing all the capture points) by joining capture points in a counter clockwise direction about their geometrical centre. The method is biassed by sample size (Jennrich and Turner 1969); hence only those individuals captured 8-12 times in two-four consecutive trapping sessions were used in this analysis. Only grid captures were used; occasional captures of individuals on the trapping lines were considered to be "expioratory sallies" (Burt 1943) and were ignored. To calculate overlaps in home range, the

home range of an individual was first mapped. The home ranges of other individuals of the same sex, and then of the opposite sex, and finally of both sexes together were then drawn over that of the first individual, so that an estimate was obtained of the percentage of that individuals area that was overlapped by the ranges of neighbouring individuals in the population. This procedure was repeated for each individual for whom a home range could be defined, and the values used to obtain mean overlaps for males, females, and for both sexes together. Home ranges and overlaps were determined with a planimeter or digitiser board.

No attempt is made here to review the very large literature on methods of home range and movement analysis, since excellent reviews exist elsewhere (Jennrich and Turner 1969, Flowerdew 1976a, Trevor-Deutsch and Hackett 1979). I selected the methods used in the present study because they are simple to use, comparable with other studies and intuitively easy to understand.

No calculations were necessary to interpret the remaining population parameters (population composition, reproduction and body size), and information on these was drawn directly from field data.

2.4.5. Analytical methods for assessment of resource use

The foods eaten by the two species of Antechinus were analysed entirely from preserved scat material. Scats from individual animals were placed in petri dishes, gently broken up, and examined under low power magnification. Invertebrate fragments were assigned to one of 24 categories of prey type and, when possible, to one of 10 categories of prey size. Minimum numbers of prey items were scored. For example, if 1-6 similar beetle tarsi were identified only one beetle

was recorded, but if 7 similar tarsi were found, 2 beetles were recorded. This method probably underestimates the numbers of a particular kind of prey that may have been eaten. In practise, however, such bias may not be extreme, since large numbers of tarsi or other identifiable fragments were seldom found in scats.

Identification of prey to Order or above was based on comparison with reference specimens collected in the enclosures, and with descriptions in CSIRO (1970, 1974), Main (1976) and McColl (1977). Size classification, where only single body parts were available, was based on the establishment of ratios of body parts to body size (overall length from the tip of the head to the tip of the abdomen) for the whole organism (Hall 1980b, see also Calver and Wooller 1982).

The diversity of types and sizes of prey eaten by Antechinus was calculated using Hurtubia's (1973) modification of the Brillouin index H. This index is calculated by the formula:

$$H = \frac{1}{N} \log e \frac{N!}{n_1!\ \ n_2!\ \ n_3!.....n_s!}$$

where N represents the total number of individuals in the collection, n_i represents the number of specimens of type i, and units are natural bels (Poole 1974). Brillouin's index is influenced by three factors: the numbers of types or taxa in the collection, the total number of individuals, and "evenness" J, where J = H/H maximum,

$$\text{and } H_{max.} = \frac{1}{N} \log e \frac{N!}{([N/S]!)^{S-R}[([N/S]+1)!]^{R}}$$

where S represents the total number of types contributing to N, [N/S] represents the integer part of N/S and R = N-S[N/S] (Poole 1974).

The method treats each scat as a sample, and its trophic diversity (Brillouin's H) is calculated separately. The prey contents for each scat sample are then pooled, one at a time, for K samples and H is recalculated at each step. The accumulated trophic diversity H_K increases with progressive pooling until an asymptote is reached. This point may be considered as an estimate of the trophic diversity of the population (Hurtubia 1973).

Hairs left by mammals visiting the hair sampling tubes were identified by cross-sectioning and scale typing methods described by Brunner and Coman (1974), using reference hairs obtained from individuals in the enclosures.

No analyses were necessary to interpret the use of other resources (time and terrestrial habitat), and information on these was drawn directly from field data.

2.4.6. Treatment of data.

The experimental design (Fig. 2.1) calls for the comparison of population parameters and patterns of resource use of one species of Antechinus when it occurs in the presence and in the absence of the other species. At each step of the experiment, three populations are to be compared. Thus, to assess the effect of A. swainsonii on A. stuartii, for example, it is necessary to compare A. stuartii populations in enclosures E1, E2 and C1, but to assess the effect of A. stuartii on A. swainsonii, it is necessary to compare A. swainsonii populations in enclosures E3, E4 and C1 (Fig. 2.1).

Comparisons between enclosures were made for separate months or for groups of months. Months were grouped to conform both to

the schedule of manipulations and to different demographic events. For example, months when females were with young (either in the pouch or in the nest) were considered together, as were months before and during mating.

To assess whether differences existed between these populations, several statistical tests were used. In general, when series of measurements were available from each population, analysis of variance (ANOVA) was used; when frequency data were available, G-tests were used. ANOVAs were performed only after Box's (1949) test had demonstrated that the variances of samples were equal, and, when necessary, after appropriate transformations had been made (Sokal and Rohlf 1969).

An important point is that all ANOVAs performed were of the Model 1 type (Sokal and Rohlf 1969). Model 1 analyses assume that differences among sample means, if any are revealed by a preliminary, overall ANOVA, are due to fixed treatment effects that are planned in advance by the investigator. In such experiments, comparisons of interest among the sample means are known and planned before the experiments are actually carried out and the results obtained. Planned comparisons are applied irrespective of the results of the preliminary, overall ANOVA. They are conducted by simply partitioning the treatment sum of squares and the treatment degrees of freedom of the preliminary ANOVA into separate, planned comparisons, and using these as part of the ANOVA (Sokal and Rohlf 1969). To distinguish the two kinds of ANOVA, F_o was used to denote the result of an overall, or preliminary comparison, whereas F_p was used to denote the result of a planned comparison.

The following planned comparisons, stated as null hypotheses (Ho), may be derived from Fig. 2.1:

	A. stuartii	A. swainsonii
May-July I 1978[1]	Ho : $\mu C1 = \mu E1 = \mu E2$	Ho : $\mu C1 = \mu E3 = \mu E4$
July II 1978-April I 1979	Ho : $\mu C1 = \mu(E1 \text{ and } E2)$	Ho : $\mu C1 = \mu(E3 \text{ and } E4)$
April II-Dec. 1979	Ho : $\mu(C1 \text{ and } E1) = \mu E2$	Ho : $\mu(C1 \text{ and } E3) = \mu E4$

where μ is the parameter mean of the population.

Although the planned comparisons were of principal interest, unexpected differences among sample means sometimes occurred between "unplanned" comparisons. Where, for example, Ho : $\mu C1 = \mu(E1 \text{ and } E2)$ and a preliminary ANOVA revealed that differences occurred among the sample means, it may be of interest to test Ho : $\mu E1 = \mu E2$. Tests of such an a posteriori hypothesis (so termed because interest in it arose only after the results had been obtained) were made using the Student-Newman-Keuls (SNK) test (Sokal and Rohlf 1969, Zar 1974).

To summarise the results of ANOVAs, the sample means were arranged in a row, and those means that were not significantly different were underlined. If the result was derived from a planned (F_p) comparison, a solid line was used in underlining, but if the result was from an overall (F_o) comparison, a broken line was used.

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[1] The null hypothesis for May-July 1978 is stated for the sake of completeness only. This is not actually a planned comparison, since there are no fixed treatment effects at this time and no a priori reason to expect that one sample mean differs from any other. Sample comparisons may still be made by a posteriori tests, however, as described in the text of this section.

If, for example, the null hypothesis stated that μC1 = μ(E1 and E2) and it was found in the planned comparison that μC1 < μ(E1 and E2), this was expressed simply as C1 E1 E2. In contrast, if (using the same null hypothesis) the planned comparison was not statistically significant but it was found in the a posteriori comparison that μCl = μE1 < μE2, this was expressed as C1 E1 E2. The actual numerical values for mean, standard deviation and sample size for each population are shown in the data summary.

To test for differences in frequency data between enclosure populations, G-tests were used. The G-test has several advantages over the conventional χ^2 test, the major one being ease of computation (Sokal and Rohlf 1969). By analogy with ANOVA, G may be used to test planned or "unplanned" comparisons, but in contrast to ANOVA, test procedures are the same for both kinds of comparisons (Sokal and Rohlf 1969). G_o and G_p were used respectively to distinguish overall from planned comparisons. In all G-tests using one degree of freedom (1 d.f.), a correction for continuity was applied when the sample size was <200 (Sokal and Rohlf 1969).

A final test statistic used in this chapter was Kendall's coefficient of concordance, W (Siegel 1956). This statistic tested the degree of association of activity periods of Antechinus between the enclosures, after capture frequencies within each of the eight 3-hourly trap intervals had been converted to ranks.

Throughout this thesis, a probability level of 5% or less ($P \leq 0.05$) is considered to be statistically significant. Unless otherwise stated, values of $P \leq 0.05$ are designated by *, values ≤ 0.01 by **, and values ≤ 0.001 by ***.

2.5 RESULTS

2.5.1. Effectiveness of the removal experiments.

Between 12 and 17 July 1978, 14 A. swainsonii were removed from enclosure E1 and from surrounding trap lines, and 19 were removed from E2 and surrounding trap lines. Very few new, extraneous individuals were captured subsequently in or close to either enclosure (Table 2.1), suggesting that little immigration occurred. When A. swainsonii was reintroduced to E1 in April 1979, however, several individuals subsequently crossed the creek barrier into E2 (Table 2.1). Until December 1979, no more than two individuals (11-14% of the number removed the previous year) were known to cross in any one month, and they were immediately returned to E1. These results suggest that, although enclosures E1 and E2 could not be kept entirely separate and free of A. swainsonii, they nevertheless permitted the numbers of this species to be kept at very low levels.

Between 12 and 19 July 1978, 23 A. stuartii were removed from enclosure E3 and from surrounding trap lines, and 17 were removed from E4 and surrounding trap lines. Several new individuals were captured subsequently in both enclosures (Table 2.2), suggesting that limited immigration had occurred. Following the reintroduction of A. stuartii to E3 in April 1979, the numbers of extraneous individuals in E4 and on surrounding trap lines increased slightly. Most of these had crossed the creek barrier from E3 to E4 (Table 2.2), and were returned immediately to E3. No more than four extraneous A. stuartii (24% of the number removed from E4 the previous year) appeared in either enclosure in any month throughout the removal experiments.

As with A. swainsonii, these results show that E3 and E4 were not always separate and entirely free of A. stuartii, but the numbers of this species were nevertheless maintained at very low levels.

2.5.2. Effectiveness of the reintroduction experiments.

Reintroductions of A. swainsonii to E1 and of A. stuartii to E3 were made on 6 April 1979 (see Fig. 2.1). Because it was impossible to reintroduce the same individuals that had been removed from these enclosures in 1978, I reintroduced the same number of individuals of each species that were known to be alive in early April (April I) 1979 in the control population, C1 (20 A. swainsonii, 21 A. stuartii). Several of these reintroduced individuals subsequently disappeared from the enclosures, so further minor additions of both species had to be undertaken from late April to July 1979. In E1, the numbers of A. swainsonii added were: 7 (April II), 3 (May), 7 (June) and 3 (July). In E3, the numbers of A. stuartii added were: 12 (April II), 9 (May), 4 (June) and 4 (July). The fact that minor reintroductions had to be made at all indicates that the two species of Antechinus are not entirely suitable for manipulation experiments. Nevertheless, the reintroductions maintained the numbers of A. swainsonii in E1 to within -1 to -3 of the monthly MNA in C1 (until May 1979), and the numbers of A. stuartii in E3 to within +2 to -5 of the monthly MNA in C1. In terms of the experimental design (Fig. 2.1), both the removal and reintroduction experiments may be considered reasonably successful.

2.5.3. Effects of the removal and reintroduction of A. swainsonii on the population parameters of A. stuartii.

2.5.3.1. Population numbers and composition

Over the entire period of study, the population numbers of A. stuartii in enclosures C1, E1 and E2 fluctuated more or less synchronously (Fig. 2.6a). In 1978 and 1979, the MNA in each enclosure was lowest from September to December, when only females >1 yr old were present, and highest from February to May due to an influx of juveniles born the previous year (Fig. 2.7).[1] Between May and August 1978, MNA in all enclosures fluctuated between 15 and 20 individuals, but over the same period in 1979, MNA in all enclosures declined before increasing again slightly in August (Fig. 2.6a) Between February and August, most individuals were males and females <1 yr old. Numbers of females >1 yr old were generally low after March or April, and only one was known to survive for more than two years (Fig. 2.7).

The removal of A. swainsonii from E1 and E2 by July II 1978 had no immediate effect on the population numbers or composition of A. stuartii, and MNA in these enclosures remained similar to that in C1 until December 1978. Thereafter, until September 1979, the numbers of A. stuartii in E1 and E2 were consistently higher than in C1 (Fig. 2.6a), although none of the separate monthly comparisons achieved statistical significance. The greatest monthly increases were in early April (April I) 1979 (the population of E1 was 57% greater than that

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[1]The terms "juvenile" and "female (or male) <1yr old" are synonymous and used interchangeably throughout the text, as are the terms "parous female" and "female >1yr old".

of C1), June 1979 (E1 was 59% greater than C1), and July 1979 (E2 was 64% greater than C1). It is worth noting that, for a control population of 20 individuals, E1 and E2 would each require populations of more than 36 (an increase of >80%) to be statistically different. It would also require exceptionally high survival (>90%) of pouch young until they were of trappable age (see section 2.5.3.2).

Considering the months February to August 1979 together, the populations of E1 and E2 were greater overall than that of C1 (χ^2 = 26.7, 16 d.f., $P < 0.05$; test for combining probability values, Sokal and Rohlf 1969). There was, however, no evident change in the numbers of A. stuartii in E1 when A. swainsonii was reintroduced there in April 1979.

The proportions of males to females did not differ between the three enclosures, whether comparisons were made monthly or over several months combined.

2.5.3.2. Survival

As with population numbers, minimum sessional survival rates of A. stuartii fluctuated more or less synchronously in the three enclosures (Fig. 2.6b). Survival was lowest in August each year (28-50%), due largely to the disappearance of all males (Fig. 2.7, Table 2.3). In other months, survival was never less than 60% (Fig. 2.6b).

Manipulations of A. swainsonii numbers had little immediate effect on the survival of A. stuartii, and there were no statistically significant differences between any of the populations in any month. The survival rates of males, females <1 yr old and females >1 yr old between the enclosures were also similar (Tables 2.3 and 2.4), and again, no statistically significant monthly differences were found.

Despite the lack of significant monthly differences, between February and June 1979 survival in populations in E1 and E2 was consistently greater than in the control population (Fig. 2.6b), and it was of interest to compare survival over these consecutive months. Thus, of those individuals known to be alive in February 1979, the following survived to April 1 1979: C1, 6/7 males, 8/15 females (64% survival); E1, 11/12 males, 14/18 females (83% survival); E2, 6/8 males, 15/18 females (81% survival). There was no significant difference in survival between enclosures ($G = 2.94$, 2 d.f., P n.s.) or between sexes ($G = 1.67$, 1 d.f., P n.s.), and the effects of survival, sex and enclosure were, overall, independent ($G = 7.26$, 7 d.f., P n.s.). Of those individuals known to be alive in April 1 1979, the following survived to June 1979: C1, 6/9 males, 7/12 females (62% survival); E1, 9/15 males, 13/17 females (69% survival); E2, 5/10 males, 10/19 females (52% survival). Again there was no significant difference in survival between enclosures ($G = 1.86$, 2 d.f., P n.s.) or between sexes ($G = 0.11$, 1 d.f., P n.s.), and the effects of survival, sex and enclosure were independent ($G = 4.03$, 7 d.f., P n.s.). Clearly, despite the trends in Fig. 2.6b, there were no differences in the minimum sessional survival of A. stuartii between the three enclosures at any time.

The above analyses refer only to independent, trappable individuals, and not to pouch, nestling or newly weaned young. What was the survival of these individuals? Before weaning in late December 1978 and early January 1979 at about three months of age (section 2.5.3.4), the survival of young was presumably dependent on the survival of lactating females >1yr old. Further, because the mean numbers of young suckled per female between September and

December 1978 were uniformly high in each enclosure (9.6 in C1, 10.0 in E1 and 9.5 in E2), it is reasonable to expect that the survival rates of young in these months closely approximated the survival rates of lactating females (Table 2.4), and hence differed little between the enclosures. After weaning, in contrast, the survival rate of newly independent A. stuartii was lower in C1 than in E1 and E2 (Table 2.5). This was probably due to reduced female survival in C1. In October 1978, when pouch young were sexed, 32 of 47 young in this enclosure were female (68%); yet females comprised only 16 of 27 juveniles (59%) captured between January and April 1979. This represents a survival rate of 50% for newly weaned females, compared with 73% for newly weaned males.

In summary, minimum survival of A. stuartii tended to be less in the presence than in the absence of A. swainsonii, but a statistically significant difference was found only for newly weaned young.

2.5.3.3 Trappability

Trappability was never less than 75% in any enclosure in any trapping session (Fig. 2.6c). There was a tendency for trappability to be relatively less in September to December in 1978 and 1979, when only females were present (Fig. 2.7), but separate monthly comparisons and comparisons of groups of months failed to reveal differences that were statistically significant. Manipulations of the numbers of A. swainsonii had no evident effect on the trappability of A. stuartii.

2.5.3.4. Reproduction

Reproductive events in A. stuartii occurred synchronously in all enclosures in the winters of both 1978 and 1979 (Table 2.6), and provided no evidence that manipulations of the numbers of A. swainsonii had effects on the timing of any stage of the reproductive cycle. Judged by the lengths of white hairs surrounding the pouch, pregnancy usually lasted 4-5 weeks. Young remained in the pouch for 5 weeks before they were left in the maternal nest; they were not captured as independent young until at least three months (92 days) of age in late December or early January. Some aspects of the behaviour of nestling young are reported elsewhere (Dickman 1982b).

2.5.3.5. Movements

Movements of male A. stuartii generally increased from January, when young individuals first appeared in traps, to August, when mating occurred (Fig. 2.8a). In contrast, the movements of females were more constant throughout the year, and Av.D. values were often less than for males (Fig. 2.8b,c).

In most trapping sessions, there were large differences in the average distances moved by different individuals. Sometimes, variances were larger than mean values. To assess the effects of removing and reintroducing A. swainsonii on the movements of A. stuartii, it was convenient to compare groups of months (Table 2.7). These results show that:

1. Prior to the removal of A. swainsonii there were no differences in the movements of A. stuartii in the three enclosures.

2. Immediately after removal, the movements of female A. stuartii increased.

3. Six to nine months after removal (between January and April 1 1979), the movements of males and females were, overall, greater in the absence than in the presence of A. swainsonii.

4. Immediately after the reintroduction of A. swainsonii to E1 (and to the end of the experiment), the movements of A. stuartii in this enclosure decreased to control levels. This was most consistently evident among females.

Hence, the movements of A. stuartii (especially females) were generally restricted in the presence of A. swainsonii.

2.5.3.6 Home range

The home range sizes of male A. stuartii were generally greater in July and August 1978 and 1979 than at other times, whereas those of females fluctuated throughout the experiment (Table 2.8). Mean male home range sizes were almost always larger than those of females, although individual ranges usually varied considerably at any time in any enclosure. The effects of removing and reintroducing A. swainsonii on the home range size of A. stuartii are summarised from Table 2.8:

1. Prior to the removal of A. swainsonii, there were no differences in home range sizes in the three enclosures.

2. Immediately after removal (and until A. swainsonii was reintroduced), the home range sizes of male and female A. stuartii increased.

3. Immediately after the reintroduction of A. swainsonii to E1 the home range sizes of A. stuartii in this enclosure decreased to control levels. There were no differences in home range sizes between the enclosures 3-4 months after reintroduction (in July and August 1979), but thereafter, the ranges of females were again smaller where A. swainsonii was present than where it was absent.

Overlaps in the home ranges of A. stuartii are shown in Tables 2.9 and 2.10. Except in the January-April I period, when their ranges were relatively small, individual males often shared 50% or more of their home ranges with other males and with females (Table 2.9). The ranges of individual females also overlapped extensively with males, but mean female/female overlaps were small (8.4-46.9%) in all enclosures from July to December in both 1978 and 1979 (Table 2.10).

There was little evidence that manipulations of the numbers of A. swainsonii influenced home range overlaps of male A. stuartii, and only one out of 13 planned comparisons was statistically significant (Table 2.9). Overlaps in the home ranges of females (Table 2.10) changed as follows:

1. Prior to the removal of A. swainsonii, mean overlaps of females with females, with males and with both sexes together, were the same.
2. Immediately after removal, overlaps of females with males and females together increased.

3. Six to nine months after removal (between January and April 1 1979), juvenile females (<1yr old) in E1 and E2 overlapped more with other juvenile females, and with males and females together, than did juvenile females in C1. In the same period, parous females (>1yr old) in E1 and E2 also overlapped more with other parous females than those in C1.

4. Immediately after the reintroduction of A. swainsonii to E1, no statistically significant differences could be detected in the overlaps of female ranges between enclosures. However, from July 1979 (3 months after reintroduction) until the end of the experiment, female/female home range overlaps were greater where A. swainsonii was absent than where it was present.

In summary, the home range sizes and home range overlaps of A. stuartii were larger in the absence than in the presence of A. swainsonii. However, these trends were statistically significant in some sampling sessions only, and differences were more evident for females than for males.

2.5.3.7 Body size

Body weight: The body weights of male A. stuartii generally increased from January until August, although a lull in growth occurred from April 1 to June 1979 (Fig. 2.9a). Females <1yr old also increased in weight from January until March 1979, but from April 1 until early August 1979 little further increase was evident (Fig. 2.9b). In contrast, the weights of females >1yr old increased

rapidly between September and October in both years (when young were in the pouch) and decreased more slowly from November (when young were in the nest) until the winter of the following year (Fig. 2.9c).

What were the effects of manipulations of A. swainsonii on the body weights of A. stuartii? The results (Fig. 2.9 and Appendices 3a,b,c) show that:

1. Prior to removal, there were no differences in the body weights of A. stuartii in the three enclosures.
2. Immediately after removal, females <1yr old weighed less in E1 and E2 than in the control population.
3. Six to nine months after removal (between January and April I 1979), males and females <1yr old weighed less in E1 and E2 than in C1.
4. After the reintroduction of A. swainsonii to E1, there were no differences in the body weights of A. stuartii in the three enclosures in some months, but in others, males and females <1yr old in E1 and E2 continued to weigh less than those in C1 (Appendices 3a,b). That is, no evident shifts in body weight were associated with the reintroduction of A. swainsonii.
5. There were no statistically significant planned differences in the body weights of females >1yr old in any month.

Head-body length: As with body weights, the head-body lengths of male A. stuartii increased until August, with a lull in growth occurring in the populations of C1 and E2 in April II and May 1979 (Fig. 2.10a, Appendix 3d). The head-body lengths of females <1yr old increased from January to August, with a lull in growth

occurring in the populations of E1 and E2 in May 1979 (Fig. 2.10b, Appendix 3e). Females >1yr old showed little variation in head-body length (means between 91 and 100 mm) throughout the experiment (Fig. 2.10c and Appendix 3f).

There was little evidence that manipulations of the numbers of A. swainsonii had consistent effects on the head-body lengths of A. stuartii: Differences were recorded only between males in E2 compared with males in C1 and E1 in April II and June 1979, and between females <1yr old in E2 compared with those in C1 and E1 in August I 1979 (Appendices 3d,e).

In summary, removal of A. swainsonii reduced the body weights of A. stuartii, whereas reintroduction had little consistent effect. Head-body lengths of A. stuartii were generally similar in the three enclosures throughout the experiments.

2.5.4. Effects of the removal and reintroduction of A. swainsonii on the patterns of resource use of A. stuartii

2.5.4.1. Arboreal and terrestrial habitat.

Antechinus stuartii visited arboreal and ground level hair sampling tubes every month in each enclosure (Fig. 2.11a,b). Levels of activity (numbers of hair tubes visited) differed between months, but generally followed differences in overall population size (compare Fig. 2.11 with Fig. 2.6a). Fig. 2.11a shows that A. stuartii was much more arboreal in the presence than in the absence of A. swainsonii: the former species was more arboreal in C1 than in E1 and E2 together between September and December 1978 ($G_{(1\ d.f.)}$ = 7.25, $P < 0.01$) and between January and April I 1979 ($G_{(1\ d.f.)}$ =

12.74, $P < 0.001$), but it was also more arboreal in C1 and E1 together than in E2 between April II and June 1979 ($G_{(1\ d.f.)} = 22.27$, $P < 0.001$). The most striking increase in arboreal activity (217%) occurred between April I and April II 1979 in E1, following the reintroduction of A. swainsonii to that enclosure after April I (Fig. 2.11a). Antechinus stuartii generally visited fewer ground level hair tubes when A. swainsonii was present than when it was absent (Fig. 2.11b), but a statistically significant difference ($G_{(1d.f.)} = 6.68$ $P < 0.01$) was observed only between April II and June 1979, when ground level activity was greater in E2 than in C1 and E1.

Overall, the activity of A. stuartii in terrestrial habitat increased after A. swainsonii was removed, but arboreal activity increased again dramatically when A. swainsonii was reintroduced.

2.5.4.2. Terrestrial habitat (structural habitat complexity)

Antechinus stuartii was captured most frequently at sites of moderate structural habitat complexity (S.H.C.), although a few captures often occurred in open or structurally very complex sites (Table 2.11). Because the proportional abundances of sites of different S.H.C. were similar between the enclosures (Section 2.4.3.), capture frequencies of Antechinus between the enclosures were compared directly. The effects of manipulations of A. swainsonii on the terrestrial habitat use of A. stuartii (Table 2.11) may be summarised as follows:

1. Prior to the removal of A. swainsonii, there were no differences in the proportional use of sites of different S.H.C. between the enclosures.

2. Immediately after removal (and until A. swainsonii was reintroduced after April 1 1979), both sexes of A. stuartii were captured in structurally more complex habitat. Between January and April 1 1979 this effect was highly statistically significant, and partitioning G revealed further differences in habitat association among the population components. Thus, in each enclosure, females >1yr old occupied the most complex habitat, followed by males and then females <1yr old in less complex habitat.

3. Immediately after the reintroduction of A. swainsonii to E1, A. stuartii shifted its use of S.H.C. back to a level similar to that in the control population. As before, males and females >1yr old were captured in more complex habitat than females <1yr old.

4. In July and August 1979 (3-4 months after the reintroduction of A. swainsonii), there were no sex differences in the use of S.H.C. in any enclosure. The planned comparison (C1 and E1) vs. E2 was not statistically significant because E1 = E2, but the habitat used by both sexes in E2 continued to be more complex than that used in C1. No differences were found in the habitat used by female A. stuartii in the three enclosures between September and December 1979.

Overall, A. stuartii was captured in structurally more complex habitat in the absence than in the presence of A. swainsonii. This effect was most evident for females >1yr old and males, and least evident for females <1yr old.

2.5.4.3. Food

Food type: The analysis of scats proved to be extremely laborious and time-consuming, hence I have examined material from five months only (Table 2.12). Overall, the remains of 23 types of food, mostly invertebrates, were found. Of these, Coleoptera (excluding Carabidae), Aranea, Amphipoda and larvae were found most frequently; others such as Dermaptera, Chilopoda, Diplopoda, Isoptera and Blattodea were found less frequently or seasonally. Some types of food, such as Collembola, Acarina and Thysanoptera were small (<2.0 mm long) and occurred sporadically in the scats; these may have been ingested accidentally. Vertebrate remains (probably of a small skink, Leiolopisma sp.) and hair were each found in two scats. In one scat the hairs appeared to be those of the House Mouse Mus musculus (only four Mus were captured on all enclosures throughout the study), but in the other scat the hairs were those of the Bush Rat Rattus fuscipes. Since adult R. fuscipes weight up to 150 g, hairs of this species may have been scavenged as carrion. Plant material was also found in several scats (Table 2.12a). In July and August 1978 fragments of leaf cuticle were found, but in April 1979, seeds and fruits of Blackberry Rubus fruticosus occurred.

The numbers of types of prey eaten by all individuals in an enclosure in any one month varied from 11 in E1 in July I 1978 (mid-winter) to 18 in E1 in April I 1979 (autumn) (Table 2.12a). Prey type diversity also differed between months, but was generally lowest in winter. The evenness with which prey types were represented in the diets varied little (Table 2.12a); hence differences in prey type diversity arose mostly from differences in the numbers of prey types represented.

The influence of manipulations of the numbers of A. swainsonii on the types of prey eaten by A. stuartii may be summarised as follows:

1. Prior to the removal of A. swainsonii there were no overall differences in the proportional frequencies or diversities of types of prey eaten by A. stuartii in the three enclosures.
2. Immediately after removal (July II and August 1978), the types of prey eaten by A. stuartii in C1 differed overall from those eaten in both E1 and E2. In July II, proportionally more Blattodea were found in the scats of A. stuartii in E2 than in either C1 or E1 ($G_{(2\ d.f.)} = 8.72$, $P < 0.05$), and more Aranea were found in scats of individuals in E1 and E2 together than in C1 ($G_{(1\ d.f.)} = 3.97$, $P < 0.05$). In August proportionally more Amphipoda were found in E1 and E2 scats combined than in C1 ($G_{(1\ d.f.)} = 4.67$, $P < 0.05$). In both July II and August, prey type diversity was higher in E1 and E2 than in C1.
3. Nine months after removal (April I 1979), the types of prey eaten by A. stuartii in C1 were still different from those eaten in both E1 and E2 together. In particular, A. stuartii in C1 ate proportionally more Coleoptera ($G_{(1\ d.f.)} = 5.59$, $P < 0.05$) and Hemiptera ($G_{(1\ d.f.)} = 6.51$, $P < 0.05$), and less Isoptera ($G_{(1\ d.f.)} = 17.81$, $P < 0.001$) than those in E1 and E2. Prey type diversity was also higher in E1 and E2 than in C1.
4. Immediately after the reintroduction of A. swainsonii (April II 1979), A. stuartii in C1 and E1 together ate more Aranea

($G_{(1\ d.f.)}$ = 7.29, $P < 0.01$) than in E2, but less Isoptera ($G_{(1\ d.f.)}$ = 17.70, $P < 0.001$). In addition, the diversity of prey types in the scats of A. stuartii in E1 decreased to near the control value.

Food size: Of the fragments identified to type from scats, only a fraction (54-84%) could be reliably assigned to a size class (Table 2.12b). In all enclosures, most prey items were <10 mm long. As with prey type diversity, the evenness with which prey size classes were represented was relatively constant between enclosures and between months; hence differences in prey size diversity arose largely from differences in the numbers of prey size classes represented (Table 2.12b).

The influence of manipulations of the numbers of A. swainsonii on the sizes of prey eaten by A. stuartii may be summarised as follows:

1. Prior to the removal of A. swainsonii, there was no difference in the proportional representation of prey sizes or in the diversity of prey sizes between the three enclosures.
2. Immediately after the removal of A. swainsonii (July II 1978), there was still no difference in the sizes of prey eaten between the enclosures. In August 1978, however, the sizes of prey eaten in E1 and E2 differed overall from those eaten in C1. In particular, proportionally more prey 1-2.4 mm long were eaten by A. stuartii in C1 than in E1 and E2 ($G_{(1\ d.f.)}$ = 4.90, $P < 0.05$), and proportionally less in the 5-7.4 mm size class ($G_{(1\ d.f.)}$ = 5.42, $P <$

0.05). Further inspection revealed that the majority of longer prey items (>5.0 mm) eaten in E1 and E2 were Amphipoda, Blattodea and Coleoptera. At least some Coleoptera were water beetles (Family Noteridae), 5.0-9.9 mm long, that were not detected in the scats of A. stuartii in C1. Prey size diversity fell in all enclosures between July I and July II/August.

3. Nine months after removal (April I 1979), the sizes of prey eaten by A. stuartii in E1 and E2 still differed overall from those eaten in C1. In C1, A. stuartii ate proportionally more items 1-2.4 mm long than in E1 and E2 ($G_{(1\ d.f.)}$ = 10.51, $P < 0.01$), but proportionally fewer items 2.5-4.9 mm long ($G_{(1\ d.f.)}$ = 7.22, $P < 0.01$). Further inspection revealed that proportionally more of the longer prey items eaten in E1 and E2 were Dermaptera, Amphipoda, Isoptera and Noterid beetles. Prey size diversities were only slightly higher in E1 and E2 than in C1.

4. Immediately after the reintroduction of A. swainsonii (April II 1979), there was no overall detectable difference in the sizes of prey eaten by A. stuartii in the three enclosures. Nevertheless, partitioning G showed that A. stuartii in C1 and E1 together ate proportionally more prey 1-2.4 mm long than in E2 ($G_{(1\ d.f.)}$ = 4.08, $P < 0.05$). Prey size diversity was also higher in E2 than in C1 and E1.

In summary, both the types and sizes of food items eaten by A. stuartii were affected by manipulations of the numbers of A. swainsonii. After removal of its larger congenor, A. stuartii ate more longer prey such as Amphipoda, Dermaptera and Isoptera, and the

diversity of prey types taken also increased. After A. swainsonii was reintroduced, these dietary shifts were largely reversed.

2.5.4.4. Periodicity of activity.

Most captures of A. stuartii occurred at night in all months in the three enclosures (Fig. 2.12). Activity was usually continuous throughout the night, but in the winter of 1978 captures, especially of females, declined temporarily after midnight. There was no evidence that manipulations of the numbers of A. swainsonii had any effect on the periodicity of activity of A. stuartii (Fig. 2.12, Table 2.13).

2.5.5 Effects of the removal and reintroduction of A. stuartii on the population parameters of A. swainsonii.

Before beginning this section, it is necessary to describe an incident that influenced the direction of the second half of my Ph.D. programme. Between mid May and early June 1979, someone illegally removed most of the A. swainsonii population from the C1 enclosure. The identity of this human intruder was never discovered, but clues to his activities were found in the destruction of small patches of vegetation, trails through the vegetation, numerous coloured flagging tapes attached to shrubs, and rats with skinned tails, presumably suffered on capture in improperly set traps. Two years later, just beyond the edge of the C1 enclosure, an illegally set trap containing a (very) dead Antechinus was also found. Because I was unprepared for such a crash in numbers in the control population, and because I was not sure whether further raids would occur, I did not attempt to reintroduce further A. swainsonii to the area. (It turned out later

that this option would also have been impossible, however, since illegal trapping and removal of A. swainsonii had also been conducted in my source areas). Instead, I decided to run the experiment until December 1979 as planned, and then examine the status of the A. swainsonii population in C1 before deciding whether to try to replicate the same experiment or to abandon C1 altogether. By December 1979, only four individuals were found in C1 (compared with 15 the previous year) so that, of necessity, the use of C1 as a control population was discontinued. A different experiment was planned and is described in Chapter 3. Comparisons of population parameters and patterns of resource use of A. swainsonii in C1, E3 and E4 have still been made for the period June-December 1979, but because of the low numbers in C1, conclusions are likely to be less reliable.

2.5.5.1. Population numbers and composition

The population numbers of A. swainsonii in the three enclosures (C1, E3 and E4) fluctuated more or less synchronously (Fig. 2.13a). MNA was lowest in each enclosure from August to October, when only females >1 yr old were present, and highest in December and January following the influx of juveniles into the trappable population (Figs. 2.13a and 2.14). Between November and July most individuals were males and females <1 yr old. Numbers of females >1 yr old declined slightly after December or January, but several individuals survived for more than two years, and one (in E4) survived for more than three years (Fig. 2.14). Consequently, in contrast to A. stuartii (Fig. 2.7), populations of A. swainsonii were often comprised of males and of females of three different age classes (Fig. 2.14). Peaks and

troughs in the numbers of A. swainsonii occurred about a month earlier than in A. stuartii, but otherwise the demographic patterns of the two species were similar. Calculation of MNA for A. swainsonii was rendered difficult because a small number of marked individuals sometimes disappeared from the trap record for 3-10 months. These individuals were not captured during grid, line or pitfall trapping, and had presumably moved outside of the enclosures. Individuals that were not captured for three or more consecutive months were not included in estimates of MNA, population composition or trappability, but they were included in estimates of survival.

The removal and reintroduction of A. stuartii had no evident effect on the population numbers of A. swainsonii (Fig. 2.13a). Until May 1979 there were no statistically significant monthly or overall differences in A. swainsonii numbers in the three enclosures, and no evident differences in population composition. Following human interference in May 1979, more A. swainsonii were found in E3 and E4 together than in C1 in both June ($G_{(1\ d.f.)} = 6.47$, $P < 0.05$) and July 1979 ($G_{(1\ d.f.)} = 5.10$, $P < 0.05$).

2.5.5.2 Survival

Minimum sessional survival rates fluctuated synchronously in the three enclosures (Fig. 2.13b). Apart from the human interference in C1, survival was lowest in July each year (17-39%, combining July I and July II 1978) due to the disappearance of all males (Fig. 2.14, Table 2.14). Survival was also relatively low (70-78%) in January 1979 in all three enclosures, again largely because of the disappearance of males but also because females >1yr old survived

poorly (compare Tables 2.14 and 2.15). In other months, survival was never less than 60% and seldom less than 80% (Fig. 2.13b).

Manipulations of the numbers of A. stuartii had little evident effect on the survival of A. swainsonii. Aside from May 1979, there were no statistically significant differences in overall survival between the enclosures in any month, and no differences in the survival rates of males and females <1 yr and >1 yr old. In May 1979 survival was lower in C1 than in E3 and E4 together: for males, $G_{(1\ d.f.)} = 15.18$, $P < 0.001$; for females, $G_{(1\ d.f.)} = 10.95$, $P < 0.001$; for males and females combined, $G_{(1\ d.f.)} = 29.75$, $P < 0.001$.

If the survival of pouch, nestling and newly weaned A. swainsonii is considered, differences in survival between the sexes emerge. In early September 1978, 7 out of 11 A. swainsonii each carried eight young in the pouch. In C1 one female carried 7 young, and in E3 one female carried 6, and another 7 young. In E4 one female had 10 nipples and 10 young, whereas all other A. swainsonii had 8 nipples. The total numbers of pouch young per enclosure were: C1, 31 (21♂, 10♀); E3, 29(16♂, 13♀); E4, 26(18♂, 8♀). Judged by the numbers of used nipples on the lactating females, all of these young were successfully transferred to nests in late September 1978, and all survived through the following month. However, when newly weaned A. swainsonii appeared in November, female young in E3 appeared to have survived poorly (Table 2.16). Here, the effects of survival, sex and enclosure departed from independence (Table 2.16) due to the poor survival of females in E3 ($G_{(1\ d.f.)} = 14.11$, $P < 0.001$). Considering males and females together, however, no overall differences in survival were found between the enclosures ($G_{(2\ d.f.)} = 1.05$, P n.s.). These findings

provide no evidence that A. stuartii affects the survival of A. swainsonii at any time.

2.5.5.3. Trappability

As with A. stuartii, trappability of A. swainsonii was never less than 75% in any enclosure in any month (Fig. 2.13c). Trappability was relatively low in July II and September 1978, especially in C1, and in August 1979 in E3, when only small numbers of females >1 yr old were present. Separate monthly comparisons and comparisons of groups of months revealed no differences in trappability between the enclosures, however, and provided no evidence that manipulations of the numbers of A. stuartii had any effect on the trappability of A. swainsonii.

2.5.5.4. Reproduction

Reproductive events in A. swainsonii occurred synchronously in the three enclosures in the winters of 1978 and 1979 (Table 2.17). Pregnancy appeared to last 4-5 weeks, and young remained in the pouch for 5½-6½ weeks before they were left in the maternal nest. The young first appeared as trappable individuals in November (Table 2.17) at the age of ⩾82 days. There was no evidence that manipulations of the numbers of A. stuartii influenced the timing of any part of the reproductive cycle of A. swainsonii.

2.5.5.5 Movements

Movements of male A. swainsonii generally increased from November to July whereas movements of females <1 yr and >1 yr old fluctuated in an apparently erratic fashion (Fig. 2.15). As with A.

stuartii, there were often large differences in the distances moved by individual animals in any month, and mean values were sometimes exceeded by their associated standard deviations. Differences in movements between the enclosures were examined by comparing groups of months (Table 2.18). There were no statistically significant differences at any time (Table 2.18), and hence no evidence that manipulations of the numbers of A. stuartii had any effect on the movements of their larger congenor.

2.5.5.6 Home range

The mean home range sizes of both male and female A. swainsonii were generally similar, and in the order of 2000-3000 m^2 (0.2-0.3 ha) (Table 2.19). There was little seasonal variation in home range size, although mean values for the period February-April I 1979 were slightly smaller than at other times throughout the experiment. The relatively large home ranges of females >1 yr old for the period July II-October 1978 and the relatively small home ranges of such females during the same period in 1979 were associated with low sample sizes. In 1978, especially in C1 and E3, I felt that the females were not making uniform use of large areas, but rather were making short movements over relatively small local areas or loci, and shifting these loci at regular intervals. This feeling was supported by the relatively small Av.D. measurements recorded between July II and October 1978 in C1 andE3 (Fig. 2.15).

Manipulations of the numbers of A. stuartii had no effects on home range sizes of A. swainsonii; there were usually considerable differences in the home range sizes of different individuals in each enclosure, and no statistically significant differences between enclosures were found at any time (Table 2.19).

Overlaps in home range were not calculated for A. swainsonii.

2.5.5.7 Body size

Body weight: The mean body weights of male and juvenile female A. swainsonii increased rapidly from November 1978 to March 1979, and then more slowly until July 1979 (Fig. 2.16 a,b). Males were heavier than females <1 yr old from December 1978 until July of the following year, and heavier than females >1 yr old from February 1979. Females >1yr old were heaviest in September 1978 when they carried young in the pouch; their mean body weights declined slowly until February 1979 after their young were weaned, and remained relatively constant before increasing to a second peak in September 1979 (Fig. 2.16c). As males aged, individual differences in body weights became pronounced. In each of the three enclosures it was not uncommon to find some males weighing almost twice as much as others. Standard deviations were correspondingly large (Fig. 2.16a). Body weight comparisons between enclosures are shown in Appendices 4a,b,c. There was no evidence that male body weights were influenced by manipulations of the numbers of A. stuartii (Appendix 4a), but in April I and May 1979 females <1 yr old were heavier in the absence than in the presence of A. stuartii (Appendix 4b). In contrast, in November 1978 females > 1 yr old were heavier in C1 than in both E3 and E4, where A. stuartii had been removed (Appendix 4c).

Head-body length: The mean head-body lengths of male and juvenile female A. swainsonii increased smoothly from November 1978 until July 1979 (Fig. 2.17a,b). Females >1 yr old were measured infrequently and are not shown.

Manipulations of the numbers of A. stuartii had little consistent effect on the head-body lengths of A. swainsonii (Fig. 2.17a,b, Appendices 4d,e). Thus, although in February 1979 the head-body lengths of males were larger in E3 and E4 than in C1 (Appendix 4d), the head-body lengths of females <1 yr old were greatest in the control population in December 1978 and February 1979, but greatest in E4 in May 1979 (Appendix 4e).

Although they are inconsistent, these findings provide evidence that, in some months, A. swainsonii was heavier and longer in the absence than in the presence of its smaller congenor.

2.5.6 Effects of the removal and reintroduction of A. stuartii on the patterns of resource use of A. swainsonii

2.5.6.1 Arboreal and terrestrial habitat

Antechinus swainsonii visited both arboreal and ground level hair sampling tubes in most months, but levels of activity were always higher on the ground (Fig. 2.18a and b). Monthly differences in the numbers of hair tubes visited reflected differences in population size, with peaks of activity occurring in December and January, and troughs occurring between August and October (Fig. 2.18).

There were no statistically significant differences in arboreal activity between enclosures in the numbers of hair tubes visited in any month or combination of months. On the ground, differences were detected when the months July to October 1978 were combined (A. swainsonii visited more hair tubes in C1 and E4 than in E3, $G_{(2d.f.)} = 8.07$, $P < 0.05$), and after the A. swainsonii population in C1 was decimated in May 1979. Between June and August 1979, A.

swainsonii visited more tubes in E4 than in C1 and E3 ($G_{(2d.f.)}$ = 9.37, $P < 0.01$), and in November and December 1979 more tubes were visited in E3 and E4 than in C1 ($G_{(2d.f.)}$ = 19.35, $P < 0.001$). None of these differences derived from planned comparisons; hence manipulations of the numbers of A. stuartii had little evident effect on the arboreal or terrestrial activity of A. swainsonii.

2.5.6.2 Terrestrial habitat (structural habitat complexity)

Antechinus swainsonii was captured most frequently at sites of relatively high S.H.C. (Table 2.20), and mean habitat scores for this species were usually slightly higher than for A. stuartii (compare Table 2.11). In contrast to the findings for A. stuartii, no differences were found at any time in the habitat used by males and females <1 yr and >1 yr old (Table 2.20). Comparisons between enclosures showed that between November 1978 and January 1979, the planned comparison C1 vs (E3 and E4) was not statistically significant, but the habitat used by A. swainsonii in C1 and E3 differed overall from that used in E4. Only one planned comparison between enclosures achieved statistical significance (in the period June-October 1979, Table 2.20); hence there was little evidence that manipulations of the numbers of A. stuartii had any consistent effect on the use of terrestrial habitat by A. swainsonii.

2.5.6.3 Food

Food type: The remains of 23 types of food were found in the scats of A. swainsonii (Table 2.21a). These types were the same as those eaten by A. stuartii, except that Thysanoptera were absent from the scats of A. swainsonii, and Isopoda were absent from the scats of A. stuartii (Compare Tables 2.12a and 2.21a). The most

frequently encountered types of prey in the scats of A. swainsonii were Coleoptera, Aranea, Amphipoda and larvae, but Chilopoda and "others" were also consistently present. Although the diet of A. swainsonii consisted largely of invertebrates, vertebrate remains (probably Leiolopisma sp.), hair and plant material were also found (Table 2.21a). In July I and II 1978 all hairs were those of A. swainsonii (possibly ingested during mating or from scavenging the bodies of dead males), but in April 1979 the hairs appeared to be those of the Eastern Pygmy-possum Cercartetus nanus. This arboreal species was never trapped at E3 or E4, but its presence was known from spotlighting it at night and from its hairs in the arboreal hair sampling tubes. In July I 1978, fragments of at least two seed cases were found in a single scat, and in April I and II 1979 the remains of berries (Rubus fruticosus and possibly Coprosma hirtella) were found.

Prey type diversity was generally similar in July I 1978 and April I and II 1979, but was reduced in July II and August 1978 due to small sample sizes (Table 2.21a). Differences in the number of prey types eaten, from 8 in C1 in August 1978 to 16 in E3 in April II 1979, more than differences in the evenness with which such types were represented, contributed to differences in prey type diversity.

The influence of manipulations of the numbers of A. stuartii on the types of prey eaten by A. swainsonii may be summarised as follows:

1) Prior to removal (July I 1978), the types of prey eaten in E3 differed from those eaten in C1 and E4. This was due largely to the higher incidence of Chilopoda remains in the scats of individuals in the former enclosure ($G_{(2d.f.)} = 7.13$, $P < 0.05$).

2) Immediately after removal (July II and August 1978), there was no overall difference in the types of prey eaten between the enclosures, but partitioning G showed that in July II 1978 proportionally fewer Amphipoda were eaten in E3 and E4 together than in C1 ($G_{(1d.F.)} = 4.16$, $P < 0.05$).

3) Nine months after removal (April I 1979), the types of prey eaten in C1 and E3 together differed from those eaten in E4. Tests showed that differences existed in the representation of three types of prey between the three enclosures: Collembola ($G_{(2d.f.)} = 9.14$, $P < 0.05$), Amphipoda ($G_{(2d.f.)} = 6.15$, $P < 0.05$) and "other invertebrates" ($G_{(2d.f.)} = 9.01$, $P < 0.05$). No planned comparisons (C1 vs E3 and E4) were, however, statistically significant.

4) Immediately after the reintroduction of A. stuartii to E3 (April II 1979), differences were found in the proportional representations of Collembola ($G_{(2d.f.)} = 7.37$, $P < 0.05$) and "other invertebrates" ($G_{(2d.f.)} = 6.21$, $P < 0.05$) between the three enclosures. (Differences were calculated also for Hemiptera and Isoptera, but for these prey types the statistical tests may have been unduly influenced by zero values, which comprised two of the six cells of the contingency tables). Only one planned comparison, for "other invertebrates", achieved statistical significance ($G_{(1d.f.)} = 6.21$, $P < 0.05$).

5) In all months, prey type diversities in C1 and E4 were usually comparable; values for these enclosures were always less than in E3 (Table 2.21a).

Food size: Between 67 and 90% of the invertebrate fragments identified to type from scats could be reliably assigned to a size class. In July II and August 1978 most prey items were <10 mm long, but sample sizes were small (Table 2.21b). In July I 1978 and April I and II 1979 appreciable numbers were >10 mm long, and 9 or 10 size classes of prey were consistently represented. Prey size diversity was relatively high in July I and April I and II, and comparable in all three enclosures. In July II and August 1978, diversity was relatively low due to the smaller number of prey size classes represented (Table 2.21b).

The influence of manipulations of the numbers of A. stuartii on the sizes of prey eaten by A. swainsonii may be summarised as follows:

1) Prior to removal, the sizes of prey eaten in C1 and E3 differed from those eaten in E4. In E4, A. swainsonii ate proportionally less prey 2.5-4.9 mm long ($G_{(2d.f.)} = 9.92$, $P < 0.01$) and more prey 7.5-9.9 mm long ($G_{(2d.f.)} = 11.00$, $P < 0.01$) than in the other two enclosures. Most of the larger items eaten by A. swainsonii in E4 were larvae, and these were eaten by three individuals only.

2) Immediately after removal (July II and August 1978), there were no differences in the sizes of prey eaten by A. swainsonii in any of the enclosures.

3) Nine months after removal (April I 1979), differences in the prey sizes eaten between the three enclosures were found for the 1.0-2.4 mm class ($G_{(2d.f.)} = 9.17$, $P < 0.05$) and the 7.5-9.9 mm class ($G_{(2d.f.)} = 8.11$, $P < 0.05$). In the planned comparison of C1 vs (E3 and E4), proportionally more prey in the latter size class were taken by A. swainsonii in C1 than in E3 and E4 ($G_{(1d.f.)} = 7.42$, $P < 0.01$). The larger prey taken in C1 were principally Coleoptera, Amphipoda and larvae.

4) Immediately after the reintroduction of A. stuartii to E3 (April II), no statistically significant differences could be detected in the sizes of prey eaten between the enclosures.

In summary, the types, sizes and diversities of food items eaten by A. swainsonii differed between the enclosures in some months. However, there was little evidence that these differences were associated with manipulations of the numbers of A. stuartii.

2.5.6.4 Periodicity of activity

Captures of A. swainsonii occurred throughout the day and night in all months in all enclosures (Fig. 2.19), but levels of activity between enclosures were usually not concordant (Table 2.22). Inspection of Fig. 2.19 suggested that this lack of concordance arose largely from the absence of a definite 24-hour cycle of activity, rather from manipulations of the number of A. stuartii.

2.6 DISCUSSION

The central question considered in this chapter is whether competition occurs between A. stuartii and A. swainsonii. The

results of the manipulation experiments, summarised in Tables 2.23 and 2.24, show that shifts occur in the population parameters and patterns of resource use in A. stuartii when the numbers of A. swainsonii are manipulated, but that reciprocal shifts in A. swainsonii are much less clear. Although these findings are strongly suggestive of interspecific competition, the first part of the discussion addresses possible alternative explanations, and also problems encountered with the experimental design. The biological consequences of competition are considered in later sections.

A first and obvious alternative explanation for the rather one-sided effect of A. swainsonii on A. stuartii is that the smaller species is eaten by its larger congenor. Hairston (1980) has argued convincingly that similar patterns of population and resource use among salamanders, although ostensibly the outcome of interspecific competition, are really due to predation. Direct observational evidence of predation was not obtained in the present study (see Chapter 6), nor has it been reported in any other study of the two species of Antechinus (Hall and Lee 1982, Kenner 1972). Indirect evidence of predation was similarly lacking: hairs were found in 11 out of 183 scats of A. swainsonii examined from five trapping sessions, but none came from A. stuartii (section 2.5.6.3). The partly arboreal habits and spectacular agility of A. stuartii probably suffice to keep it out of reach of the larger species; hence the predation alternative may be rejected.

A second alternative explanation for the shifts in population parameters and patterns of resource use, especially by A. stuartii, is that they were caused by the presence of the superfluous third species, the Bush Rat Rattus fuscipes. If previously unsuspected

interactions occur between rats and the two species of Antechinus, it is conceivable that removal of A. swainsonii or A. stuartii would induce changes in the rat population which could, in turn, influence population parameters and resource use by the remaining species of Antechinus. Diffuse competition probably occurs in relatively diverse communities of small dasyurids and murid rodents near Sydney (Fox 1981), and competitive interactions have been suspected between A. stuartii and R. fuscipes in Queensland (Braithwaite 1973).

In the present study, mutually detrimental interactions between rats and Antechinus are likely to have been minimal and unimportant. Within the enclosures, R. fuscipes is strictly herbivorous (Stewart 1979b), and hence there is little or no overlap in food resources with Antechinus spp. Rats construct their own nests and subterranean burrows (Warneke 1961, Woodside 1983), and hence overlap only slightly with Antechinus spp. in their nest requirements. In addition, all rats captured within the enclosures and on the trapping lines were individually ear-tagged, sexed, weighed and released along with Antechinus. Although these data have not yet been fully analysed and are not presented here, aspects of the demography of R. fuscipes in E1 and E2 in 1978 and 1979 have been assessed elsewhere (Woodside 1983). Woodside found no evidence of changes in the demography or social behaviour of R. fuscipes when the numbers of A. swainsonii were manipulated, suggesting that interactions between rats and A. swainsonii, if they occur, are not mutually harmful. Other evidence, obtained by calculating traditional measures of numerical and spatial association, suggests that interactions between the two species of Antechinus are much stronger and more negative than interactions between either species of Antechinus and

R. fuscipes (Dickman and Woodside in press). In view of these studies, it seems reasonable to conclude that shifts in the population parameters and resource use by one species of Antechinus were caused only by changes in the numbers of the other species, and not by any interaction with the rat.

Although removing rats from the enclosures may have simplified the interpretation of competition between the two species of Antechinus, removal was not conducted for several reasons. First, there are few areas in Australia where A. stuartii and A. swainsonii together occur in the absence of R. fuscipes (compare maps in Dickman 1982a for Antechinus, and Watts and Aslin 1981 for R. fuscipes). Hence the removal of rats from the enclosures would have produced a situation that was artificial for these specific areas, and for both species of Antechinus over their entire ranges. Second, R. fuscipes may actually be beneficial to Antechinus by constructing runways or providing (as carrion) a source of food (see section 2.5.4.3). Third, removal of rats would preclude any later assessment of possible rat-Antechinus interactions. And finally, why stop at removing rats? Throughout much of the year large numbers of insectivorous birds and reptiles occurred in the enclosures, and nectarivorous and insectivorous mammals (pygmy-possums and gliders) were present in the trees. Any of these species may be regarded as potential competitors of Antechinus, but their wholesale removal would, to say the least, be unethical and impractical. This final point is further discussed in Chapter 7.

A third alternative explanation for the observed shifts in resource use and population parameters is that the individuals in the experimental enclosures were genetically different from those in the

control enclosure. Genetical variation has been found to be important in determining the outcomes of competition in Tribolium beetles (Lerner and Dempster 1962), but it is irrelevant here. The enclosures were not absolutely isolated, and even a relatively small percentage of individuals moving into an out of the preferred valley habitats every few generations would be sufficient to prevent genetical divergence (see Lewontin 1974). Also, actual electrophoretic comparisons of variable enzyme systems between the enclosure populations have revealed no differences in gene frequencies (section 7.2).

None of the above alternative explanations for the shifts in population parameters and patterns of resource use of Antechinus, especially A. stuartii, is as complete or convincing as that of interspecific competition. At this point the null hypothesis of no competition may be rejected and restated: "Antechinus stuartii is affected adversely by competition from A. swainsonii, whereas A. swainsonii is probably affected much less by competition from its smaller congenor". The effects of competition, especially of A. swainsonii on A. stuartii, are now discussed in more detail.

The most obvious consequence of removing A. swainsonii was that population sizes of A. stuartii increased. Increases occurred in all three enclosures after breeding, but were greatest in E1 and E2 due to enhanced survival of newly weaned young. Reduced survival of weanlings in C1 may have arisen from direct harrassment by A. swainsonii, or because they were killed by lactating mothers who were unable to meet the energetic costs of feeding all their young in the presence of competitor individuals.

Antechinus swainsonii was the more terrestrial of the two species of Antechinus, and it was generally captured in structurally more complex habitat than its smaller congenor (compare Tables 2.11 and 2.20). The removal of A. swainsonii was followed by increases in movements, home range sizes and home range overlaps in A. stuartii, by a shift towards use of more complex habitat, and also by a decrease in the use of trees by this species. Antechinus stuartii evidently has a three dimensional home range, but its relative use of the vertical component depends on the presence or absence of A. swainsonii on the ground. These findings strongly support the suggestion of Hall and Lee (1982) that A. stuartii uses trees to avoid confrontations with its larger congenor, and suggest that the major arena for competition occurs on the ground. Differences in arboreal activity may also facilitate coexistence among other species of mammals, such as Venezuelan Mouse Opossums (O'Connell 1979) and some rodents (Taylor and McCarley 1963, McCracken 1978, Imaizumi 1979).

The shifts described above provide strong evidence of interspecific competition. In discussing diet, however, the evidence is ostensibly not so convincing. Shifts in the diet of A. stuartii certainly occurred when A. swainsonii was removed and reintroduced, but invertebrate food, unlike space and time, is a renewable resource that interacts with the animals using it, and it may change rapidly in abundance and availability. Hence, without measurements of the food resource it is not possible to state confidently that shifts in the diet of one species are due only to manipulations in the density of a competitor species. In an attempt to address this problem, month by month censuses were made of the invertebrate populations in all five

enclosures throughout the period of study. The findings are presented in detail in Chapter 4, but are summarised briefly here for convenience. First, invertebrates that move freely on the forest litter surface were most abundant and diverse in summer, but least so in winter. Fluctuations in their abundance and diversity occurred concordantly in all enclosures. Second, the more sessile invertebrates that live in the forest litter remained abundant and diverse all year round. Patterns of abundance and diversity were again concordant in all enclosures. These findings demonstrated that patterns of food availability were similar between the enclosures at all times, and suggest that observed shifts in diets of Antechinus were due only to the effects of the manipulation experiments. These effects are now considered in more detail below.

Comparison of Tables 2.12a and 2.21a shows that, although the two species of Antechinus ate broadly similar types of prey, there were differences in the proportional representation of prey types in the diets. Overall, A. stuartii tended to eat more prey such as Dermaptera, Isoptera, Diptera, Blattodea, Hemiptera and Orthoptera than A. swainsonii. These prey are generally inhabitants of logs, tree bark or the surface of the litter, and they tended to be well represented in pitfall traps (Chapter 4). In contrast, A. swainsonii tended to eat more prey such as Isopoda, Amphipoda, Oligochaeta and larvae that are more strictly terrestrial and are inhabitants of soil and sub-surface litter. Ostensibly, these findings support the general view that A. stuartii is an agile, partly arboreal predator, whereas A. swainsonii is a soil-fossicking insectivore (Wakefield and Warneke 1963, 1967; Calaby 1967; Recher et al. 1975; Braithwaite et al. 1978).

These conclusions were, however, challenged by the results of the removal experiments. Following the removal of A. swainsonii, for example, A. stuartii ate more Amphipoda and Isoptera, but less Hemiptera and Coleoptera than in the control population. (Differences were also recorded in the proportions of Blattodea and Aranea eaten). The Amphipoda all belonged to a strictly terrestrial species Arcitalitrus sylvaticus (J.A. Friend, personal communication), whereas many of the Coleoptera and Hemiptera (especially nymphs of the Family Lygaeidae) were almost certainly arboreal. The switch to eating proportionally more terrestrial and fewer arboreal prey in A. stuartii suggests that this species is an opportunistic predator, and that, when given access to terrestrial sources of food by the removal of its larger congenor, it will eat a variety of types of prey there. In addition, there were proportionally more invertebrates 2.5-4.9mm long in samples of forest litter than in pitfall traps (Chapter 4). The tendency for A. stuartii to eat these longer, terrestrial prey items when given access to them by the removal of A. swainsonii (section 2.5.4.3.) again reflects an opportunistic and competition-mediated switch in diet.

Changes in the proportions of prey types eaten by A. swainsonii also occurred between the enclosures (section 2.5.6.3), but these changes concerned mostly terrestrial prey such as Collembola and Amphipoda. There was no further evidence that A. swainsonii ate arboreal prey items in the absence of its smaller and semi-arboreal congenor.

Hall (1980b) concluded that the two species of Antechinus draw prey opportunistically from the same large population of prey. The above findings fully support this conclusion, but suggest further that

the types and sizes of prey eaten depend also on their accessibility. And, as earlier sections have shown, access of A. stuartii to terrestrial populations of prey is hindered by the presence of its terrestrial congenor, A. swainsonii.

Both species of Antechinus breed seasonally, but the timing of reproductive events in each species was unaffected by manipulations of the numbers of the other species. The above findings nevertheless confirm the earlier work of Wood (1970), Braithwaite (1973), Moore (1974) and others that mating occurs only over a short period (about 2 weeks) in winter, after which all males die. Mating is also remarkably synchronous from year to year in any locality (Wood 1970, Braithwaite 1973), and invites speculation on what triggers mating and why mating is so precisely timed.

Neither the proximate nor the ultimate factors controlling reproduction are clearly known, but Lee et al. (1977) and Braithwaite and Lee (1979) have suggested that mating is so timed that lactation and the weaning of young coincide with a flush in insect abundance in spring and summer. Wainer (1976) has further suggested that reproductive phase differences in a two species system (A. stuartii and A. minimus in Victoria) arise from dietary preferences for different insect groups that peak at different times, but this proposal has not been adequately tested. Hall (1980b) found that the diets of A. stuartii and A. swainsonii overlapped broadly, while Dickman (1982a) postulated that differences in the timings of matings of the two species at different altitudes were too great to be explicable solely in terms of differences in diet. The question of seasonal breeding is returned to in Chapter 7, where I suggest that, on a geographical scale, differences in the times of matings of the two species may lead to a reduction in levels of interspecific competition.

There were two unexpected findings in the results. The first was that the consequences of competition in A. stuartii were more obvious in females than in males. In the presence of A. swainsonii, female survival, movements and home ranges were more affected than in males. There is no obvious explanation for these findings, since male A. stuartii are closer in size to A. swainsonii and may be expected to compete more intensely than the smaller females. Some differences may, however, be more apparent than real: sample sizes of females were usually larger than of males, and variances were often smaller; hence differences of statistical significance were easier to obtain.

The second unexpected finding in the results was that the body weights of male and juvenile female A. stuartii were less in the absence than in the presence of A. swainsonii. Since the foregoing sections have suggested that the removal of A. swainsonii allowed A. stuartii access to a wider range of terrestrial habitats and to terrestrial populations of prey, it is of interest to ask why this should be so. There are three possible explanations. First, A. stuartii exploited cryptic prey that were flushed out and made available by the foraging activities of A. swainsonii (resource enhancement - see Charnov et al. 1976). Removal of the larger species would have rendered these prey unavailable, so that the food intake and body weights of A. stuartii declined. However, this explanation is unlikely, since the diversity of prey types in the diet of A. stuartii actually increased after A. swainsonii was removed (Table 2.12a). The second explanation is that small A. stuartii individuals suffered disproportionately in competition with A. swainsonii. Removal of the larger species would then have increased

the survival of these small individuals and so reduced the body weight mean of the population while simultaneously increasing the variance. Again, there is no evidence for this explanation, since variances in body weights differ little between enclosures (Appendices 3a,b,c). The third explanation is that removal of A. swainsonii allowed the numbers of A. stuartii to increase so that intraspecific interference competition occurred. Interference could have reduced access to food so that body weights declined. There is some evidence for this explanation, since reductions in body weight were greatest in the months (especially February-April I 1979) when the population sizes in E1 and E2 were unusually high (compare Fig. 2.6a with Appendices 3a,b). The importance of intraspecific competition is discussed at length below.

The inference that intraspecific competition occurred at all follows from the expectation that overlaps in resource use, and the potential for competition, should always be greater between conspecific individuals than between congenors. Hence, when two species compete, it may be assumed that individuals of each species also compete among themselves. For A. stuartii, the immediate consequence of removing A. swainsonii was to directly alleviate interspecific competition, but intraspecific competition was presumably also reduced, as individuals shifted and expanded the ranges of resources they used. Indeed, these shifts were almost certainly caused by intraspecific population pressure. However, the additional, long term consequence of removing A. swainsonii was to allow A. stuartii populations to increase in size. These increases - by up to 64% more in E1 and E2 than in the control population (section 2.5.3.1) - not only produced unusually high population densities, but

they may also have led to fertile conditions for increased intraspecific competition.

It is not immediately clear why this should be so, because resources in the experimental enclosures may not have been limiting: until the illegal removal of individuals from the control population in May 1979, the total numbers and biomass of both species of Antechinus in C1 were never less than the numbers and biomass of A. stuartii alone in E1 and E2. If, as suggested above, A. stuartii was able to exploit the terrestrial food resource of A. swainsonii, food should have been relatively abundant in E1 and E2 and hence have pre-empted intraspecific competition for this resource. However, the key is that increased frequencies of intraspecific contacts in the dense A. stuartii populations in E1 and E2 interfered with individuals access to resources, especially to food. Antechinus stuartii is basically a solitary animal, and most interactions other than those of mother and dependent young are aggressive (Braithwaite 1973, Lee 1972, Settle and Croft 1982a,b). High frequencies of such interactions could have reduced food intake and have led, in turn, to the reduced mean body weights.

Apart from the high densities of A. stuartii in E1 and E2 between February and April 1979, several other pieces of evidence suggested that the potential for intraspecific interference contacts in these enclosures was high. First, A. stuartii was considerably less arboreal in E1 and E2 than in C1; consequently there was little opportunity for individuals to avoid contact with each other on the ground. Second, home ranges generally overlapped more extensively in E1 and E2 than in C1; this would again have increased the chances of intraspecific contacts. Third, survival of newly-weaned

A. stuartii was enhanced in E1 and E2 (Table 2.5), so that average family sizes and frequencies of contacts among family members were probably increased.

There are two further observations that may be attributable to intraspecific competition. The first observation is that overlaps in the home ranges of individual juvenile females with other females were relatively small, especially in July and August (Table 2.10). Lee (1972) has shown that, in staged dyad encounters, levels of aggression among female A. stuartii increase towards the time of mating. In the field, increased levels of aggression may contribute to reduced overlap among females, and in this sense they may be thought to be territorial (Brown 1964, Kaufmann 1983). Female aggression and territory formation may arise in the face of a declining food supply before mating (Chapter 4) to ensure individuals priority of access to this resource. The decline in food may be less serious for males than for females, since males were captured consistently in structurally more complex habitats than females (Table 2.11) and thus had access to a more constant supply of food there (Chapter 4). Moreover, males may eat foods such as snails which appear to be less available to females. (The evidence for this is admittedly indirect and based on the increased incidence in pre-breeding males of a parasitic trematode Brachylaime antechini, for which the only known intermediate host is the snail Strangesta capillacea (Moore 1974, Peisley and Howell 1975). If the removal of A. swainsonii effectively increased the food available to A. stuartii, female-female overlaps in July and August (just prior to mating) might also be expected to increase, since the territorial need to defend scarce food is decreased. This occurred in both 1978 and 1979, but only in the latter year was the increase statistically significant (Table 2.10).

The second observation is that Antechinus mothers differed in the proportions of males to females they carried in the pouch. In A. stuartii the sex ratio was biassed towards females (section 2.5.3.2), whereas in A. swainsonii it was biassed towards males (section 2.5.5.2). Several authors have discussed sex ratio deviations (Kolman 1960, Trivers and Willard 1973, Myers 1978, Clutton-Brock et al. 1982), but an explanation for Antechinus has been proposed by A. Cockburn (personal communication). Cockburn has proposed that adjustments of sex ratios may facilitate reduction of competition between mothers and their daughters. In species where the expectation for females of breeding in a second year is relatively high and where daughters remain in or near the maternal range (such as A. swainsonii), individual reproductive output may be maximised by the production of relatively few female offspring, which reduces the probability of mother-daughter conflict in the following year. In contrast, in species such as A. stuartii where the expectation of breeding in a second year is remote, individual reproductive effort may be maximised by the production of more female offspring or equal numbers of both sexes.

2.7 SUMMARY

This chapter considered the question of whether competition occurs between A. stuartii and A. swainsonii. Five enclosures were established in May 1978, each containing relatively dense populations of both species. Antechinus stuartii was removed from two enclosures in July 1978 and later reintroduced to one, whereas A. swainsonii was removed from two other enclosures and later returned to one. Populations of both species were not manipulated in the remaining

enclosure; this served as a control. Comparisons of the population parameters and patterns of resource use were made for each species when it occurred in the presence and in the absence of the other species.

Manipulations of the numbers of A. swainsonii produced several effects on A. stuartii that were consistent with the interpretation of competition. These were: increases in numbers, survival of weanlings, movements, home range areas and overlaps; shifts in arboreal activity, terrestrial habitat use, and the types and sizes of food eaten. Unexpectedly, some effects, such as increases in survival, movements, home ranges and overlaps, were more evident in juvenile females than in males or parous females. A second anomalous finding was that mean body weights of A. stuartii declined when A. swainsonii was removed. Since the decline coincided with unusually high population densities in A. stuartii, however, I have suggested that this was due to increased levels of intraspecific competition. Competition with A. swainsonii had little evident effect on trappability, reproduction, body length and periodicity of activity of A. stuartii.

Manipulations of the numbers of A. stuartii were sometimes followed by changes in the population paramters or resource use of A. swainsonii. Some changes were consistent with the interpretation of competition, such as the increase (in two sampling sessions) in body weight of juvenile A. swainsonii when A. stuartii was removed, but more often, they occurred irrespective of the presence or absence of the smaller species. Hence, the competitive effects of A. stuartii on A. swainsonii were considered to be small.

Several alternative explanations of the above findings were discussed and rejected; none was as complete or as convincing as that of interspecific competition. The findings of the present Chapter show, then, that A. stuartii and A. swainsonii do compete, but further that the strongest effect is that of the larger species on the smaller species. Due to decimation of the A. swainsonii population in C1 in 1979, no attempt could be made to replicate precisely the experimental design followed in this chapter. In following chapters different questions are asked. What are the effects of high and low numbers of A. swainsonii on population parameters and resource use in A. stuartii? What is the scarce resource for which competition occurs and what is the mechanism of competition?

Table 2.1 The numbers of extraneous Antechinus swainsonii in enclosures E1 and E2 and on surrounding trap lines in 1978 and 1979.

	1978						1979											
	July II	A	S	O	N	D	Jan.	F	M	AI	M	J	J	A	S	O	N	D
E1																		
In enclosure	0	0	0	0	0	1	1	0	0	0	None extraneous							
On trap lines	1	0	0	0	1	0	1	1	0	0								
E2																		
In enclosure	0	0	0	0	0	0	1	0	0	0	1,1*	1*	2*	1*	0	1*	0	4*
On trap lines	0	0	0	0	0	0	0	1	0	1	1*	0	1	0	0	0	2*	0

*Denotes individuals that moved from E1. Antechinus swainsonii was removed from E1 and E2 in July 1978 after the first of two trapping sessions (July I and July II) in that month, and reintroduced only to E1 after the first of two trapping sessions (April I and April II) in April 1979.

Table 2.2 The numbers of extraneous Antechinus stuartii in enclosures E3 and E4 and on surrounding trap lines in 1978 and 1979.

	1978						1979											
	July II	A	S	O	N	D	Jan.	F	M	AI	M	J	J	A	S	O	N	D
E3																		
In enclosure	0	1	0	1	0	0	0	3	2	1	None extraneous							
On trap lines	1	1	0	0	0	0	0	0	1	1								
E4																		
In enclosure	2	0	0	0	0	0	0	1	1	1	1	2*	1*	1,1*	0	1*	0	1*
On trap lines	0	0	0	0	0	0	0	1	1	3	0	1*	1	2	0	0	0	0

*Denotes individuals that moved from E3. Antechinus stuartii was removed from E3 and E4 in July 1978 after the first of two trapping sessions (July I and July II) in that month, and reintroduced only to E3 after the first of two trapping sessions (April I and April II) in April 1979.

Table 2.3 Minimum sessional survival (%) of male Antechinus stuartii. Sample sizes are shown in brackets.

	C1	E1	E2
	Antechinus swainsonii not manipulated.		
May 1978	89 (9)	100 (7)	67 (9)
Jun.	90 (10)	86 (7)	100 (8)
Jul. I	100 (9)	89 (9)	83 (12)
	Antechinus swainsonii removed from E1 and E2		
Jul. II	78 (9)	67 (9)	91 (11)
Aug.	0 (10)	0 (8)	0 (12)
Jan. 1979	100 (1)	100 (3)	100 (1)
Feb.	86 (7)	92 (12)	100 (8)
Mar.	86 (7)	100 (12)	78 (9)
Apr. I	67 (9)	81 (16)	70 (10)
	Antechinus swainsonii reintroduced only to E1		
Apr. II	60 (10)	86 (14)	78 (9)
May	89 (9)	92 (13)	92 (13)
Jun.	78 (9)	69 (13)	85 (13)
Jul.	88 (8)	89 (9)	85 (13)
Aug.	0 (11)	0 (13)	0 (13)

Table 2.4 Minimum sessional survival (%) of female Antechinus stuartii. Sample sizes are shown in brackets.

	C1		E1		E2	
	<1yr	>1yr	<1yr	>1yr	<1yr	>1yr
	Antechinus swainsonii not manipulated					
May 1978	88 (8)	100 (1)	86 (7)	100 (1)	70 (10)	- (0)
Jun.	75 (8)	100 (1)	86 (7)	0 (1)	88 (8)	- (0)
Jul. I	100 (7)	0 (1)	100 (7)	- (0)	100 (8)	- (0)
	Antechinus swainsonii removed from E1 and E2					
Jul. II	86 (7)	- (0)	78 (9)	- (0)	75 (8)	- (0)
Aug.	63 (8)	- (0)	100 (8)	- (0)	83 (6)	- (0)
Sep.	- (0)	83 (6)	- (0)	63 (8)	- (0)	80 (5)
Oct.	- (0)	60 (5)	- (0)	100 (5)	- (0)	100 (4)
Nov.	- (0)	100 (5)	- (0)	80 (5)	- (0)	100 (4)
Dec.	- (0)	100 (5)	- (0)	100 (4)	- (0)	100 (4)
Jan. 1979	50 (2)	100 (5)	80 (5)	100 (4)	100 (4)	100 (4)
Feb.	70 (10)	100 (5)	93 (14)	100 (4)	86 (14)	100 (4)
Mar.	78 (9)	40 (5)	93 (14)	50 (4)	88 (17)	100 (4)
Apr. I	80 (10)	100 (2)	87 (15)	100 (2)	93 (15)	75 (4)
	Antechinus swainsonii reintroduced only to E1					
Apr. II	89 (9)	100 (2)	86 (14)	100 (2)	87 (15)	67 (3)
May	78 (9)	50 (2)	100 (12)	50 (2)	73 (15)	50 (2)
Jun.	71 (7)	0 (1)	83 (12)	100 (2)	75 (12)	100 (1)
Jul.	83 (6)	- (0)	80 (10)	50 (2)	89 (9)	100 (1)
Aug.	71 (7)	- (0)	67 (9)	0 (1)	80 (10)	100 (1)
Sep.	- (0)	100 (5)	- (0)	100 (6)	- (0)	78 (9)
Oct.	- (0)	83 (6)	- (0)	83 (6)	- (0)	71 (7)
Nov.	- (0)	80 (5)	- (0)	80 (5)	- (0)	80 (5)
Dec.	- (0)	100 (4)	- (0)	75 (4)	- (0)	75 (4)

Table 2.5 Survival of newly weaned Antechinus stuartii in late December 1978 and early January 1979.

	Number of nestling young in December 1978	Numbers surviving until January to April 1 1979	Overall survival (%)
C1	48	27	56
E1	40	35	88
E2	38	31	82

$G_{(2d.f.)} = 12.67,\ P < 0.01.$

The numbers of nestling young in December 1978 were obtained by counting the numbers of used nipples on lactating females (Woolley 1966). The survival of these young as weanlings in late December 1978 was assessed by counting the numbers of new juveniles that appeared in each enclosure between January and April 1 the following year. Since nestling young were not marked individually, these calculations assume that no individuals born outside the enclosures moved into the enclosures prior to April.

Table 2.6 The range in timing of reproductive events in Antechinus stuartii in 1978 and 1979.

Enclosure	Last male captured	Pregnancy	Birth	Young in nest	End of lactation	First juvenile captured
C1	3 Sept.	22* Aug.-28 Sept. (N=16)	23-29 Sept (N=11)	27 Oct.-2 Nov. (N=10)	8 Jan.	6 Jan.
E1	1 Sept.	24* Aug.-30 Sept. (N=18)	21-31 Sept. (N=14)	27 Oct.-2 Nov. (N=9)	29 Dec.	12 Jan.
E2	4 Sept.	20* Aug.-29 Sept. (N=17)	25-30 Sept. (N=14)	30 Oct.-3 Nov. (N=10)	11 Jan.	3 Jan.

*These dates were estimated from the condition of the hairs surrounding the pouch (Woolley 1966). Sample sizes (N) are in brackets.

Table 2.7 Movements of Antechinus stuartii. Values are mean average distances moved (m) ± standard deviation. Sample sizes are in brackets.

		C1	E1	E2	F_o	F_p	Conclusion
			Antechinus swainsonii not manipulated				
May-July I 1978	♂	43.3±15.9 (27)	52.9±26.1 (21)	47.4±29.4 (26)	0.93	-	C1 E1 E2
	♀	36.0±11.5 (23)	43.8±20.8 (20)	34.9±18.7 (24)	1.66	-	C1 E1 E2
	♂+♀	40.1±14.5 (50)	48.5±23.8 (41)	41.4±25.4 (50)	1.88	-	C1 E1 E2
			Antechinus swainsonii removed from E1 and E2				
July II-Aug. 1978	♂	59.6±31.1 (19)	67.0±33.2 (16)	62.2±26.9 (20)	0.26	0.30	C1 E1 E2
	♀	30.0±5.0 (15)	50.5±23.2 (15)	47.9±23.2 (13)	5.11*	10.08**	C1 E1 E2
	♂+♀	46.6±27.6 (34)	59.0±29.6 (31)	56.6±26.1 (33)	1.86	3.59	C1 E1 E2
Sept.-Dec. 1978	♀	31.7±8.7 (20)	41.5±21.4 (20)	35.7±19.9 (15)	1.62	2.30	C1 E1 E2
Jan.-Apr. I 1979	♂	37.9±28.2 (21)	42.2±17.7 (29)	50.3±19.8 (23)	1.86	1.94	C1 E1 E2
	♀<1yr	34.0±17.8 (24)	40.3±20.3 (42)	43.0±18.1 (41)	1.73	3.04	C1 E1 E2
	♀>1yr	34.3±19.1 (18)	41.8±22.5 (16)	44.6±19.8 (16)	1.15	2.15	C1 E1 E2
	♂+♀	35.4±21.9 (63)	41.2±19.7 (87)	45.4±18.9 (80)	4.39*	6.95**	C1 E1 E2
			Antechinus swainsonii reintroduced only to E1				
Apr. II-June 1979	♂	44.6±15.3 (24)	46.7±19.9 (34)	66.6±23.5 (31)	10.81***	21.46***	C1 E1 E2
	♀	46.3±21.5 (27)	41.9±17.6 (40)	56.6±34.5 (46)	3.46*	6.48*	C1 E1 E2
	♂+♀	45.5±18.7 (51)	44.1±18.7 (74)	60.6±30.8 (77)	10.57***	21.00***	C1 E1 E2
July-Aug. 1979	♂	67.4±23.1 (22)	78.1±38.5 (25)	81.8±37.5 (30)	1.15	1.18	C1 E1 E2
	♀	39.4±19.5 (19)	36.8±14.6 (27)	50.4±15.7 (30)	5.46**	10.64**	C1 E1 E2
	♂+♀	54.4±25.5 (41)	56.6±35.2 (52)	66.1±32.6 (60)	2.01	3.91*	C1 E1 E2
Sept.-Dec. 1979	♀	38.4±15.6 (19)	40.1±18.7 (20)	48.5±14.4 (24)	2.48	4.86*	C1 E1 E2

For Jan.-April I 1979, females >1 yr and <1 yr old are considered separately; for other months they are grouped together.

Table 2.8 Home ranges of Antechinus stuartii. Values are mean minimum areas (m^2) ± standard deviation. Sample sizes are in brackets.

		C1	E1	E2	F_o	F_p	Conclusion
			Antechinus swainsonii not manipulated				
May-July I 1978	♂	2054±894 (7)	2248±780 (7)	2365±757 (8)	0.28	-	C1 E1 E2
	♀	1421±483 (8)	1590±534 (7)	1397±609 (7)	0.27	-	C1 E1 E2
	♂+♀	1716±752 (15)	1919±728 (14)	1913±833 (15)	0.33	-	C1 E1 E2
			Antechinus swainsonii removed from E1 and E2				
July II-Aug. 1978	♂	2468±499 (7)	3164±464 (6)	3297±758 (9)	3.89*	7.61*	C1 E1 E2
	♀	1555±480 (7)	2239±412 (7)	2419±512 (5)	6.12*	11.81**	C1 E1 E2
	♂+♀	2012±668 (14)	2666±636 (13)	2983±790 (14)	6.94**	12.51**	C1 E1 E2
Sept.-Dec. 1978	♀	1801±801 (6)	2716±709 (5)	2570±371 (4)	2.83	5.55*	C1 E1 E2
Jan.-Apr. I 1979	♂	1405±427 (6)	1862±435 (7)	2741±817 (7)	8.55**	9.49**	C1 E1 E2
	♀<1yr	1182±510 (8)	1618±467 (11)	1828±494 (10)	3.97*	6.96*	C1 E1 E2
	♀>1yr	1163±708 (4)	2234±1202 (4)	1960±409 (4)	1.76	3.30	C1 E1 E2
	♂+♀	1252±511 (18)	1807±647 (22)	2157±719 (21)	9.85***	16.46***	C1 E1 E2
			Antechinus swainsonii reintroduced only to E1				
Apr. II-June 1979	♂	2177±793 (8)	2235±671 (11)	3210±964 (8)	4.40*	8.75**	C1 E1 E2
	♀	1658±691 (8)	2245±1262 (13)	2586±902 (13)	2.05	2.46	C1 E1 E2
	♂+♀	1917±767 (16)	2240±1013 (24)	2824±954 (21)	4.57*	8.00**	C1 E1 E2
July-Aug. 1979	♂	2719±902 (8)	2306±581 (7)	2587±914 (9)	0.05	0.03	C1 E1 E2
	♀	1758±548 (6)	1598±537 (7)	2039±654 (8)	1.08	1.92	C1 E1 E2
	♂+♀	2307±893 (14)	1953±651 (14)	2329±827 (17)	1.02	0.66	C1 E1 E2
Sept.-Dec. 1979	♀	1676±393 (5)	1322±611 (5)	2303±665 (6)	4.12*	7.30*	C1 E1 E2

For Jan.-April I 1979, females >1 yr and <1 yr old are considered separately; for other months they are considered together.

Table 2.9 Overlaps in home ranges of male Antechinus stuartii. Values are mean overlap (%) and 95% confidence limits (cl).

	Overlap		C1	E1	E2	F_o	F_p	Conclusion
			Antechinus swainsonii not manipulated					
			N = 7	N = 7	N = 8			
May-July 1978	♂/♂	$\bar{x}$	51.2	41.2	40.3	0.17	-	C1 E1 E2
		cl	28.5-73.5	12.2-78.8	7.4-79.4			
	♂/♀	$\bar{x}$	53.3	64.9	46.5	0.80	-	C1 E1 E2
		cl	32.4-73.6	38.4-87.3	21.3-72.6			
	♂/♂+♀	$\bar{x}$	72.7	80.9	53.8	2.10	-	C1 E1 E2
		cl	60.7-83.2	59.5-95.5	23.2-82.9			
			Antechinus swainsonii removed from E1 and E2					
			N = 7	N = 6	N = 9			
July II-Aug. 1978	♂/♂	$\bar{x}$	52.6	86.8	69.1	2.78	3.60	C1 E1 E2
		cl	21.9-82.4	65.1-98.8	48.6-86.2			
	♂/♀	$\bar{x}$	49.5	58.7	71.5	1.43	1.96	C1 E1 E2
		cl	25.8-73.3	32.4-82.5	50.5-88.4			
	♂/♂+♀	$\bar{x}$	74.7	94.1	87.9	2.20	3.69	C1 E1 E2
		cl	49.8-93.0	75.3-(100.0)	75.9-96.1			
			N = 6	N = 7	N = 7			
Jan.-Apr. I 1979	♂/♂	$\bar{x}$	19.2	21.0	45.8	1.22	0.72	C1 E1 E2
		cl	0.5-56.3	1.0-56.6	16.2-77.2			
	♂/♀<1yr	$\bar{x}$	53.2	47.2	66.0	0.40	0.03	C1 E1 E2
		cl	21.3-83.7	8.5-88.1	33.0-91.9			
	♂/♀>1yr	$\bar{x}$	21.9	48.8	9.5	2.03	0.07	C1 E1 E2
		cl	0.9-59.1	10.8-87.6	(0.0)-42.9			
	♂/♂+♀	$\bar{x}$	72.7	93.4	88.4	3.28	5.95*	C1 E1 E2
		cl	53.7-88.1	81.7-99.4	72.7-98.6			
			Antechinus swainsonii reintroduced only to E1					
			N = 8	N = 11	N = 8			
Apr. II-June	♂/♂	$\bar{x}$	51.5	66.4	68.6	0.63	0.35	C1 E1 E2
		cl	29.9-72.0	40.1-87.6	35.5-93.5			
	♂/♀	$\bar{x}$	71.5	80.8	82.1	0.46	0.26	C1 E1 E2
		cl	58.8-82.5	58.5-95.8	61.4-95.9			
	♂/♂+♀	$\bar{x}$	83.1	88.6	92.4	0.43	0.55	C1 E1 E2
		cl	72.5-91.4	68.6-99.1	71.3-(100.0)			
			N = 8	N = 7	N = 9			
July-Aug. 1979	♂/♂	$\bar{x}$	69.5	45.6	51.8	1.37	0.29	C1 E1 E2
		cl	50.5-85.6	13.9-79.5	31.0-72.4			
	♂/♀	$\bar{x}$	67.4	45.5	75.7	3.47*	3.76	C1 E1 E2
		cl	51.2-81.7	20.6-71.6	59.2-89.1			
	♂/♂+♀	$\bar{x}$	90.4	67.8	80.5	4.39*	0.01	C1 E1 E2
		cl	79.0-97.6	48.1-84.6	69.9-89.3			

All data were submitted to the arcsine transformation before statistical analysis. For this reason, although the above values were transformed back to percentages, confidence limits were generally not symmetrical about the mean (Zar 1974). Brackets denote confidence limits <0 or >100.

Table 2.10 Overlaps in home ranges of female Antechinus stuartii. Values are mean overlap (%) and 95% confidence limits (cl).

	Overlap		C1	E1	E2	F_o	F_p	Conclusion
			Antechinus swainsonii not manipulated					
			N = 8	N = 7	N = 7			
May-	♀/♀	$\bar{x}$	36.4	49.8	51.4	0.45	-	C1 E1 E2
July I		cl	14.8-61.1	24.5-75.1	15.4-86.5			
1978	♀/♂	$\bar{x}$	58.0	55.3	32.2	0.90	-	C1 E1 E2
		cl	21.3-90.1	27.0-81.9	4.4-70.4			
	♀/♂+♀	$\bar{x}$	83.2	68.2	77.1	0.62	-	C1 E1 E2
		cl	61.6-96.9	36.9-92.4	52.6-94.3			
			Antechinus swainsonii removed from E1 and E2					
			N = 7	N = 7	N = 5			
July II-	♀/♀	$\bar{x}$	17.6	28.7	46.9	3.21	4.21	C1 E1 E2
Aug.		cl	3.4-39.6	14.8-45.1	26.6-67.8			
1978	♀/♂	$\bar{x}$	75.8	66.8	77.8	0.33	0.12	C1 E1 E2
		cl	47.8-95.1	43.9-86.1	41.6-98.8			
	♀/♂+♀	$\bar{x}$	74.7	91.4	93.7	3.23	6.33*	C1 E1 E2
		cl	55.5-89.9	77.3-99.0	79.8-99.8			
			N = 6	N = 5	N = 4			
Sept.-	♀/♀	$\bar{x}$	26.5	33.9	36.9	0.21	0.39	C1 E1 E2
Dec. 1978		cl	4.0-59.4	8.9-65.2	5.4-77.1			
			N = 8	N = 11	N = 10			
	♀/♀<1yr	$\bar{x}$	28.9	61.9	60.2	4.05*	8.08**	C1 E1 E2
Jan.-		cl	4.6-63.3	47.9-75.0	46.3-73.3			
Apr. I	♀/♀>1yr	$\bar{x}$	26.4	50.0	12.3	1.79	0.04	C1 E1 E2
1979		cl	8.0-50.7	13.7-86.4	(0.0)-46.5			
(Females	♀/♂	$\bar{x}$	51.6	55.5	87.5	5.66**	3.08	C1 E1 E2
<1yr		cl	18.7-83.7	35.7-74.4	81.6-92.4			
old)	♀/♂+♀	$\bar{x}$	69.8	94.0	91.6	9.63***	18.87***	C1 E1 E2
		cl	55.2-82.5	86.3-98.6	85.5-96.1			
			N = 4	N = 4	N = 4			
	♀/♀<1yr	$\bar{x}$	52.3	46.3	19.5	0.65	0.51	C1 E1 E2
Jan.-		cl	17.3-86.0	(0.0)-100.0	(0.0)-96.6			
Apr. I	♀/♀>1yr	$\bar{x}$	1.5	19.1	25.2	3.47	6.74*	C1 E1 E2
1979		cl	(0.0)-13.1	(0.0)-74.2	19.3-31.6			
(Females	♀/♂	$\bar{x}$	26.9	76.9	43.4	1.37	1.56	C1 E1 E2
<1yr		cl	(0.0)-85.7	20.8-(100.0)	(0.0)-(100.0)			
old)	♀/♂+♀	$\bar{x}$	73.4	94.3	51.0	5.70*	0.06	C1 E1 E2
		cl	56.1-87.6	70.5-(100.0)	9.7-91.4			

Table 2.10. (Cont'd.)

	Overlap		C1	E1	E2	F_o	F_p	Conclusion		
			Antechinus swainsonii reintroduced only to E1							
			N = 8	N = 13	N = 13					
	♀/♀	$\bar{x}$	38.9	66.1	65.0	1.76	0.55	C1	E1	E2
Apr. 11-		cl	24.5-54.4	36.4-90.1	50.8-78.0					
June	♀/♂	$\bar{x}$	83.7	64.6	50.0	3.19	4.10	C1	E1	E2
1979		cl	75.6-90.5	46.9-80.5	25.6-74.4					
	♀/♂+♀	$\bar{x}$	88.5	87.5	81.5	0.50	0.98	C1	E1	E2
		cl	78.7-95.6	73.3-96.8	68.2-91.7					
			N = 6	N = 7	N = 8					
	♀/♀	$\bar{x}$	16.9	9.8	30.6	2.96	5.14*	C1	E1	E2
Jul.-		cl	2.3-41.1	2.5-21.2	15.5-48.3					
Aug.	♀/♂	$\bar{x}$	84.7	71.6	75.2	0.67	0.08	C1	E1	E2
1979		cl	68.7-95.7	45.0-91.9	54.2-91.3					
	♀/♂+♀	$\bar{x}$	86.4	72.2	78.5	0.82	0.01	C1	E1	E2
		cl	64.8-98.6	45.5-92.4	63.1-90.7					
			N = 5	N = 5	N = 6					
Sep.-	♀/♀	$\bar{x}$	11.8	8.4	37.7	2.42	4.74*	C1	E1	E2
Dec. 1979		cl	0.0-40.6	(0.0)-36.2	9.3-71.9					

All data were submitted to the arcsine transformation before statistical analysis. (See footnote to Table 2.9). Brackets denote confidence limits <0 or >100. For January-April I 1979, females <1yr and >1yr old are considered separately; for other months they are considered together.

Table 2.11 Frequency of capture of Antechinus stuartii at sites of different structural habitat complexity (S.H.C.). The number of captures (N), mean S.H.C. ($\bar{x}$) and standard deviation (s.d.) are given.

May-July I 1978

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♂	(2)	4	3	2	22	11	24	11	2	8	(3)	92	8.41	2.21
	♀<1yr	1	3	1	5	10	15	18	9	6	2	2	72	8.44	2.01
	♀>1yr	0	0	0	1	2	1	3	0	3	0	1	11	9.18	2.14
E1	♂	2	1	5	3	14	16	17	4	4	4	0	70	8.06	1.98
	♀<1yr	2	4	5	3	7	11	9	8	2	4	(3)	58	8.14	2.56
	♀>1yr	0	0	0	0	0	2	1	2	0	0	0	5	9.00	1.00
E2	♂	1	3	3	8	12	10	19	17	3	2	(2)	80	8.33	2.05
	♀<1yr	(2)	6	2	7	10	14	20	6	6	4	(3)	80	8.21	2.35

Summary[1] SHC x E x S, $G_{o\ (52\ d.f.)} = 57.84$

July II-August 1978

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♂	(3)	1	0	8	5	14	17	10	2	1	2	63	8.27	2.07
	♀	0	3	2	4	1	5	11	15	7	2	(2)	52	9.02	1.70
E1	♂	(1)	2	1	0	3	9	10	14	8	4	(2)	54	9.28	2.10
	♀	0	1	2	1	2	8	10	8	9	5	1	47	9.36	1.52
E2	♂	0	0	1	3	4	2	12	18	11	5	1	57	9.63	1.70
	♀	0	0	1	0	3	5	4	8	9	6	(4)	40	10.13	1.92

Summary[1]

SHC x E x S, $G_{o\ (52\ d.f.)} = 82.43^{**}$

SHC x E, $G_{o(20\ d.f.)} = 42.22^{**}$

C1 vs (E1 + E2), $G_{p(10\ d.f.)} = 29.15^{**}$

SHC x S, $G_{o(10\ d.f.)} = 14.41$

E x S, $G_{o(2\ d.f.)} = 0.61$

Table 2.11. (Cont'd.)

September-December 1978

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♀	0	2	1	7	6	11	15	16	4	2	1	65	8.63	1.86
E1	♀	0	2	1	2	5	5	9	17	12	4	(3)	60	9.50	2.00
E2	♀	(1)	1	3	1	4	2	10	11	6	7	2	48	9.33	2.36

Summary[1]

SHC x E (or S), $G_{o\ (20\ d.f.)} = 26.68$

C1 vs (E1 + E2), $G_{p\ (10\ d.f.)} = 19.05^{*}$

January-April I 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♂	3	1	5	11	9	8	14	9	0	1	0	61	7.52	2.00
	♀<1yr	(6)	4	12	13	18	9	4	1	2	0	0	69	6.35	1.84
	♀>1yr	0	0	4	2	4	16	7	9	6	2	2	52	8.79	1.95
E1	♂	1	0	3	1	17	10	17	28	12	4	5	98	9.19	1.92
	♀<1yr	(4)	8	18	11	20	34	17	15	3	0	2	132	7.38	2.06
	♀>1yr	0	0	1	3	1	10	10	7	4	5	(5)	46	9.54	2.06
E2	♂	0	0	2	10	8	9	12	24	3	5	0	73	8.75	1.82
	♀<1yr	(5)	11	16	22	14	12	26	19	21	1	1	148	7.74	2.44
	♀>1yr	0	1	0	1	1	12	2	8	5	4	4	38	9.63	2.10

Summary[1]

SHC x E x S, $G_{o\ (84\ d.f.)} = 316.99^{***}$

SHC x E, $G_{o\ (20\ d.f.)} = 51.10^{***}$

C1 vs (E1 + E2), $G_{p\ (10\ d.f.)} = 29.35^{**}$

SHC x S, $G_{o\ (20\ d.f.)} = 149.99^{***}$

E x S, $G_{o\ (4\ d.f.)} = 21.88^{***}$

Table 2.11. (Cont'd.)

April 11-June 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♂	1	6	4	13	14	18	19	10	0	0	(1)	86	7.57	1.85
	♀<1yr	(3)	4	6	16	11	9	3	4	1	2	0	59	6.81	2.06
	♀>1yr	0	1	0	1	2	6	1	3	2	1	0	17	8.53	2.00
E1	♂	4	4	9	9	24	17	19	10	11	1	0	108	7.73	2.10
	♀<1yr	(6)	5	10	14	15	22	21	16	1	1	(2)	113	7.53	2.17
	♀>1yr	0	0	0	2	2	3	4	3	3	3	0	20	9.25	1.92
E2	♂	1	0	1	8	8	15	21	22	10	13	(2)	101	9.24	1.94
	♀<1yr	(4)	5	3	6	9	18	32	28	14	2	(4)	125	8.70	2.16
	♀>1yr	0	1	2	3	3	4	1	4	5	1	(3)	27	8.89	2.64

Summary[1]

SHC x E x S,	G_o (84 d.f.) = 201.83***
SHC x E,	G_o (20 d.f.) = 80.65***
(C1 + E1) vs E2,	G_p (10 d.f.) = 67.67***
SHC x S,	G_o (20 d.f.) = 32.66*
E x S,	G_o (4 d.f.) = 8.66

July-August 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♂	(4)	1	5	4	11	9	16	13	2	3	(1)	69	8.10	2.26
	♀	(2)	3	6	7	15	5	8	12	5	2	0	65	7.78	2.25
E1	♂	(1)	5	3	2	12	15	25	7	7	1	0	78	8.18	1.91
	♀	1	5	3	4	9	22	15	14	5	4	1	83	8.34	2.07
E2	♂	1	1	7	4	12	12	29	14	5	5	(3)	93	8.61	2.04
	♀	0	4	0	6	8	19	22	18	10	4	(4)	95	8.93	1.96

Summary[1]

SHC x E x S,	G_o (52 d.f.) = 79.04**
SHC x E,	G_o (20 d.f.) = 38.73**
(C1 + E1) vs E2,	G_p (10 d.f.) = 16.46
C1 vs E1,	G_o (10 d.f.) = 22.27*
C1 vs E2,	G_o (10 d.f.) = 23.29**
SHC x S,	G_o (10 d.f.) = 15.04
E X S,	G_o (2 d.f.) = 0.23

Table 2.11. (Cont'd.)

September-December 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♀	1	1	2	3	6	9	11	13	5	0	(1)	52	8.58	1.94
E1	♀	0	5	1	0	7	13	11	16	9	1	0	63	8.70	1.96
E2	♀	0	2	1	3	5	14	18	11	14	2	(2)	72	9.08	1.85

Summary[1]		
SHC x E (or S),	$G_{o\ (20\ d.f.)}$	= 22.29
(C1 + E1) vs E2,	$G_{p\ (10\ d.f.)}$	= 9.50

[1] The G statistic was used to test the joint independence of S.H.C., sex/age class (S) and enclosure (E). If dependence was found, G was partitioned to examine which pairs of criteria were associated.

Antechinus swainsonii was removed from E1 and E2 between July I and July II 1978, and reintroduced only to E1 between April I and April II 1979. A few captures occured in S.H.C. categories 1, 2, 14 and 15. These were grouped with captures in category 3 or 13 and are shown in brackets. For January-June 1979, females < 1 yr and > 1 yr old are considered separately in G tests; for other months they are considered together.

Table 2.12 The dietary diversity of Antechinus stuartii. N = Number of individuals.
(a) Prey type diversity

	July I 1978			July II 1978			August 1978			April I 1979			April II 1979		
Prey type	C1	E1	E2	C1	E1	E2	C1	E1	E2	C1	E1	E2	C1	E1	E2
	N=16	N=16	N=16	N=15	N=17	N=15	N=18	N=16	N=17	N=20	N=31	N=27	N=18	N=26	N=25
Collembola	(1	0	0)	0	3	5	(2	0	1)	2	1	6	1	4	0
Coleoptera	15	21	14	10	8	19	21	13	15	21	26	15	15	21	18
Dermaptera	(0	0	1)	2	2	1	(0	1	0)	4	14	9	3	6	11
Aranea	14	15	9	17	7	11	10	6	8	10	12	10	15	14	9
Acarina	(1	1	0)	(1	0	0)	(0	0	0)	(0	1	0)	(0	0	0)
Chilopoda	(1	0	2)	(1	0	2)	(1	1	1)	4	4	2	2	1	4
Diplopoda	(0	0	0)	(4	0	0)	(1	2	0)	2	7	5	4	4	7
Amphipoda	2	12	7	4	1	2	5	9	16	3	10	8	2	4	7
Isoptera	4	1	2	0	4	2	(0	0	4)	0	4	29	2	0	16
Oligochaeta	(0	0	1)	(0	1	1)	(1	1	0)	(0	0	1)	(0	1	2)
Lepidoptera	(0	0	0)	(0	0	0)	(0	3	0)	(1	0	1)	(0	0	2)
Diptera	(0	0	0)	(1	3	0)	(0	0	1)	(1	0	0)	(0	1	1)
Formicoidea	(0	1	2)	(0	1	1)	4	1	2	(0	0	0)	(1	0	1)
Other Hymenoptera	(2	0	1)	(0	1	2)	(0	0	0)	(0	1	0)	(0	0	0)
Blattodea	1	3	5	1	8	2	1	5	4	3	5	4	3	2	3
Hemiptera	(1	0	1)	(0	1	0)	(0	0	0)	9	3	8	2	11	5
Orthoptera	(0	1	1)	(1	0	0)	(0	1	0)	1	2	3	4	1	2
Thysanoptera	(0	0	0)	(0	0	0)	(0	0	1)	(1	1	0)	(0	0	0)
Larvae	2	7	9	7	3	3	6	5	12	2	6	11	6	9	18
Other invertebrates	3 1	2	3	6	4	6	4	3	1	5	4	3	4	4	
Hair	(0	0	0)	(0	1	0)	(0	0	0)	(0	1	0)	(0	0	0)
Vertebrates	(0	0	0)	(0	0	0)	(0	0	0)	(0	0	1)	(0	1	0)
Plant	(0	1	0)	(0	0	1)	(1	0	1)	2	8	5	1	2	4
Total no. prey items	47	64	57	52	50	56	59	52	69	67	111	122	64	86	114
No. prey types represented	12	11	14	12	15	14	12	13	13	16	18	17	15	16	17
Evenness J	0.77	0.74	0.84	0.81	0.90	0.80	0.79	0.86	0.82	0.81	0.86	0.87	0.85	0.84	0.88
Diversity H	1.63	1.59	1.92	1.74	2.06	1.83	1.73	1.91	1.86	1.97	2.25	2.27	2.00	2.08	2.28
G_o (d.f.)	11.75(12)			34.87**(16)			16.14(12)			70.29***(26)			53.16**(26)		
G_p (d.f.)	-			23.80**(8)			12.98*(6)			35.12***(13)			38.04***		

(b) *Prey size diversity*

Prey size class (mm)	July I 1978			July II 1978			August 1978			April I 1979			April II 1979		
	C1 N=16	E1 N=16	E2 N=16	C1 N=15	E1 N=17	E2 N=15	C1 N=18	E1 N=16	E2 N=17	C1 N=20	E1 N=31	E2 N=27	C1 N=18	E1 N=26	E2 N=25
0.0-0.9	3	5	2	3	1	3	5	2	1	5	2	3	1	3	1
1.0-2.4	9	6	4	10	11	15	23	10	17	17	7	13	15	10	10
2.5-4.9	6	9	12	10	6	7	11	15	14	4	18	24	16	11	27
5.0-7.4	5	12	9	3	2	4	1	3	12	8	21	15	7	15	11
7.5-9.9	3	10	5	3	4	5	3	6	8	4	12	7	7	4	17
10.0-12.4	(1	1	1)	(0	1	2)	4	2	2	2	0	3	3	2	5
12.5-14.9	(0	0	1)	(0	0	0)	(0	0	2)	(0	1	2)	1	2	3
15.0-17.4	2	1	4	(1	0	1)	(1	1	0)	(0	1	0)	(0	1	2)
17.5-19.9	(1	2	0)	(0	1	0)	(0	1	1)	2	4	3	0	1	4
⩾ 20.0	(0	1	1)	(0	1	1)	1	2	1	1	4	1	(1	0	2)
Total no. prey items	30	47	39	30	27	38	49	42	58	43	70	71	51	49	82
No. prey size classes represented	8	9	9	6	8	8	8	9	9	8	9	9	8	9	10
Evenness J	0.89	0.85	0.85	0.85	0.79	0.83	0.73	0.81	0.79	0.83	0.81	0.81	0.80	0.82	0.82
Diversity H	1.54	1.64	1.59	1.30	1.36	1.48	1.34	1.53	1.55	1.51	1.62	1.62	1.47	1.59	1.72
G_o (d.f.)	$11.45_{(10)}$			$3.01_{(8)}$			$23.19^{*}_{(12)}$			$32.62^{**}_{(14)}$			$21.93_{(14)}$		
G_p (d.f.)	-			$2.21_{(4)}$			$16.95^{**}_{(6)}$			$21.18^{**}_{(7)}$			$4.87_{(7)}$		

Antechinus swainsonii was removed from E1 and E2 between July I and July II 1978, and reintroduced only to E1 between April I and April II 1979. G-tests were performed on the raw frequency data, excluding values in brackets. Data for males and females were pooled.

Table 2.13 Comparison of activity periods of Antechinus stuartii in three enclosures, using Kendall's coefficient of concordance, W.

	Males			Females			Both		
	W	χ^2	P	W	χ^2	P	W	χ^2	P
June-July I 1978	0.96	20.2	<0.01	0.85	17.9	<0.05	0.95	20.0	<0.01
July II-Aug. 1978	0.93	19.6	<0.01	0.89	18.7	<0.01	0.97	20.4	<0.01
Sept.-Dec. 1978	-	-	-	0.82	17.3	<0.05	-	-	-
Jan.-Apr. I 1979	0.90	18.8	<0.01	0.88	18.4	<0.05	0.89	18.8	<0.01
Apr. II-June 1979	0.95	19.9	<0.01	0.88	18.5	=0.01	0.98	20.6	<0.01
July-Aug. 1979	0.91	19.1	<0.01	0.80	16.9	<0.05	0.91	19.1	<0.01
Sept.-Dec. 1979	-	-	-	0.86	18.0	<0.05	-	-	-

All χ^2 values are associated with 7 d.f. Values of $P < 0.05$ show that the frequencies of captures within 3-hour time periods are concordant between enclosures.

Table 2.14 Minimum sessional survival (%) of male Antechinus swainsonii. Sample sizes are shown in brackets.

	C1	E3	E4
	Antechinus stuartii not manipulated		
May 1978	91 (11)	89 (9)	82 (11)
Jun.	90 (10)	100 (9)	90 (10)
Jul. I	18 (11)	30 (10)	0 (10)
	Antechinus stuartii removed from E3 and E4		
Jul. II	0 (4)	0 (3)	- (0)
Nov.	83 (6)	100 (5)	80 (5)
Dec.	88 (8)	91 (11)	93 (15)
Jan. 1979	71 (14)	67 (15)	71 (14)
Feb.	91 (10,1)	83 (12)	92 (13)
Mar.	100 (11,1)	100 (9,1)	92 (12,1)
Apr. I	92 (12,1)	90 (9,1)	92 (12,1)
	Antechinus stuartii reintroduced only to E3		
Apr. II	100 (11,1)	90 (9,1)	100 (11,1)
May.	29 (13,1)	100 (8,1)	92 (11,1)
Jun.	75 (3,1)	89 (9)	91 (11)
Jul.	0 (4)	0 (9)	0 (12)
Nov.	- (0)	75 (4)	67 (3)
Dec.	50 (2)	75 (8)	89 (9)

Where two values are given in brackets, the first denotes the number of individuals regularly present in the enclosure, the second the number of individuals that were absent from the trap record for $\geq$ 3 months. Both values were summed to obtain estimates of survival.

Table 2.15 Minimum sessional survival (%) of female Antechinus swainsonii. Sample sizes are shown in brackets.

	C1		E3		E4	
	<1yr	>1yr	<1yr	>1yr	<1yr	>1yr
	Antechinus stuartii not manipulated					
May 1978	80 (5)	100 (2)	100 (5)	100 (2)	100 (5)	50 (2)
Jun.	100 (4)	100 (2)	100 (5)	100 (2)	80 (5)	100 (1)
Jul. I	100 (4)	50 (2)	83 (6)	100 (2)	100 (4)	100 (1)
	Antechinus stuartii removed from E3 and E4					
Jul. II	75 (4)	100 (1)	100 (5)	100 (2)	100 (4)	100 (1)
Aug.	- (0)	100 (4)	- (0)	86 (7)	- (0)	100 (4,1)
Sep.	- (0)	100 (4)	- (0)	100 (4,2)	- (0)	80 (4,1)
Oct.	- (0)	100 (4)	- (0)	100 (4,2)	- (0)	100 (3,1)
Nov.	100 (4)	100 (4)	100 (1)	100 (4,2)	100 (1)	100 (3,1)
Dec.	75 (3,1)	75 (4)	100 (3)	100 (4,2)	80 (5)	100 (3,1)
Jan. 1979	100 (5,1)	67 (3)	83 (6)	67 (4,2)	100 (5)	75 (3,1)
Feb.	100 (4,2)	67 (3)	100 (5)	100 (3,1)	100 (5)	100 (2,1)
Mar.	100 (5,2)	100 (2)	80 (5)	75 (3,1)	100 (4,1)	100 (2,1)
Apr. I	86 (6,1)	100 (2)	100 (4)	100 (3)	100 (4,1)	100 (2,1)
	Antechinus stuartii reintroduced only to E3					
Apr. II	83 (5,1)	100 (2)	100 (4)	100 (3)	80 (4,1)	67 (2,1)
May	17 (6)	50 (2)	100 (4)	100 (3)	100 (3,1)	100 (2)
Jun.	100 (1)	100 (1)	100 (4)	67 (3)	75 (3,1)	100 (2)
Jul.	100 (1)	0 (1)	75 (4)	100 (2)	75 (3,1)	100 (2)
Aug.	- (0)	100 (1)	- (0)	100 (5)	- (0)	60 (5)
Sep.	- (0)	100 (1)	- (0)	100 (4,1)	- (0)	100 (3)
Oct.	- (0)	100 (1)	- (0)	100 (4,1)	- (0)	100 (3)
Nov.	- (0)	100 (1)	50 (2)	100 (4,1)	100 (2)	100 (3)
Dec.	100 (1)	100 (1)	100 (4)	80 (4,1)	67 (3)	100 (3)

See footnote to Table 2.14.

Table 2.16 Survival of newly weaned Antechinus swainsonii in late October and early November 1978.

	Sex	Number of nestling young in October 1978	Numbers surviving until November 1978 to January 1979	Overall survival (%)
C1	♂	21	16	76
	♀	10	7	70
E3	♂	16	16	100
	♀	13	6	46
E4	♂	18	16	89
	♀	8	6	75

Dependence of survival x sex x enclosure: $G_{(7d.f.)} = 17.52$, $P<0.05$.

The numbers of nestling young in October 1978 were obtained by counting numbers of used nipples on lactating females (Woolley 1966). The sexes of these young were checked in early September 1978. (In contrast to A. stuartii, precise numbers of sexed young were obtained because all the lactating females and young counted in September were present in October, and no new females entered the enclosures in the intervening time). The survival of these young as weanlings in late October 1978 was assessed by counting the numbers of new juveniles that appeared in each enclosure between November 1978 and January 1979. The calculations assume that no individuals born outside the enclosures moved into the enclosures prior to January.

Table 2.17 The range in timing of reproductive events in Antechinus swainsonii in 1978 and 1979.

Enclosure	Last male captured	Pregnancy	Birth	Young in nest	End of lactation	First juvenile captured
C1	24 July	3* July-17 Aug. (N=6)	10-18 Aug. (N=5)	19-27 Sept. (N=4)	25 Nov.	6 Nov.
E3	19 July	12* July-22 Aug. (N=11)	12-23 Aug. (N=11)	22-26 Sept. (N=7)	12 Nov.	13 Nov.
E4	13 July	5* July-18 Aug. (N=9)	9-19 Aug. (N=8)	17-29 Sept. (N=6)	?	7 Nov.

* These dates were estimated from the condition of the hairs surrounding the pouch. Sample sizes (N) are in brackets.

Table 2.18 Movements of Antechinus swainsonii. Values are mean average distances moved (m) ± standard deviation. Sample sizes are in brackets.

		C1	E3	E4	Fo	Fp	Conclusion
			Antechinus stuartii not manipulated				
May-July 1978	♂	50.7±42.3 (29)	63.7±40.3 (26)	55.7±34.5 (29)	0.76	-	C1 E3 E4
	♀	36.6±20.9 (17)	46.1±24.1 (21)	39.2±15.8 (16)	1.06	-	C1 E3 E4
	♂+♀	45.5±36.3 (46)	55.8±34.8 (47)	49.8±30.1 (45)	1.09	-	C1 E3 E4
			Antechinus stuartii removed from E3 and E4				
July II-Oct. 1978	♀	41.2±18.7 (17)	37.8±29.0 (22)	51.5±22.4 (15)	1.46	0.05	C1 E3 E4
Nov.1978-Jan. 1979	♂	37.7±19.8 (26)	43.1±23.2 (29)	41.6±18.6 (30)	0.49	0.90	C1 E3 E4
	♀<1yr	36.8±17.6 (11)	26.2±9.0 (9)	41.1±15.1 (9)	2.48	0.32	C1 E3 E4
	♀>1yr	38.2±11.4 (10)	38.2±26.0 (11)	46.1±18.6 (9)	0.50	0.21	C1 E3 E4
	♂+♀	37.6±17.5 (47)	38.9±22.6 (49)	42.3±17.8 (48)	0.76	0.75	C1 E3 E4
Feb.-Apr. 1 1979	♂	41.6±17.6 (25)	40.4±23.7 (29)	37.5±18.9 (28)	0.29	0.29	C1 E3 E4
	♀<1yr	43.5±29.9 (13)	31.6±12.1 (14)	32.4±13.3 (11)	1.37	2.73	C1 E3 E4
	♀>1yr	44.9±7.8 (7)	42.0±14.1 (9)	51.1±20.6 (9)	0.80	0.06	C1 E3 E4
	♂+♀	42.6±20.6 (45)	38.3±19.9 (52)	38.9±18.8 (48)	0.66	1.30	C1 E3 E4
			Antechinus stuartii reintroduced only to E3				
Apr. II-May 1979	♂	44.9±23.8 (22)	51.3±15.7 (14)	56.4±29.6 (19)	1.14	1.70	C1 E3 E4
	♀<1yr	41.2±19.4 (10)	41.9±14.6 (7)	37.2±8.3 (6)	0.17	0.33	C1 E3 E4
	♀>1yr	40.5±18.4 (4)	38.5±23.1 (6)	53.5±36.4 (4)	0.42	0.83	C1 E3 E4
	♂+♀	43.4±21.7 (36)	46.0±17.5 (27)	52.0±27.9 (29)	1.18	2.15	C1 E3 E4
June-July 1979	♂	59.0±22.6 (7)	71.8±33.7 (15)	66.1±34.8 (18)	0.38	0.02	C1 E3 E4
	♀	30.5±8.4 (4)	46.1±21.3 (11)	45.0±15.7 (12)	1.25	0.20	C1 E3 E4
	♂+♀	48.6±23.1 (11)	60.9±31.4 (26)	57.7±30.2 (30)	0.66	0.00	C1 E3 E4
Aug.-Oct. 1979	♀	52.3±17.5 (3)	34.3±14.6 (9)	42.0±11.5 (10)	2.12	0.30	C1 E3 E4
Nov.-Dec. 1979	♂	52.0 (1)	35.7±20.8 (9)	30.4±15.8 (9)	0.36	-	-
	♀<1yr	48.0 (1)	32.2±16.4 (6)	30.8±11.8 (5)	0.02	-	-
	♀>1yr	41.0 (2)	35.7±8.2 (6)	48.0±8.6 (4)	5.26*	-	-
	♂+♀	45.5±10.5 (4)	34.7±16.1 (21)	34.4±14.8 (18)	0.94	0.17	C1 E3 E4

For some months, females <1 yr and >1 yr old are considered separately; for other months they are grouped together.

Table 2.19 Home ranges of Antechinus swainsonii. Values are mean minimum areas (m^2) ± standard deviation. Sample sizes are in brackets.

		C1	E3	E4	F_o	F_p	Conclusion
			Antechinus stuartii not manipulated				
May–July 1978	♂	2110±1245 (8)	3026±2141 (7)	25[illegible]±1156 (7)	0.64	–	C1 E 3 E4
	♀	2140±757 (5)	2556±1003 (6)	[illegible]941±940 (4)	0.47	–	C1 E3 E4
	♂+♀	2122±1047 (13)	2809±1665 (13)	2355±1062 (11)	0.93	–	C1 E3 E4
			Antechinus stuartii removed from E3 and E4				
July II–Oct. 1978	♀	3322±940 (3)	3212±728 (5)	2474±1386 (3)	0.70	0.34	C1 E3 E4
Nov.1978–Jan. 1979	♂	2303±911 (5)	2068±707 (7)	2514±943 (8)	0.50	0.00	C1 E3 E4
	♀<1yr	2728±1118 (3)	2541±671 (3)	2045±778 (3)	0.49	0.49	C1 E3 E4
	♀>1yr	2211±776 (4)	3224±1301 (3)	2495±573 (3)	1.08	1.21	C1 E3 E4
	♂+♀	2379±860 (12)	2444±919 (13)	2409±813 (14)	0.02	0.03	C1 E3 E4
Feb.–Apr. 1 1979	♂	1920±902 (8)	1794±593 (7)	2156±793 (7)	0.39	0.02	C1 E3 E4
	♀	1763±702 (6)	2562±879 (7)	1927±618 (6)	2.09	1.87	C1 E3 E4
	♂+♀	1853±797 (14)	2178±823 (14)	2050±698 (13)	0.62	1.06	C1 E3 E4
			Antechinus stuartii reintroduced only to E3				
Apr. II–May 1979	♂	2454±1166 (7)	2399±942 (6)	2470±1357 (10)	0.01	0.01	C1 E3 E4
	♀	3060±902 (5)	2229±520 (5)	2268±446 (4)	2.38	0.90	C1 E3 E4
	♂+♀	2706±1065 (12)	2322±748 (11)	2412±1153 (14)	0.46	0.10	C1 E3 E4
June–July 1979	♂	3035±247 (2)	3166±1803 (6)	2183±1064 (8)	1.64	–	–
	♀	1945 (1)	2718±788 (4)	3167±1217 (4)	0.38	–	–
	♂+♀	2672±653 (3)	2987±1438 (10)	2511±1166 (12)	0.40	0.65	C1 E3 E4
Aug.–Oct. 1979	♀	2360 (1)	1362±634 (3)	1885±778 (3)	0.82	–	–

For the period November 1978-January 1979, females <1 yr and >1 yr old are considered separately; for other months they are considered together.

Table 2.20 Frequency of capture of Antechinus swainsonii at sites of different structural habitat complexity (S.H.C.). The number of captures (N), mean S.H.C. ($\bar{x}$) and standard deviation (s.d.) are given.

May-July 1 1978

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
	♂	1	2	4	4	4	18	16	21	8	12	(4)	94	9.20	2.18
C1	♀<1yr	0	1	1	0	5	6	6	7	4	0	2	32	8.94	1.98
	♀>1yr	0	0	0	2	2	2	1	5	5	2	(4)	23	10.09	2.21
	♂	2	0	6	7	7	11	10	17	13	5	(6)	84	9.00	2.40
E3	♀<1yr	(1)	0	2	4	2	4	9	7	8	2	(5)	44	9.34	2.40
	♀>1yr	0	2	1	0	4	1	4	1	3	1	2	19	8.74	2.75
	♂	0	3	1	4	9	17	17	14	16	4	(3)	88	9.05	1.98
E4	♀<1yr	0	0	0	2	2	6	8	7	2	1	1	29	9.07	1.60
	♀>1yr	1	0	0	0	2	1	2	4	0	1	1	12	9.00	2.59

Summary[1] SHC x E x S, $G_{o(52\ d.f.)} = 60.52$

July 11-October 1978

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1	♀	0	1	0	3	5	7	12	10	6	1	2	47	9.04	1.83
E3	♀	(4)	1	2	1	5	12	10	18	10	2	1	66	8.79	2.26
E4	♀	1	2	2	0	4	4	13	6	3	1	3	39	8.77	2.36

Summary[1] SHC x E (or S), $G_{o(20d.f.)} = 23.43$

C1 vs E3 + E4, $G_{p(10d.f.)} = 10.47$

November 1978-January 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
	♂	0	0	0	6	5	11	8	21	14	6	(3)	74	9.54	1.82
C1	♀<1yr	0	2	0	1	0	3	5	12	6	2	2	33	9.67	2.04
	♀>1yr	0	1	1	2	1	8	7	8	2	1	(2)	33	8.94	2.00
	♂	1	2	0	6	4	12	15	15	18	2	1	76	9.09	1.96
E3	♀<1yr	0	0	1	2	4	2	2	7	8	2	0	28	9.32	1.98
	♀>1yr	(1)	0	2	0	0	4	4	10	9	2	(3)	35	9.80	2.18
	♂	0	1	0	6	7	17	28	20	4	2	2	87	8.86	1.56
E4	♀<1yr	0	0	0	2	0	4	7	7	4	1	1	26	9.46	1.61
	♀>1yr	(2)	0	1	0	2	4	8	2	7	2	1	29	9.07	2.42

Summary[1]

SHC x E x S, $G_{o(84\ d.f.)} = 120.07^{**}$

SHC x E, $G_{o(20d.f.)} = 32.08^{*}$

C1 vs (E3 + E4), $G_{p(10d.f.)} = 13.33$

(C1 + E3) vs E4, $G_{(10d.f.)} = 21.76^{*}$

SHC x S, $G_{o(20d.f.)} = 30.79$

E x S, $G_{o(4d.f.)} = 2.66$

Table 2.20 (cont.)

February-April I 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
	♂	(2)	0	2	2	9	9	15	20	16	4	(4)	83	9.33	2.04
C1	♀<1yr	0	1	1	0	3	9	5	8	7	4	1	39	9.36	1.95
	♀>1yr	0	2	1	1	2	4	4	5	3	0	1	23	8.57	2.29
	♂	1	3	0	3	8	12	17	15	16	3	3	81	9.12	2.05
E3	♀<1yr	0	2	2	4	4	4	10	9	3	4	2	44	8.84	2.29
	♀>1yr	1	1	0	2	2	5	2	8	5	1	4	31	9.35	2.51
	♂	(2)	1	5	2	12	8	31	17	15	11	3	107	9.16	2.11
E4	♀<1yr	1	4	2	2	1	7	14	5	3	1	3	43	8.47	2.48
	♀>1yr	0	1	0	1	1	3	3	4	4	2	0	19	9.26	2.08

Summary[1] SHC x E x S, $G_{o(84\ d.f.)} = 93.42$

C1 vs (E3 + E4), $G_{p(10d.f.)} = 8.26$

April II-May 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
	♂	1	0	1	1	2	3	15	33	7	2	4	69	9.71	1.63
C1	♀<1yr	0	1	0	1	3	2	5	6	6	0	1	25	9.24	1.96
	♀>1yr	0	0	0	2	2	3	3	2	0	0	0	12	8.08	1.38
	♂	0	1	0	0	2	7	12	8	4	4	4	42	9.67	1.88
E3	♀<1yr	0	0	0	1	2	0	5	5	6	1	2	22	9.95	1.79
	♀>1yr	1	0	1	0	0	2	4	4	4	1	1	18	9.39	2.38
	♂	1	1	1	2	3	2	10	20	14	5	3	62	9.74	2.00
E4	♀<1yr	1	0	0	0	2	1	5	8	3	1	0	21	9.29	1.90
	♀>1yr	0	0	1	0	0	4	2	4	1	1	0	13	9.08	1.75

Summary[1] SHC x E x S, $G_{o(52d.f.)} = 66.88$

(C1 + E3) vs E4, $G_{p(10d.f.)} = 5.58$

June-October 1979

	sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
	♂	3	1	0	1	2	3	4	3	2	0	2	21	8.14	3.00
C1	♀	0	0	2	1	2	4	6	8	2	1	2	28	9.14	2.01
	♂	1	2	2	1	4	4	8	12	8	2	4	48	9.23	2.40
E3	♀	0	2	1	1	4	5	18	22	9	6	2	70	9.51	1.79
	♂	0	0	1	3	3	9	12	15	17	1	2	63	9.51	1.66
E4	♀	1	0	1	0	2	5	14	20	18	4	1	66	9.80	1.60

Summary[1] SHC x E x S, $G_{o(52d.f.)} = 61.26$

(C1 + E3) vs E4, $G_{p(10d.f.)} = 20.09^{*}$

[1] The G statistic was used to test the joint independence of S.H.C., sex/age class (S) and enclosure (E). If dependence was found, G was partitioned to examine which pairs of criteria were associated. Antichinus stuartii was removed from E3 and E4 between July I and July II 1978 and reintroduced only to E3 between April I and April II 1979. A few captures occurred in S.H.C. categories 1,2,14 and 15. These were grouped with captures in category 3 or 13 and are shown in brackets. For November 1978-April I 1979, females <1yr and >1yr old are considered separately in G-tests; for other months they are considered together.

Table 2.21 The dietary diversity of Antechinus swainsonii. N = number of individuals.
(a) Prey type diversity

	July I 1978			July II 1978			August 1978			April I 1979			April II 1979		
	C1	E3	E4	C1	E3	E4	C1	E3	E4	C1	E3	E4	C1	E3	E4
Prey type	N=17	N=17	N=15	N=7	N=10	N=4	N=4	N=7	N=4	N=18	N=16	N=16	N=17	N=15	N=16
Collembola	(2	0	0)	(0	4	0)	(0	0	2)	2	5	0	0	5	1
Coleoptera	29	15	16	11	8	5	4	6	11	23	13	21	17	26	19
Dermaptera	(0	0	1)	(0	0	0)	(0	1	0)	2	0	2	(1	0	3)
Aranea	15	23	9	7	9	5	2	6	6	8	11	8	17	21	10
Acarina	(1	3	0)	(0	1	0)	(0	0	0)	(0	3	0)	(2	1	0)
Chilopoda	2	8	1	1	2	3	1	3	1	1	3	2	8	6	2
Diplopoda	0	2	2	(1	0	2)	(0	2	0)	2	4	2	2	4	4
Isopoda	(0	0	0)	(1	0	1)	(0	1	0)	2	4	2	0	2	3
Amphipoda	18	10	16	20	10	3	2	1	6	18	10	30	18	13	10
Isoptera	(0	0	0)	(0	0	0)	(0	0	1)	(0	1	0)	(0	0	3)
Oligochaeta	(2	1	0)	(1	0	0)	(1	0	2)	2	0	2	(3	1	0)
Lepidoptera	(0	0	0)	(0	0	0)	(0	0	0)	(0	1	0)	(0	0	1)
Diptera	(0	0	0)	(0	0	0)	(0	0	0)	(0	0	0)	(1	1	0)
Formicoidea	(0	1	0)	(0	0	0)	(1	0	0)	(3	0	0)	(4	0	0)
Other Hymenoptera	(0	0	0)	(0	0	0)	(0	0	0)	(0	0	1)	(0	1	0)
Blattodea	(1	2	0)	(2	1	0)	(1	0	1)	2	0	2	(4	0	0)
Hemiptera	(1	0	0)	(0	0	0)	(0	0	0)	(2	0	0)	0	5	0
Orthoptera	(0	0	0)	(0	0	0)	(0	0	0)	(0	0	1)	(0	1	0)
Larvae	25	11	17	4	2	2	3	4	2	13	9	23	18	10	12
Other invertebrates	4	7	5	2	3	1	0	4	2	3	5	0	4	4	10
Hair	1	5	3	(0	1	0)	(0	0	0)	(0	0	0)	(0	0	1)
Vertebrates	(0	0	1)	(0	0	0)	(0	0	0)	(0	0	1)	(0	0	0)
Plant	(0	2	0)	(0	0	0)	(0	0	0)	3	2	4	(0	1	1)
Total no. prey items	101	90	71	50	41	22	15	28	34	86	71	101	99	102	80
No. prey types represented	12	13	10	10	10	8	8	9	10	15	13	14	13	16	14
Evenness J	0.74	0.85	0.81	0.75	0.86	0.93	0.93	0.91	0.85	0.81	0.91	0.74	0.85	0.80	0.85
Diversity H	1.68	1.98	1.69	1.51	1.69	1.54	1.44	1.64	1.62	1.96	2.06	1.77	1.98	2.01	2.00
$G_{o(d.f.)}$	$30.90^{**}_{(14)}$			$9.75_{(10)}$			$11.39_{(10)}$			$42.16^{*}_{(24)}$			$38.92^{**}_{(18)}$		
$G_{p(d.f.)}$	-			$6.97_{(5)}$			$3.84_{(5)}$			$4.85_{(12)}$			$16.67_{(9)}$		

Table 2.21 (cont.)
(b) Prey size diversity

	July I 1978			July II 1978			August 1978			April I 1979			April II 1979		
	C1	E3	E4	C1	E3	E4	C1	E3	E4	C1	E3	E4	C1	E3	E4
Prey size class (mm)	N=17	N=17	N=15	N=7	N=10	N=4	N=4	N=7	N=4	N=18	N=16	N=16	N=17	N=15	N=16
0.0- 0.9	8	2	5	2	1	1	(0	1	1)	4	3	7	9	5	10
1.0- 2.4	11	8	8	9	4	2	2	4	3	11	21	10	14	15	8
2.5- 4.9	18	18	4	7	4	2	4	3	7	4	8	14	18	28	14
5.0- 7.4	12	16	17	10	9	2	2	5	5	5	8	17	15	20	18
7.5- 9.9	12	5	17	12	7	3	2	4	6	20	12	11	7	7	4
10.0-12.4	5	6	1	(1	0	1)	(0	0	0)	5	3	9	5	5	3
12.5-14.9	2	4	1	1	2	1	(1	0	1)	2	2	5	6	1	3
15.0-17.4	4	2	0	(2	1	0)	(0	1	0)	(1	0	2)	1	2	2
17.5-19.9	4	1	2	(1	2	0)	(0	2	0)	4	2	1	1	1	3
⩾ 20.0	2	3	1	(0	0	3)	(1	1	0)	2	3	2	3	1	2
Total no. prey items	78	65	56	45	30	15	12	21	23	58	62	78	79	85	67
No. prey size classes represented	10	10	9	9	8	8	6	8	6	10	9	10	10	10	10
Evenness J	0.91	0.85	0.79	0.83	0.88	0.96	0.93	0.92	0.88	0.85	0.85	0.90	0.88	0.78	0.87
Diversity H	1.90	1.75	1.54	1.58	1.52	1.48	1.23	1.51	1.30	1.73	1.67	1.87	1.84	1.63	1.80
$G_{o(d.f.)}$		$35.67^{**}_{(18)}$			$3.05_{(10)}$			$2.25_{(6)}$			$27.99^{*}_{(16)}$			$16.67_{(18)}$	
$G_{p(d.f.)}$		-			$1.85_{(5)}$			$0.74_{(3)}$			$13.75_{(8)}$			$7.43_{(9)}$	

Antechinus stuartii was removed from E3 and E4 between July I and July II 1978 and was reintroduced only to E3 between April I and April II 1979. G-tests were performed on the raw frequency data, excluding values in brackets. Data for males and females were pooled.

Table 2.22 Comparison of activity periods of Antechinus swainsonii in three enclosures, using Kendall's coefficient of concordance, W.

	Males			Females			Both		
	W	χ^2	P	W	χ^2	P	W	χ^2	P
June-July I 1978	0.63	13.1	n.s.	0.21	4.5	n.s.	0.45	9.4	n.s.
July II-Oct. 1978	-	-	-	0.41	8.7	n.s.	-	-	-
Nov. 1978-Jan. 1979	0.39	8.1	n.s.	0.13	2.8	n.s.	0.27	5.6	n.s.
Feb.-Apr. I 1979	0.09	1.8	n.s.	0.08	1.7	n.s.	0.12	2.6	n.s.
Apr. II-May 1979	0.44	9.2	n.s.	0.67	14.1	<0.05	0.63	13.2	n.s.
June-July 1979	0.57	11.9	n.s.	0.22	4.6	n.s.	0.56	11.8	n.s.
Aug.-Oct. 1979	-	-	-	0.21	4.4	n.s.	-	-	-

All χ^2 values are associated with 7 d.f. Values of $P < 0.05$ show that the frequencies of captures within 3-hour time periods are concordant between enclosures. Not significant (n.s.) values denote a lack of such concordance.

Table 2.23. Summary of the effects of removal and reintroduction of A. swainsonii on the population parameters and resource use of A. stuartii.

	Effects of removal			Effects of reintroduction		
	♂	♀	Both	♂	♀	Both
Population parameters						
Numbers	-	-	√	-	-	-
Survival	√	√	√	-	-	-
Trappability	-	-	-	-	-	-
Reproduction	-	-	-	-	-	-
Movements	-	√	√	√	√√	√√
Home range	√√	√√	√√	√	√	√
Home range overlap	-	√	√	-	√	√*
Body weight	√*	√*		√*	√*	
Body length	-	-		√*	√	
Resources						
Habitat (arboreal)			√			√
Habitat (terrestrial)	√√	√√	√√	√	√	√
Food type			√√			√√
Food size			√			-
Time	-	-	-	-	-	-

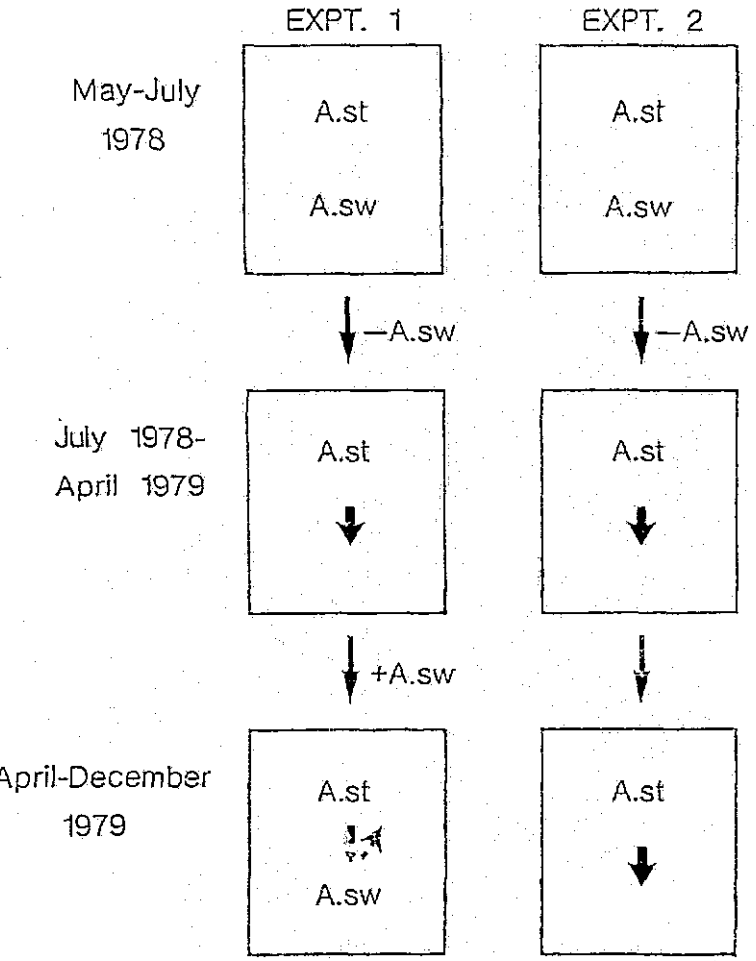
√ denotes that statistically significant effects occurred in some sampling sessions (months or groups of months) only; √√ that effects occurred in all sampling sessions; - that no statistically significant effects were detected at any time. All effects were consistent with the interpretation of interspecific competition, except where marked *.

Table 2.24. Summary of the effects of removal and reintroduction of A. stuartii on the population parameters and resource use of A. swainsonii.

	Effects of removal			Effects of reintroduction		
	♂	♀	Both	♂	♀	Both
Population parameters						
Numbers	-	-	-	-	-	-
Survival	-	-	-	-	-	-
Trappability	-	-	-	-	-	-
Reproduction	-	-	-	-	-	-
Movements	-	-	-	-	-	-
Home range	-	-	-	-	-	-
Home range overlap						
Body weight	-	√		-	√	
Body length	√	√*		-	√	
Resources						
Habitat (arboreal)			-			-
Habitat (terrestrial)	-	-	√*	-	-	√
Food type			-			√*
Food size			√*			-
Time	-	-	-	-	-	-

√ denotes that statistically significant effects occurred in some sampling sessions (months or groups of months) only; - that no statistically significant effects were detected at any time. Effects were consistent with the interpretation of interspecific competition, except where marked *.

Fig. 2.1 Requirements for the experimental demonstration of competition between A. stuartii (A.st) and A. swainsonii (A.sw). All steps are described in detail in the text. Rectangles (EXPT. 1 - EXPT. 4 and CONTROL) represent enclosures. Solid arrows within rectangles represent an expansive shift in population parameters or patterns of resource use when one species is removed, broken arrows a return shift when that species is reintroduced. The effect of A. swainsonii on A. stuartii is assessed by comparing populations in E1, E2 and C1, whereas the effect of A. stuartii on A. swainsonii is assessed by comparing populations in E3, E4 and C1.


EXPT. 1
EXPT. 2
May-July
1978
A.st
A.sw
A.st
A.sw
—A.sw
—A.sw
July 1978-
April 1979
A.st
A.st
+A.sw
April-December
1979
A.st
A.sw
A.st
A.st

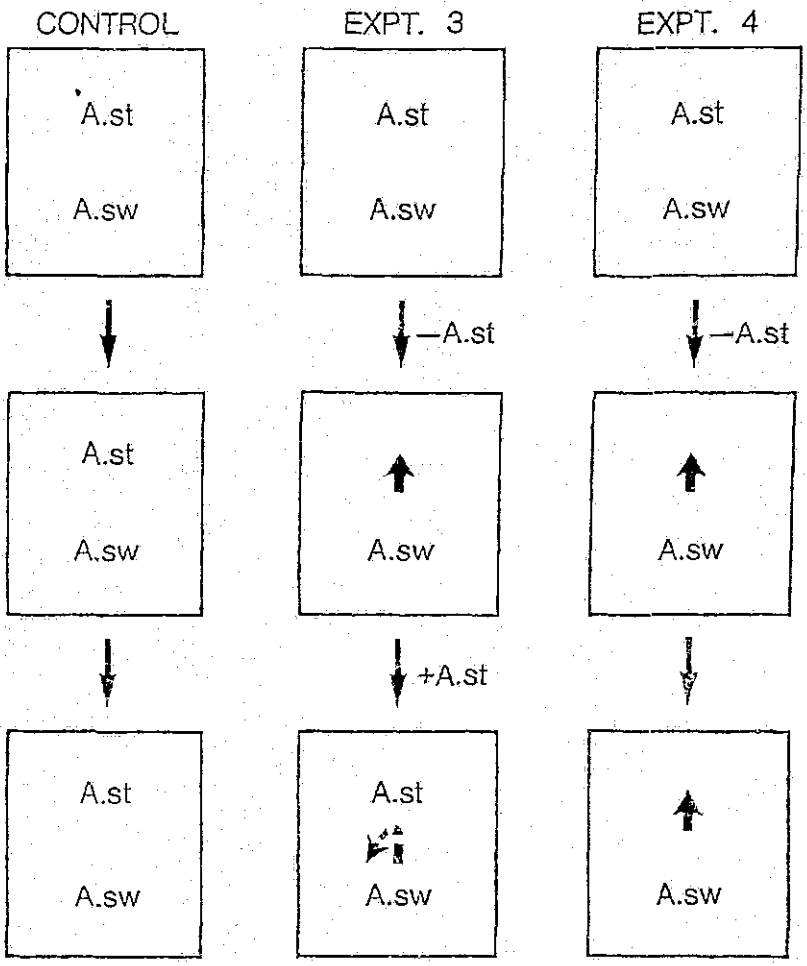

CONTROL
EXPT. 3
EXPT. 4
A.st
A.sw
A.st
A.sw
A.st
A.sw
—A.st
—A.st
A.st
A.sw
A.sw
A.sw
+A.st
A.st
A.sw
A.st
A.sw
A.sw

Fig. 2.2 Rainfall and temperature regimes of the enclosures: (a) and (c), enclosures E1 and E2; (b) and (d), enclosures E3 and E4. The control enclosure is <1 km from E3 and E4, and may be expected to have a similar climate. In (a) and (b), shading represents the monthy rainfall average over the eleven years (1966-1976) prior to the commencement of this study, the solid line represents monthly rainfall throughout the study. In (c) and (d), the broken lines represent average monthly maximum and minimum temperatures between 1966 and 1976, the solid lines represent temperatures throughout this study.

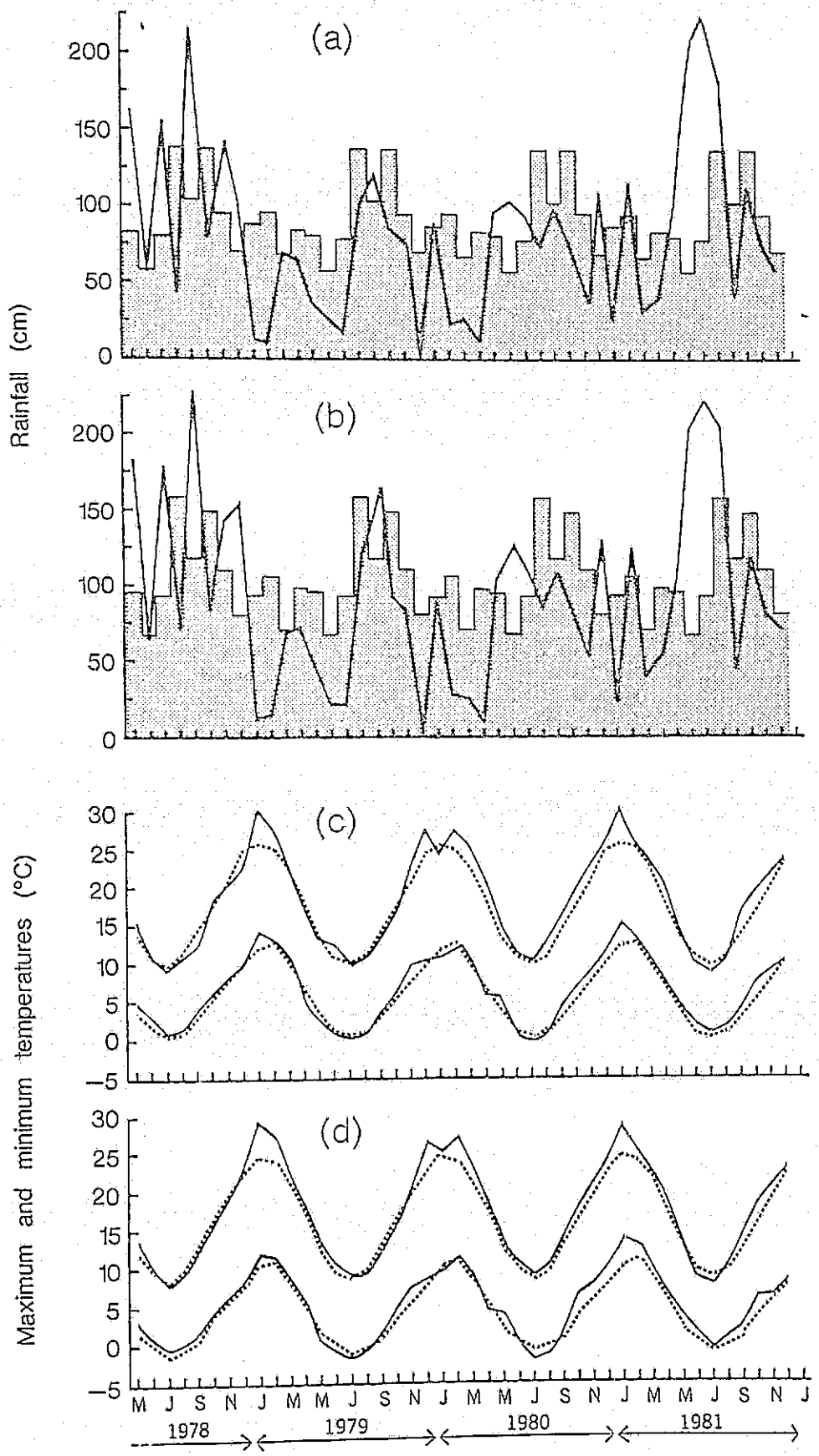

(a)
(b)
(c)
(d)
Rainfall (cm)
Maximum and minimum temperatures (°C)
200
150
100
50
0
30
25
20
15
10
5
0
−5
M J S N J M M J S N J M M J S N J M M J S N J
1978
1979
1980
1981

Fig. 2.3 Vegetation of (a) the enclosures and (b) the surrounding slopes. Note that the relatively dense fern understorey and litter cover of the enclosures is absent on the slopes.

Fig. 2.3 (a)

Fig. 2.3 (b)

Fig. 2.4 The enclosures. (a) the control enclosure, C1; (b) experimental enclosures E1 and E2. E1 lies on the south bank of Lees Creek, E2 on the north bank; (c) experimental enclosures E3 and E4. E3 lies on the west bank of Blundell Creek, E4 on the east bank. Solid circles represent grid trapping stations, open circles line trapping stations. The major creeks are shown in solid heavy lines, minor watercourses in broken heavy lines.

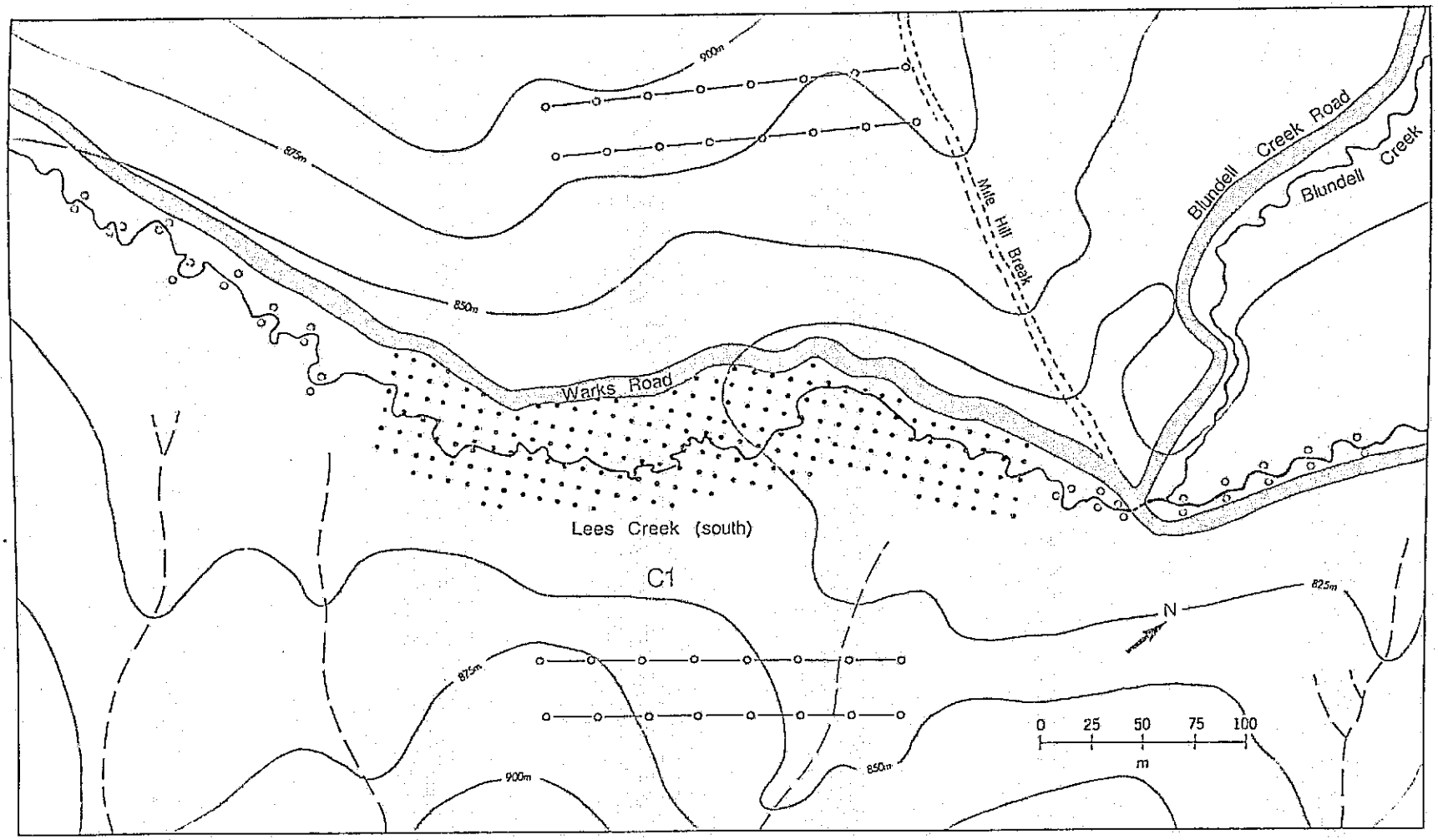

900m
875m
850m
Mile Hill Break
Blundell Creek Road
Blundell Creek
Warks Road
Lees Creek (south)
C1
N
825m
875m
900m
850m
0 25 50 75 100
m

Fig. 2.4 (a)

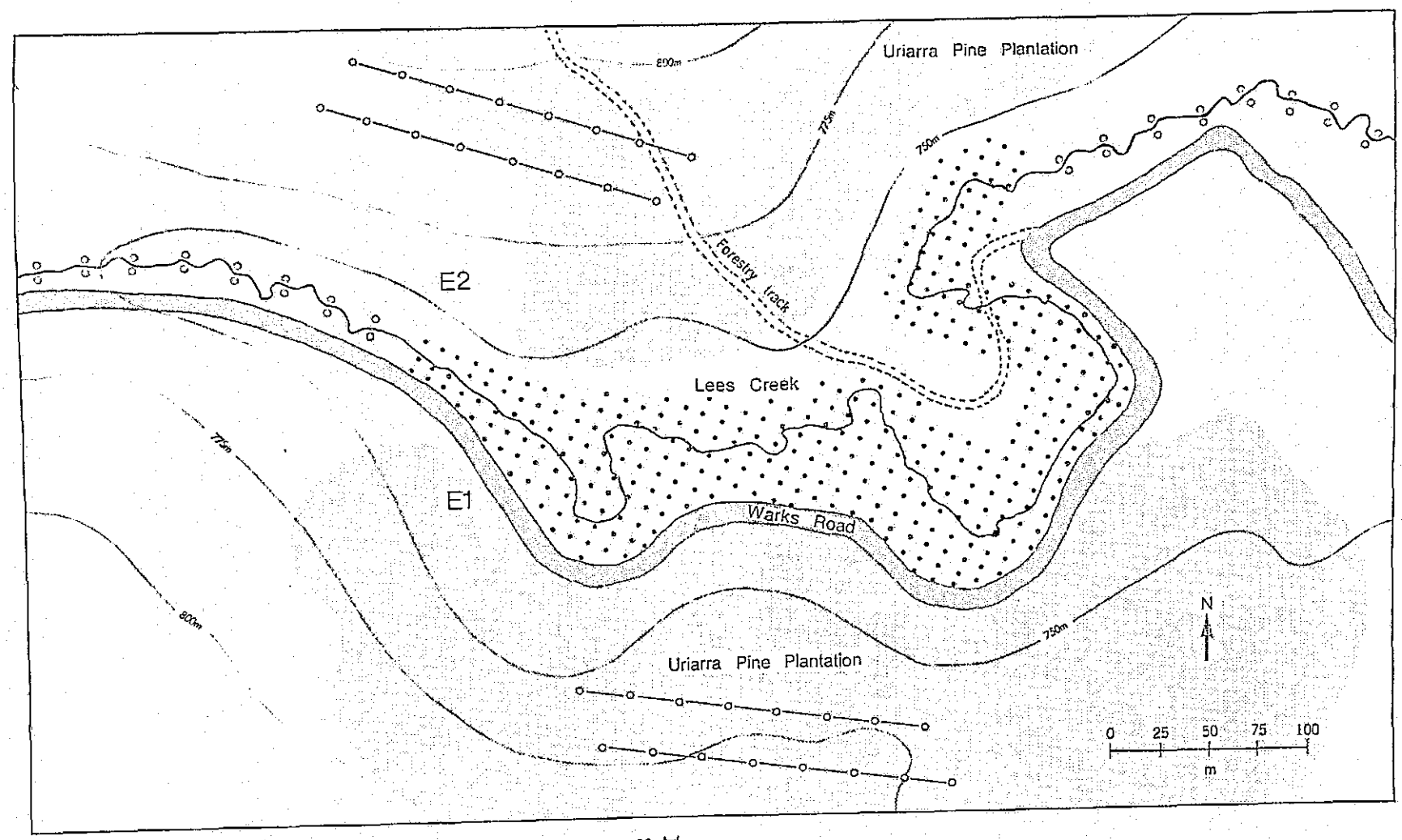

Uriarra Pine Plantation
850m
775m
750m
Forestry track
E2
Lees Creek
E1
775m
Warks Road
800m
750m
Uriarra Pine Plantation
N
0 25 50 75 100
m

Fig. 2.4 (b)

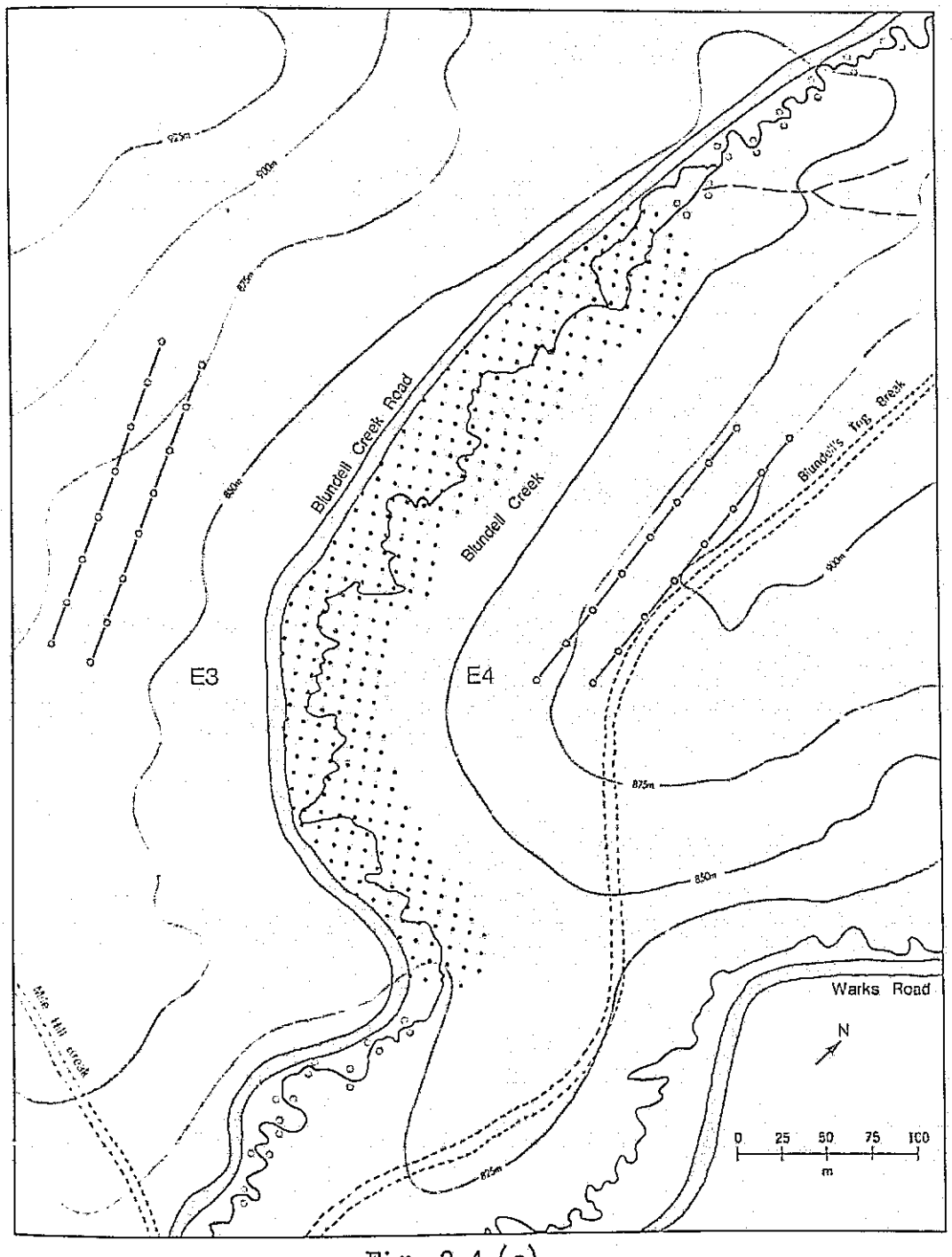

Blundell Creek Road
Blundell Creek
Blundell's Trig Break
E3
E4
875m
850m
Warks Road
N
0 25 50 75 100
m

Fig. 2.4 (c)

Fig. 2.5 Residence and transience of Antechinus in the enclosures. Animals were considered to be resident in the enclosures if <10% of their total captures occurred outside the enclosures, and transient or resident on the trapping lines if >10% of their total captures occurred outside the enclosures.

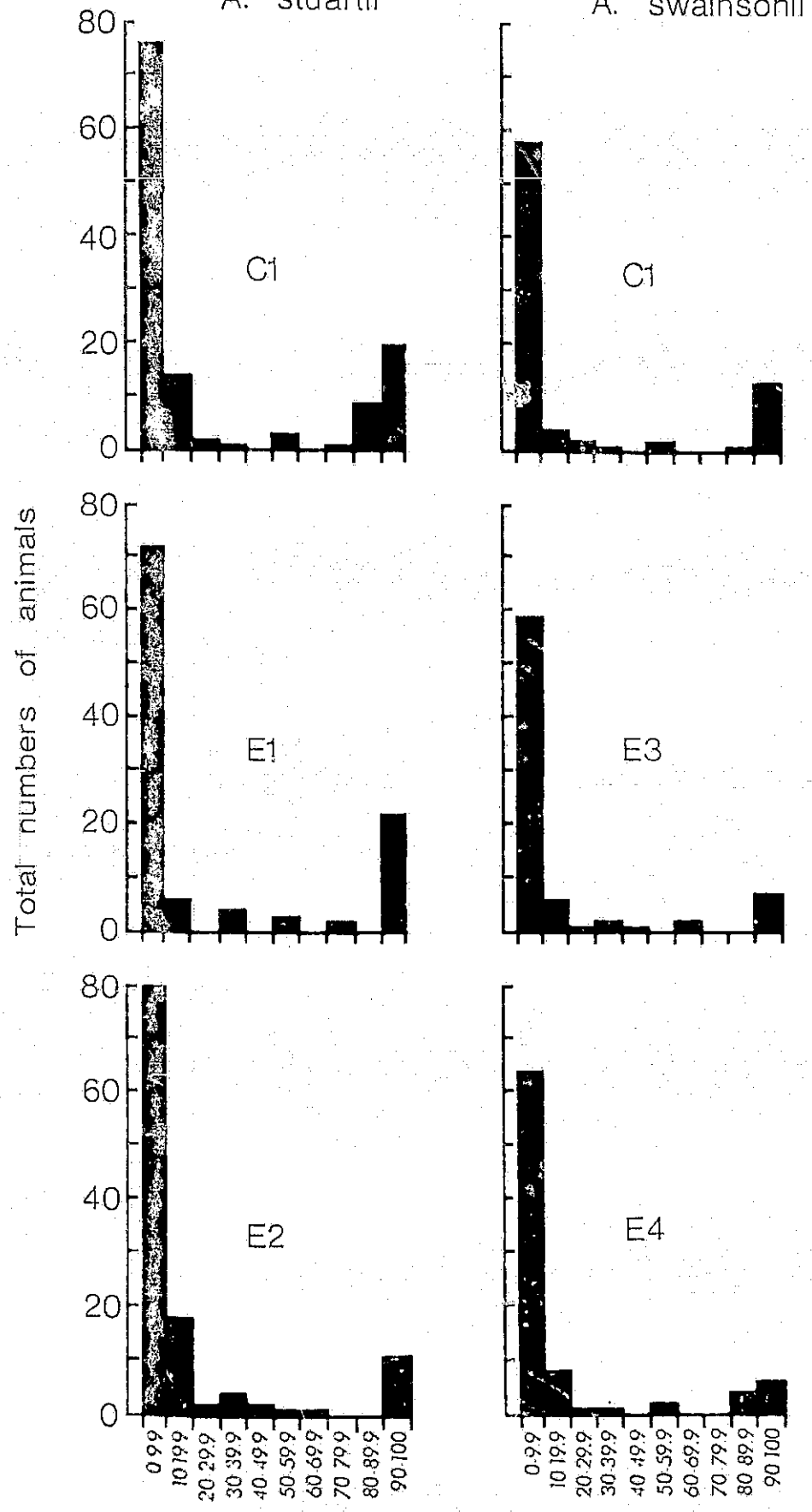

A. stuartii
A. swainsonii
C1
C1
E1
E3
E2
E4
Total numbers of animals
0
20
40
60
80
0-9.9
10-19.9
20-29.9
30-39.9
40-49.9
50-59.9
60-69.9
70-79.9
80-89.9
90-100
Percentage of total captures occurring outside the enclosures

Fig. 2.6 Population parameters of A. stuartii in enclosures C1, E1 and E2. (a), minimum numbers known to be alive; (b), minimum sessional survival of individuals known to be alive; (c), trappability of individuals known to be alive. July I and July II 1978 are represented by the symbols J and J^* respectively, April I and April II 1979 by A and A^* respectively.

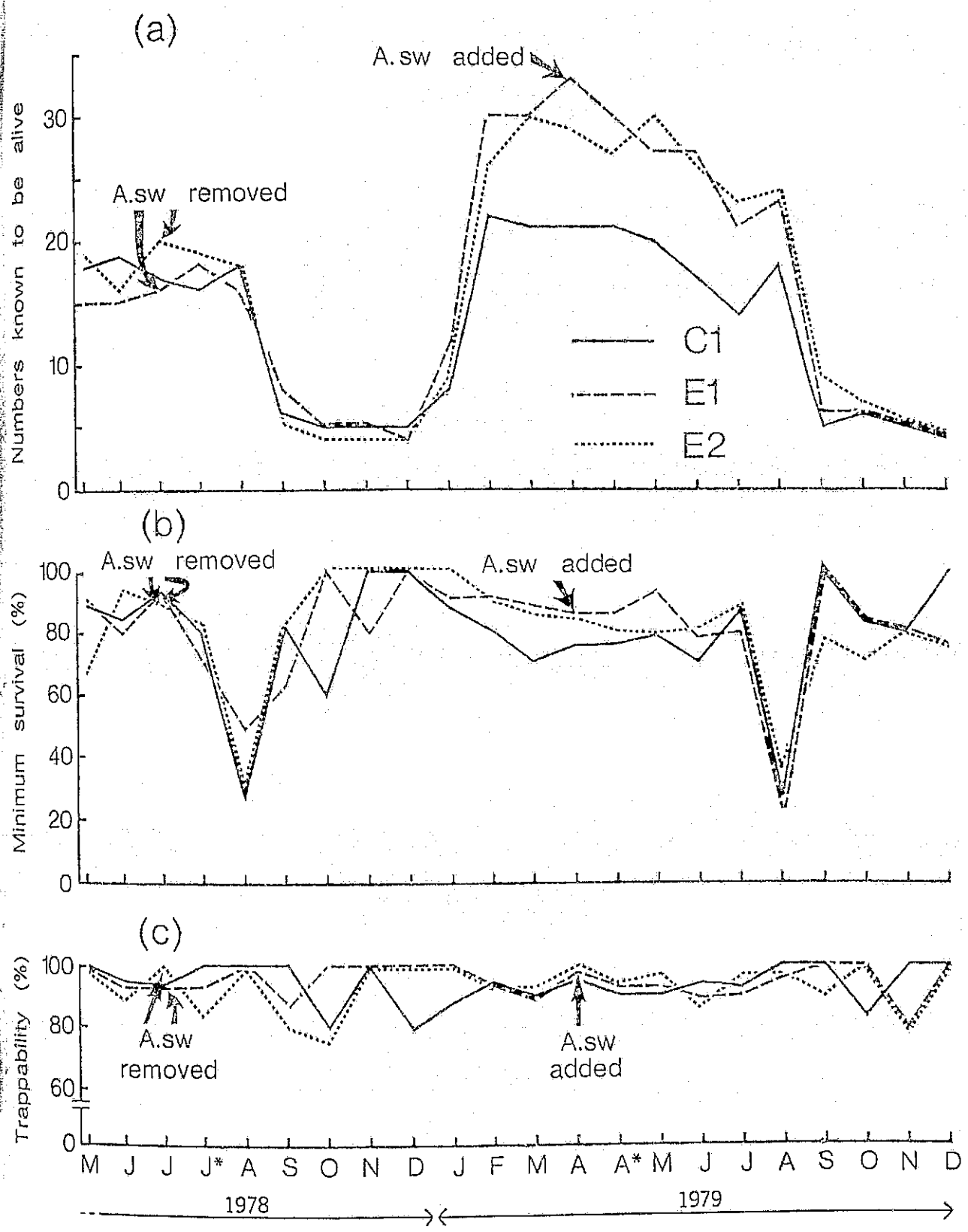

(a)
A. sw added
A.sw removed
Numbers known to be alive
30
20
10
0
C1
E1
E2
(b)
A.sw removed
A.sw added
Minimum survival (%)
100
80
60
40
20
0
(c)
Trappability (%)
100
80
60
0
A.sw removed
A.sw added
M J J J* A S O N D J F M A A* M J J A S O N D
1978
1979

Fig. 2.7 Population composition of A. stuartii in enclosures C1, E1 and E2. Different female year classes are represented by solid, hatched and stippled shading, male year classes by no shading. J^* and A^* represent July II 1978 and April II 1979 respectively.

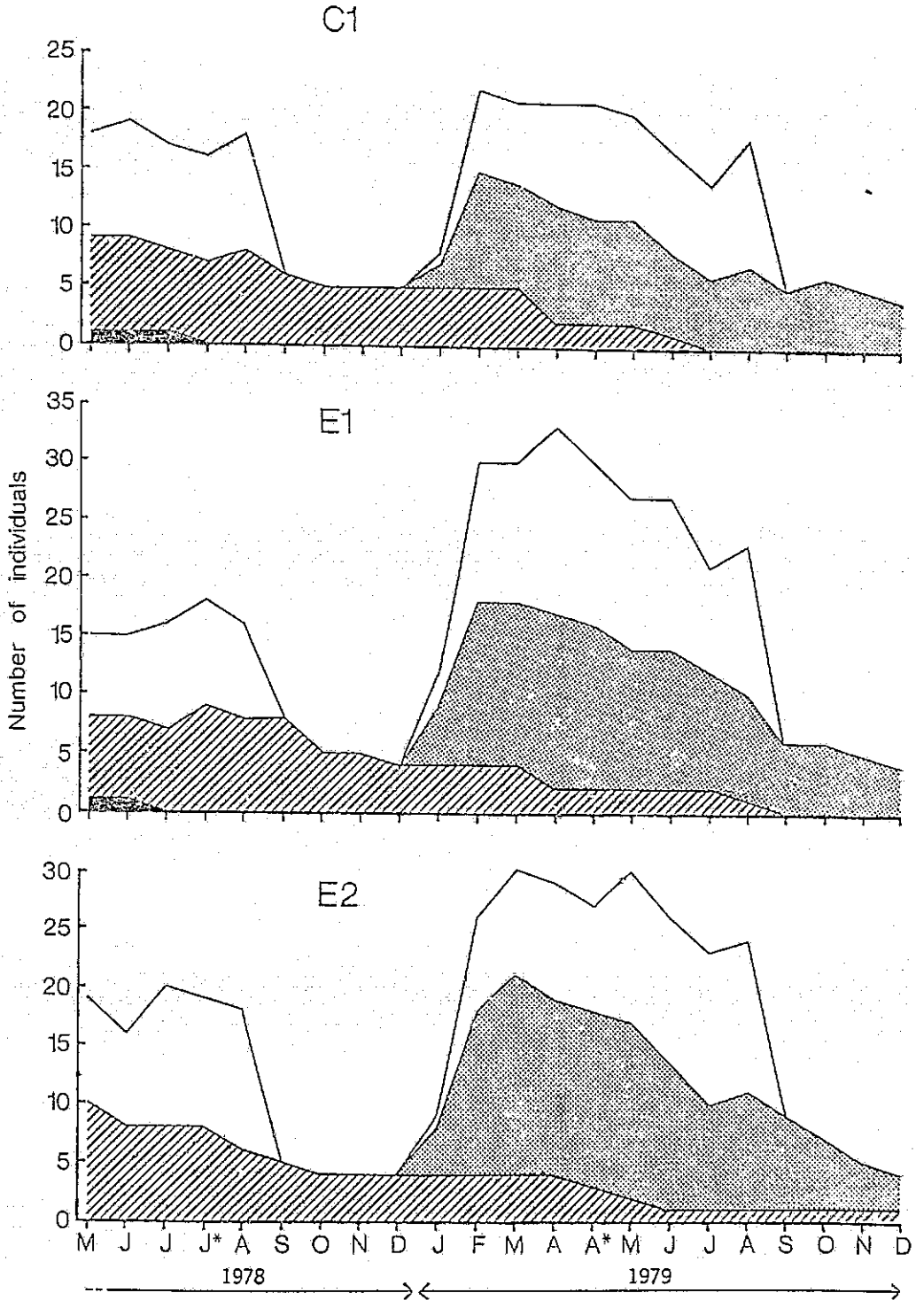

C1
E1
E2
Number of individuals
25
20
15
10
5
0
35
30
M J J J* A S O N D J F M A A* M J J A S O N D
1978
1979

Fig. 2.8 Average distances moved by A. stuartii in enclosures C1, E1 and E2 (a) males, (b) females <1 yr old, (c) females >1 yr old. Solid circles represent means for C1, open inverted triangles means for E1, and open upright triangles means for E2. J^*, A^* and A^* represent July II 1978, April II 1979 and August II 1979 respectively.

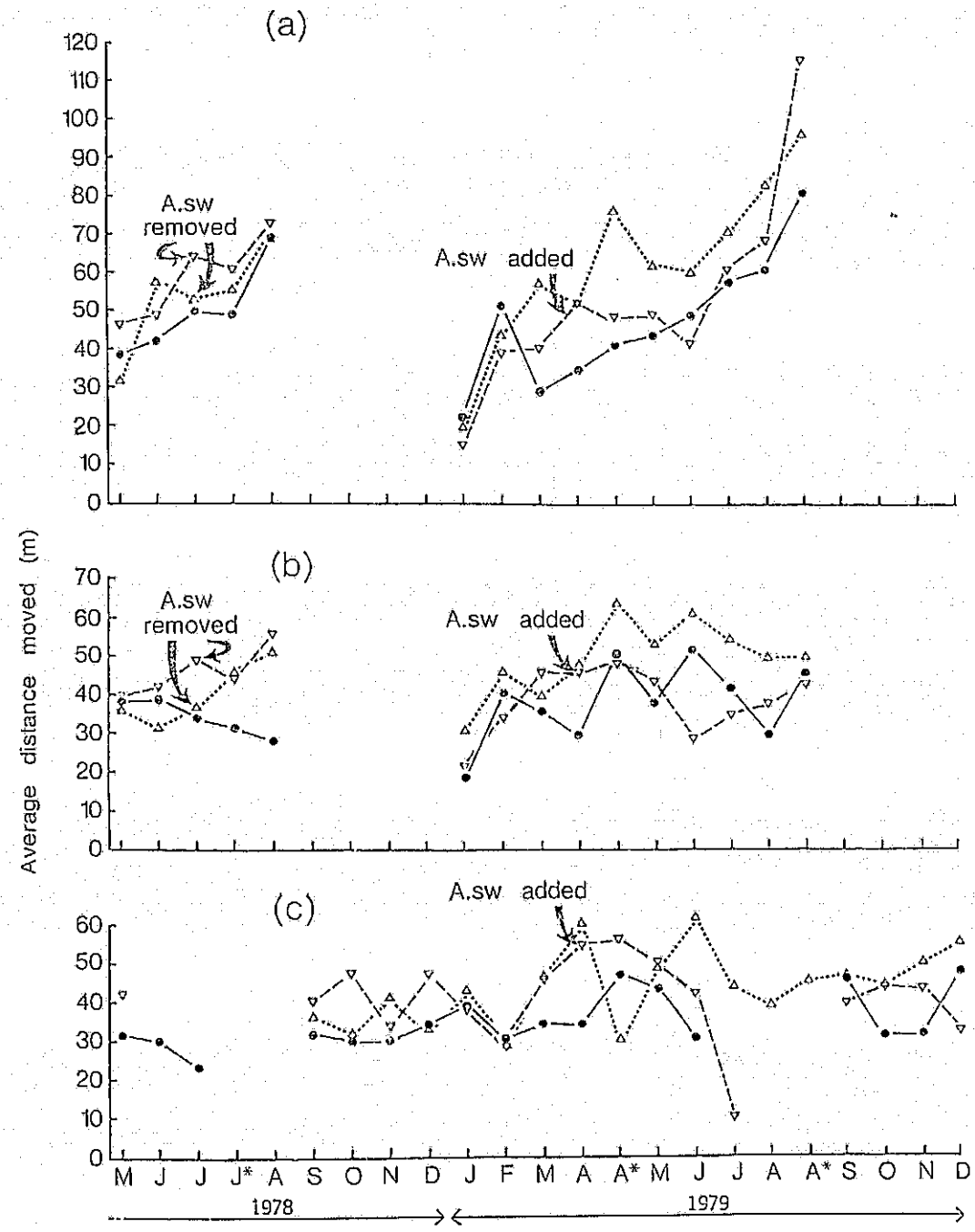

(a)
A.sw removed
A.sw added
(b)
A.sw removed
A.sw added
(c)
A.sw added
Average distance moved (m)
M J J J* A S O N D J F M A A* M J J A A* S O N D
1978
1979

Fig. 2.9 Body weights of A. stuartii in enclosures C1, E1 and E2. (a) males, (b) females <1 yr old, (c) females >1 yr old. Solid circles represent means for C1, open inverted triangles means for E1, and open upright triangles means for E2. Vertical lines represent standard deviations about the means (sample sizes are given in Appendices 3a,b,c). J^*, A^* and A^* represent July II 1978, April II 1979 and August II 1979 respectively.

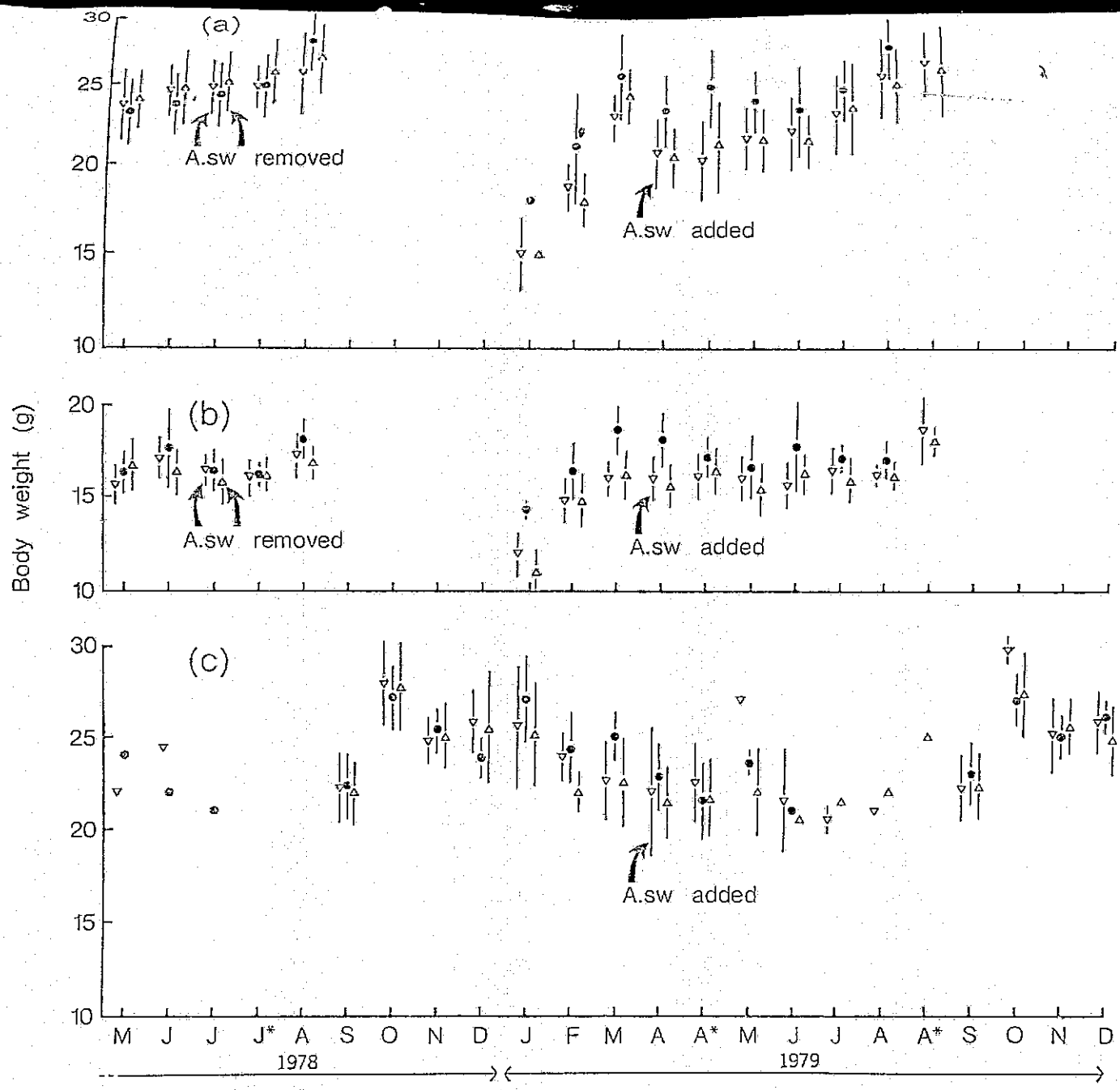

(a)
A.sw removed
A.sw added
(b)
A.sw removed
A.sw added
(c)
A.sw added
Body weight (g)
10
15
20
25
30
M J J J* A S O N D J F M A A* M J J A A* S O N D
1978
1979

Fig. 2.10 Head-body lengths of A. stuartii in enclosures C1, E1 and E2. (a) males, (b) females <1 yr old, (c) females >1 yr old. Solid circles represent means for C1, open inverted triangles means for E1, and open upright triangles means for E2. Vertical lines represent standard deviations about the means (sample sizes are given in Appendices 3d,e,f). J^*, A^* and A^* represent July II 1978, April II 1979 and August II 1979 respectively.

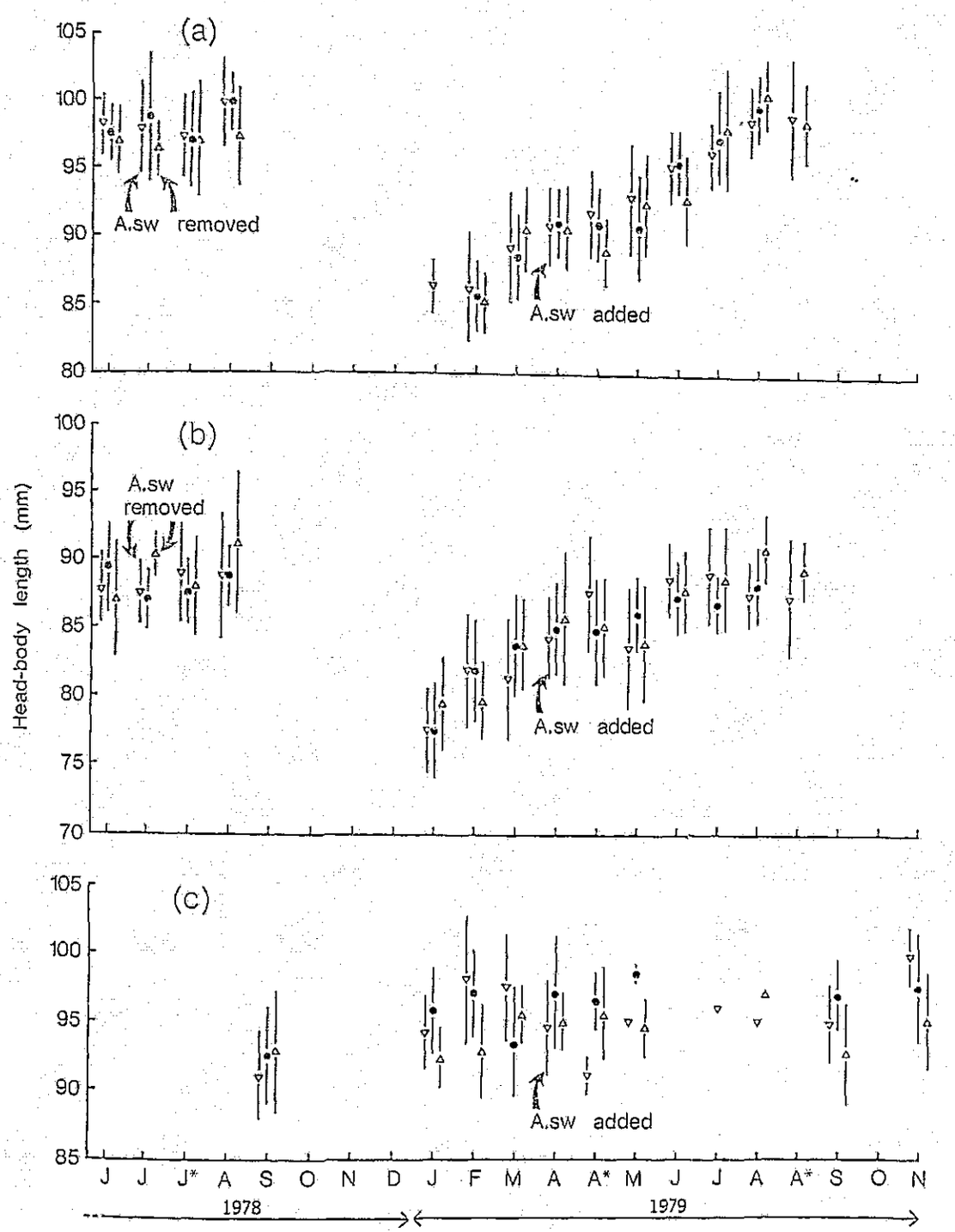
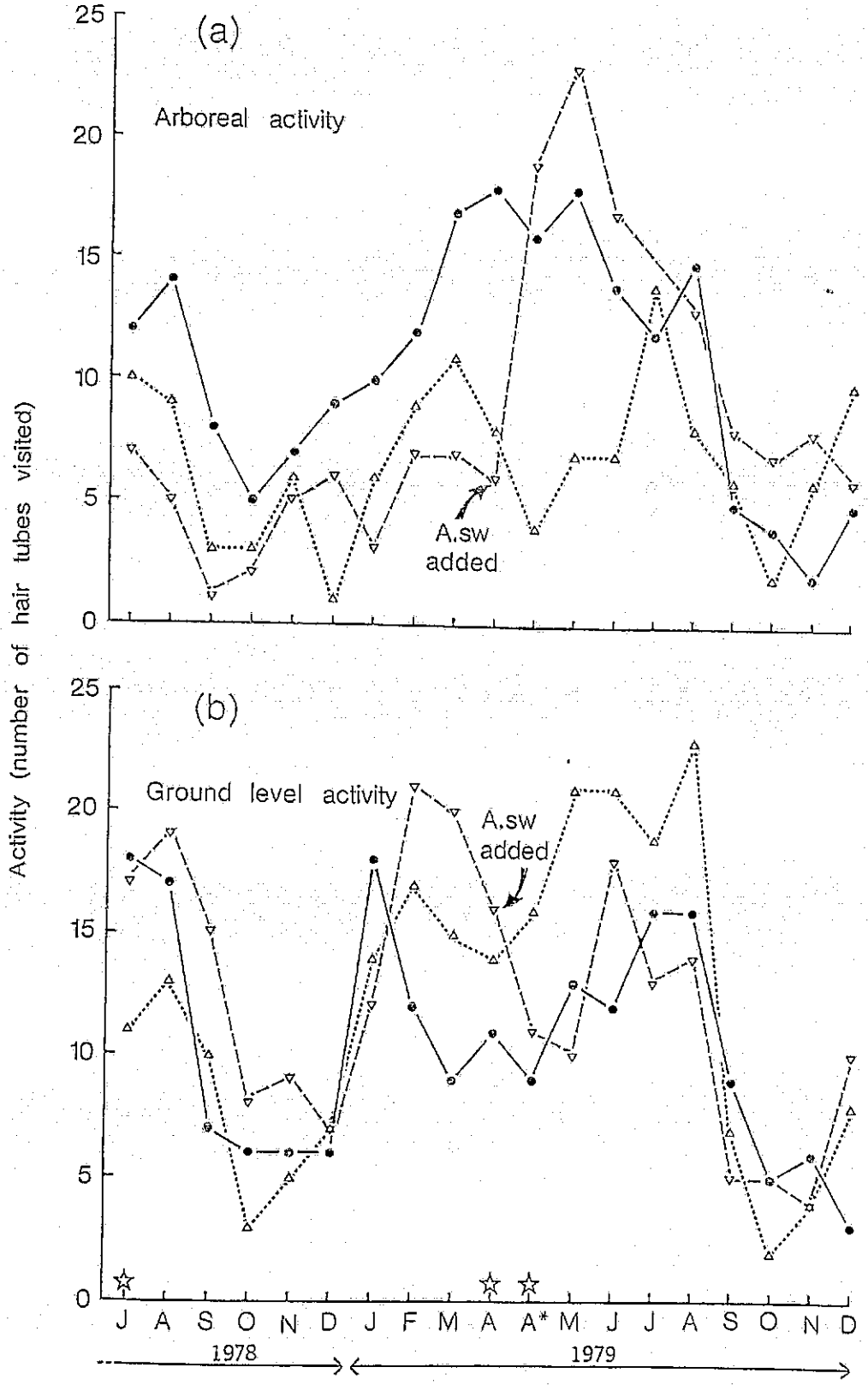

(a)
105
100
95
90
85
80
A.sw removed
A.sw added
(b)
100
95
90
85
80
75
70
A.sw removed
A.sw added
Head-body length (mm)
(c)
105
100
95
90
85
A.sw added
J J J* A S O N D J F M A A* M J J A A* S O N
1978
1979

Fig. 2.11 Activity of A. stuartii in enclosures C1, E1 and E2. (a) arboreal activity (b) ground level activity. Solid circles represent numbers of hair tubes visited in C1, open inverted triangles those in E1, open upright triangles those in E2. Tapes from hair sampling tubes were usually checked at intervals of 25-31 days; in months marked by open stars they were checked at intervals of <25 days. A^{*} represents April II 1979.


(a)
Arboreal activity
A.sw added
(b)
Ground level activity
A.sw added
Activity (number of hair tubes visited)
25
20
15
10
5
0
J A S O N D J F M A A* M J J A S O N D
1978
1979

Sept.-Dec. 1979
July-August 1979
April-June 1979
Time (h)
1200 1500
1500 1800
1800 2100
2100 2400
000 300
300 600
600 900
900 1200
0
10
20
30
40
50
60

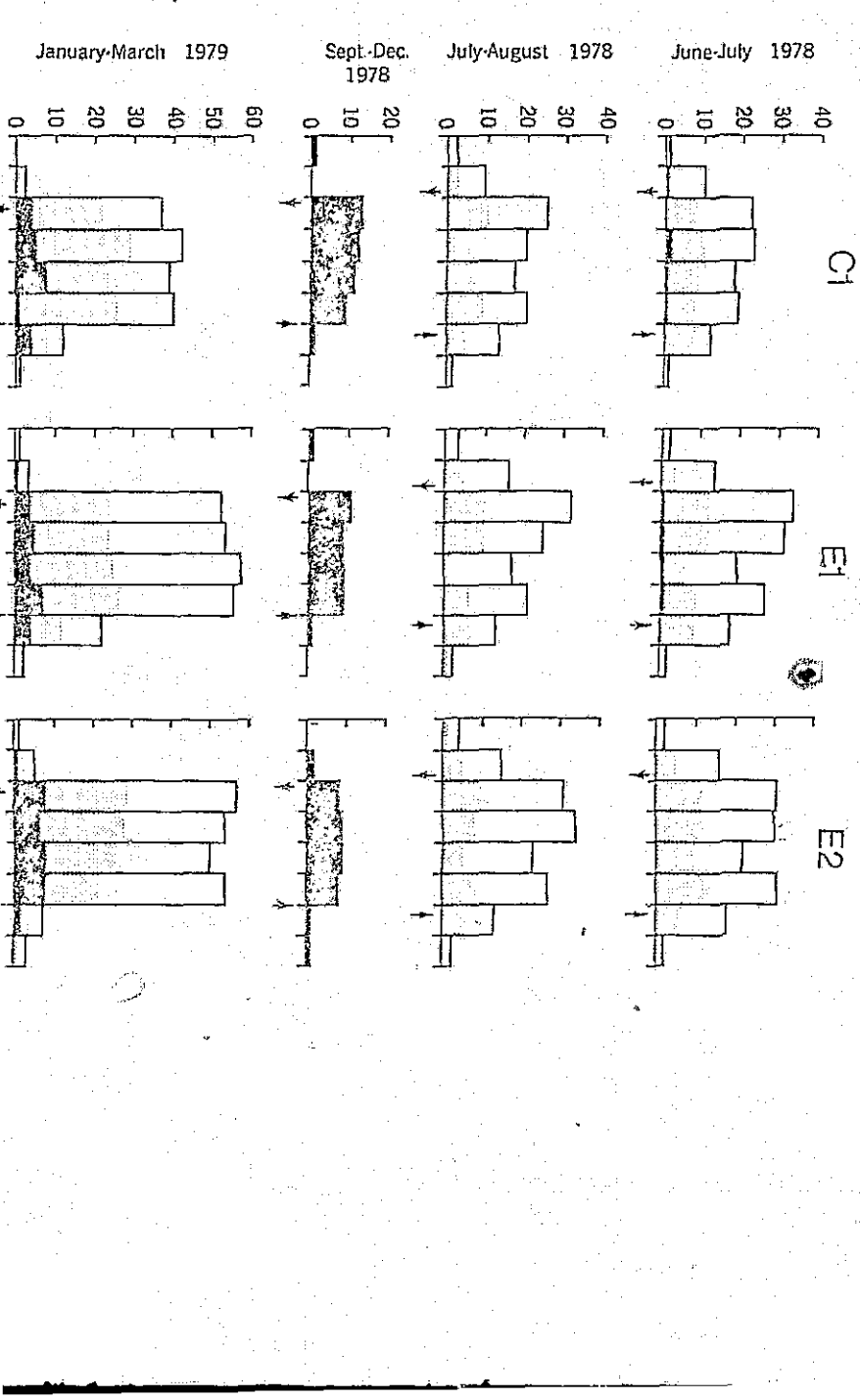

Number of captures
January-March 1979
Sept.-Dec. 1978
July-August 1978
June-July 1978
0
10
20
30
40
50
60
C1
E1
E2

Fig. 2.13 Population parameters of A. swainsonii in enclosures C1, E3 and E4. Solid lines represent the population in C1, dashed lines the population in E3 and dotted lines the population in E4. (a), minimum numbers known to be alive; (b), minimum sessional survival of individuals known to be alive; (c), trappability of individuals known to be alive. J^* and A^* represent July II 1978 and April II 1979 respectively.

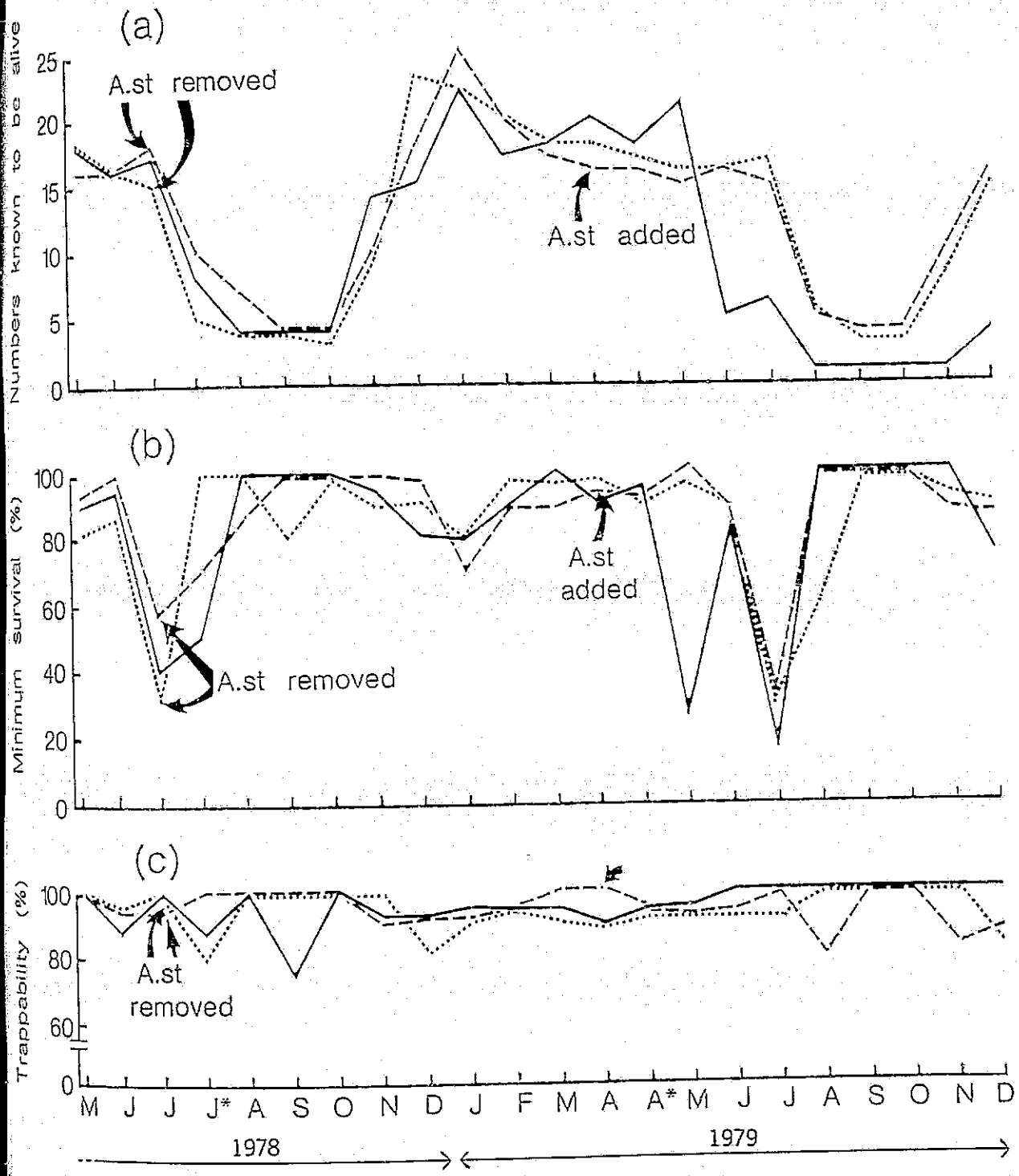
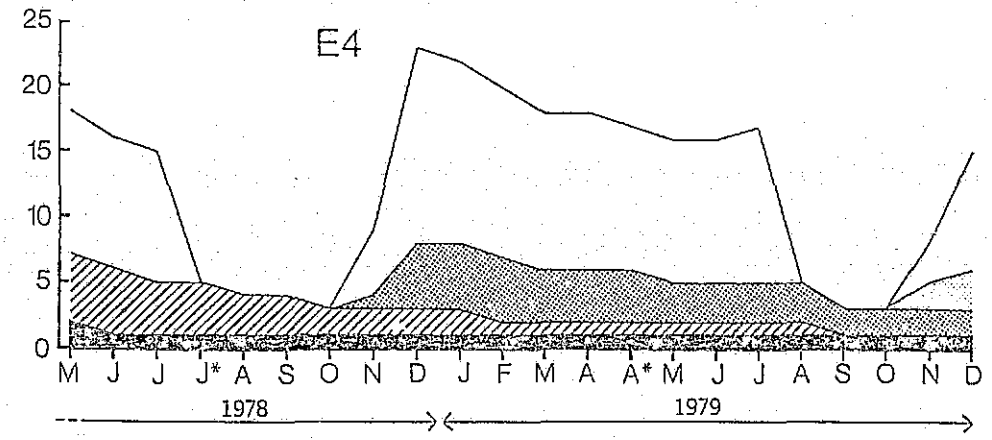

(a)
A.st removed
A.st added
Numbers known to be alive
25
20
15
10
5
0
(b)
A.st added
A.st removed
Minimum survival (%)
100
80
60
40
20
0
(c)
A.st removed
Trappability (%)
100
80
60
0
M J J J* A S O N D J F M A A* M J J A S O N D
1978
1979

Fig. 2.14 Population composition of A. swainsonii in enclosures C1, E3 and E4. Different female year classes are represented by solid, hatched and stippled shading, male year classes by no shading. J^* and A^* represent July 11 1978 and April 11 1979 respectively.


E4
25
20
15
10
5
0
M J J J* A S O N D J F M A A* M J J A S O N D
1978
1979

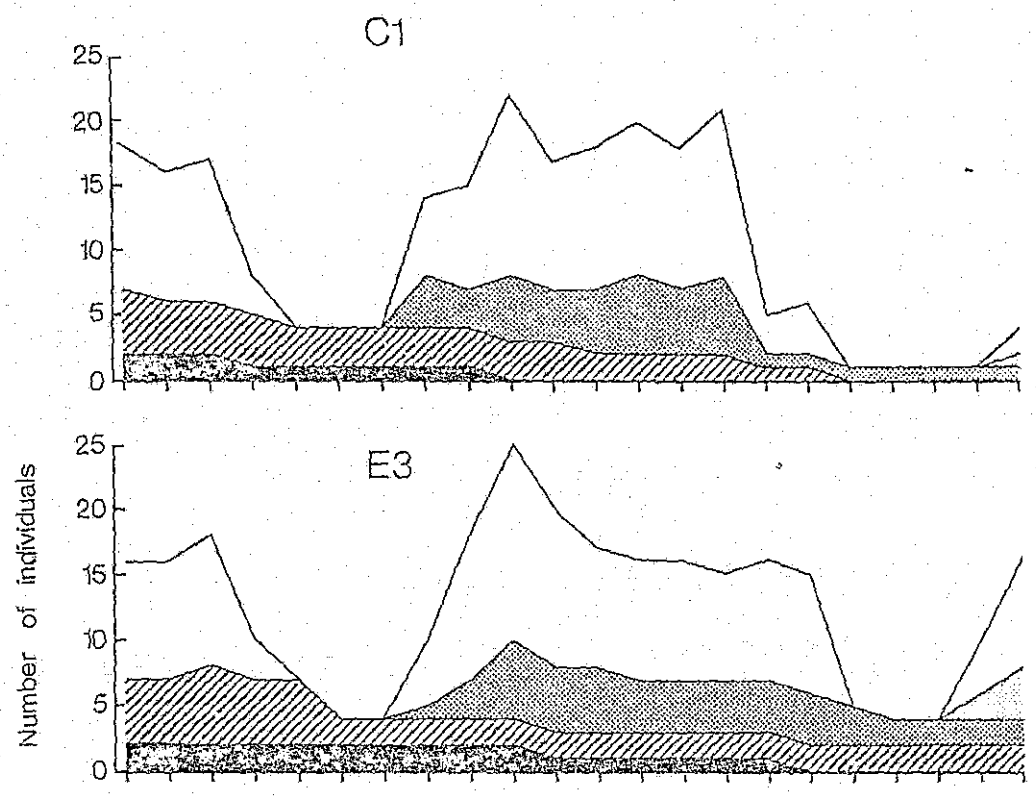

C1
E3
25
20
15
10
5
0
Number of individuals

Fig. 2.15 Average distances moved by A. swainsonii in enclosures C1, E3 and E4. (a) males, (b) females <1yr old, (c) females >1yr old. Solid circles represent means for C1, open inverted triangles means for E3, and open upright triangles means for E4. J^* and A^* represent July II 1978 and April II 1979 respectively.

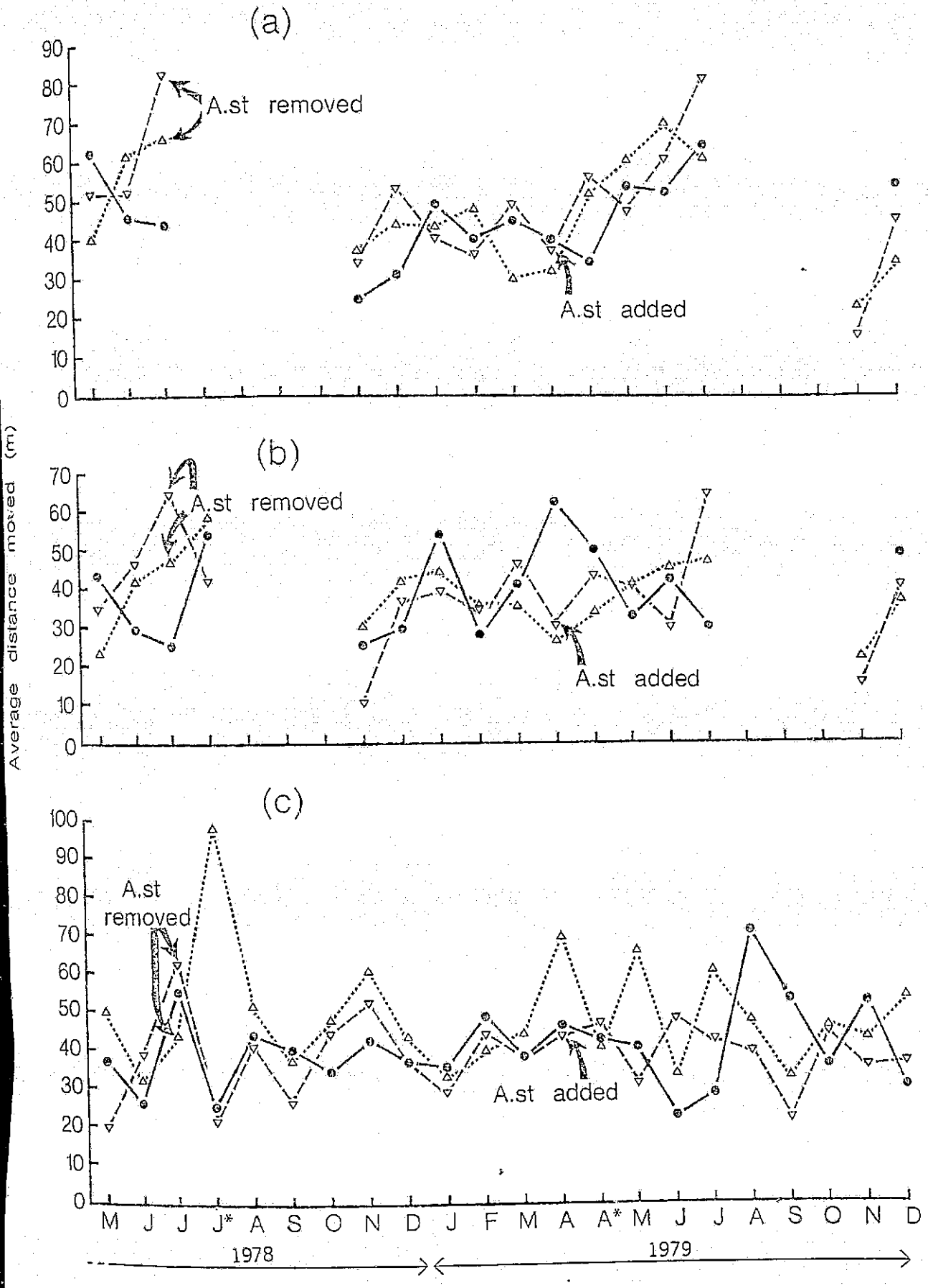

(a)
A.st removed
A.st added
(b)
A.st removed
A.st added
(c)
A.st removed
A.st added
Average distance moved (m)
M J J J* A S O N D J F M A A* M J J A S O N D
1978
1979

Fig. 2.16 Body weights of A. swainsonii in enclosures C1, E3 and E4. (a) males, (b) females <1 yr old, (c) females >1 yr old. Solid circles represent means for C1, open inverted triangles means for E3, and open upright triangles means for E4. Vertical lines represent standard deviations about the means (sample sizes are given in Appendices 4a,b,c). J^* and A^* represent July 11 1978 and April 11 1979 respectively.

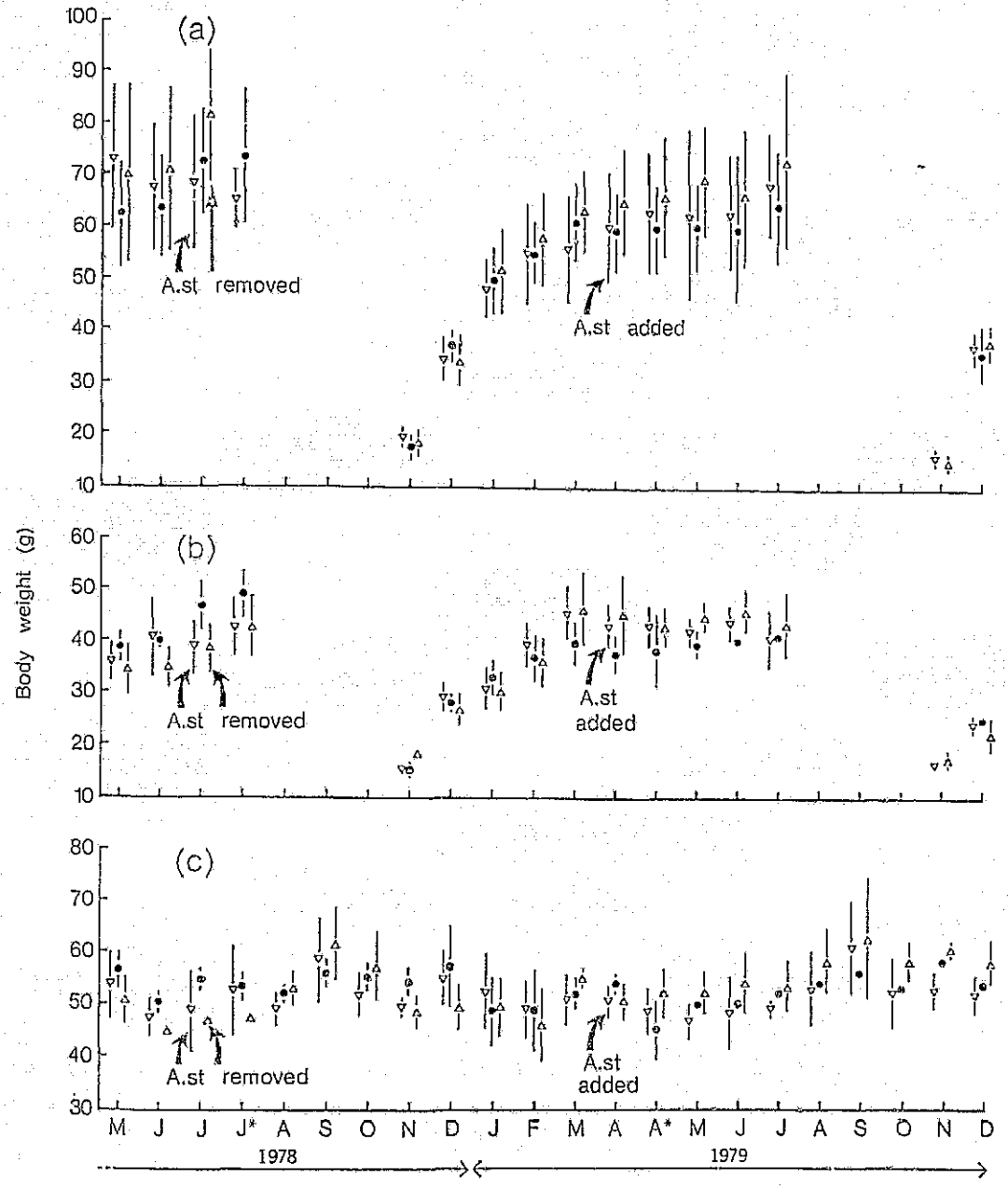

(a)
A.st removed
A.st added
(b)
A.st removed
A.st added
(c)
A.st removed
A.st added
Body weight (g)
M J J J* A S O N D J F M A A* M J J A S O N D
1978
1979

Fig. 2.17 Head-body lengths of A. swainsonii in enclosures C1, E3 and E4. (a) males, (b) females <1 yr old. Solid circles represent means for C1, open inverted triangles means for E3, and open upright triangles means for E4. Vertical lines represent standard deviations about the means (sample sizes are given in Appendices 4d,e). J^* and A^* represent July II 1978 and April II 1979 respectively.

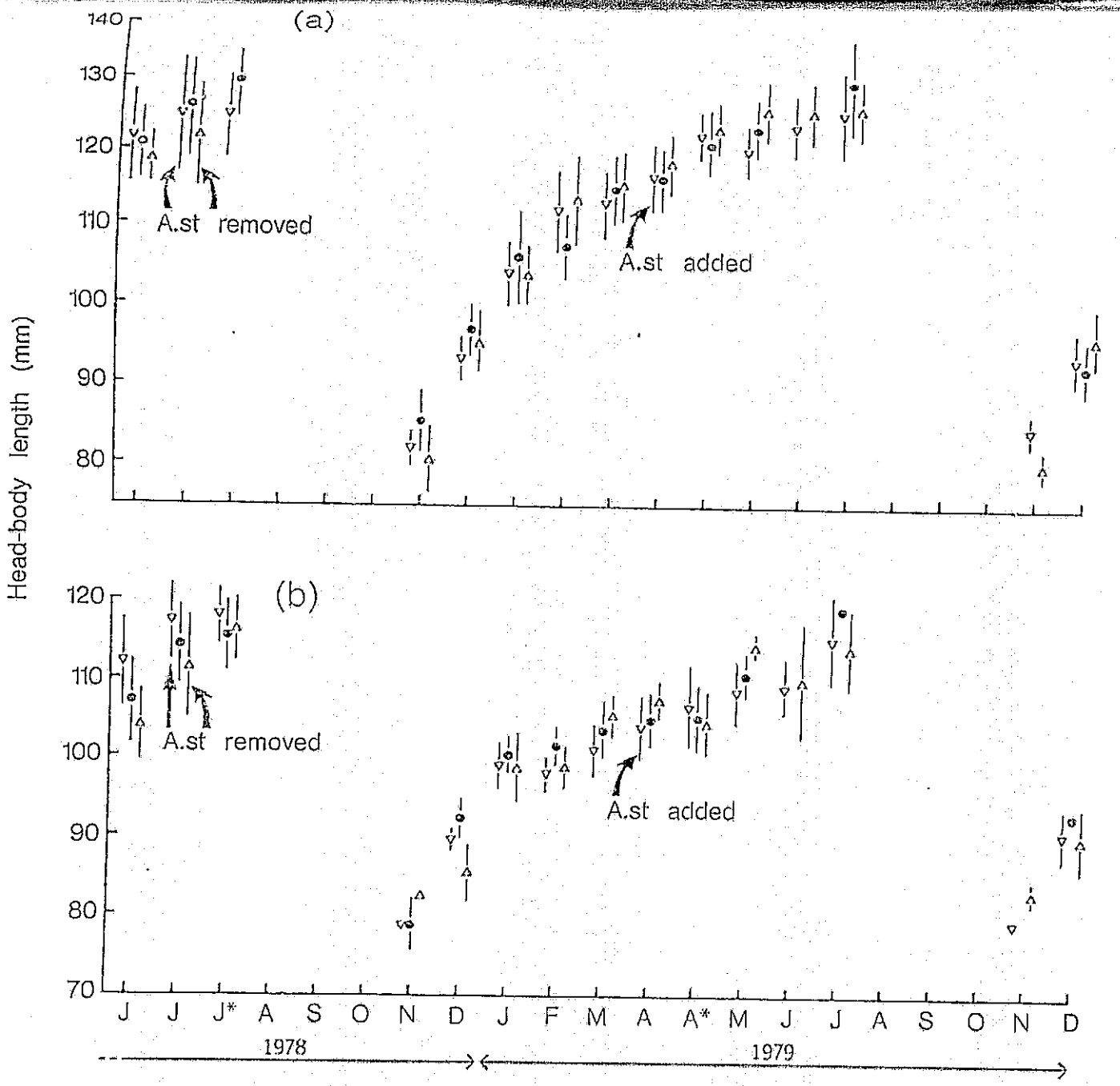

(a)
(b)
Head-body length (mm)
A.st removed
A.st added
A.st removed
A.st added
J J J* A S O N D J F M A A* M J J A S O N D
1978
1979

Fig. 2.18 Activity of A. swainsonii in enclosures C1, E3 and E4. (a) arboreal activity, (b) ground level activity. Solid circles represent numbers of hair tubes visited in C1, open inverted triangles those in E3, open upright triangles those in E4. Tapes from hair sampling tubes were usually checked at intervals of 25-31 days; in months marked by open stars they were checked at intervals of <25 days. A^{*} represents April II 1979.

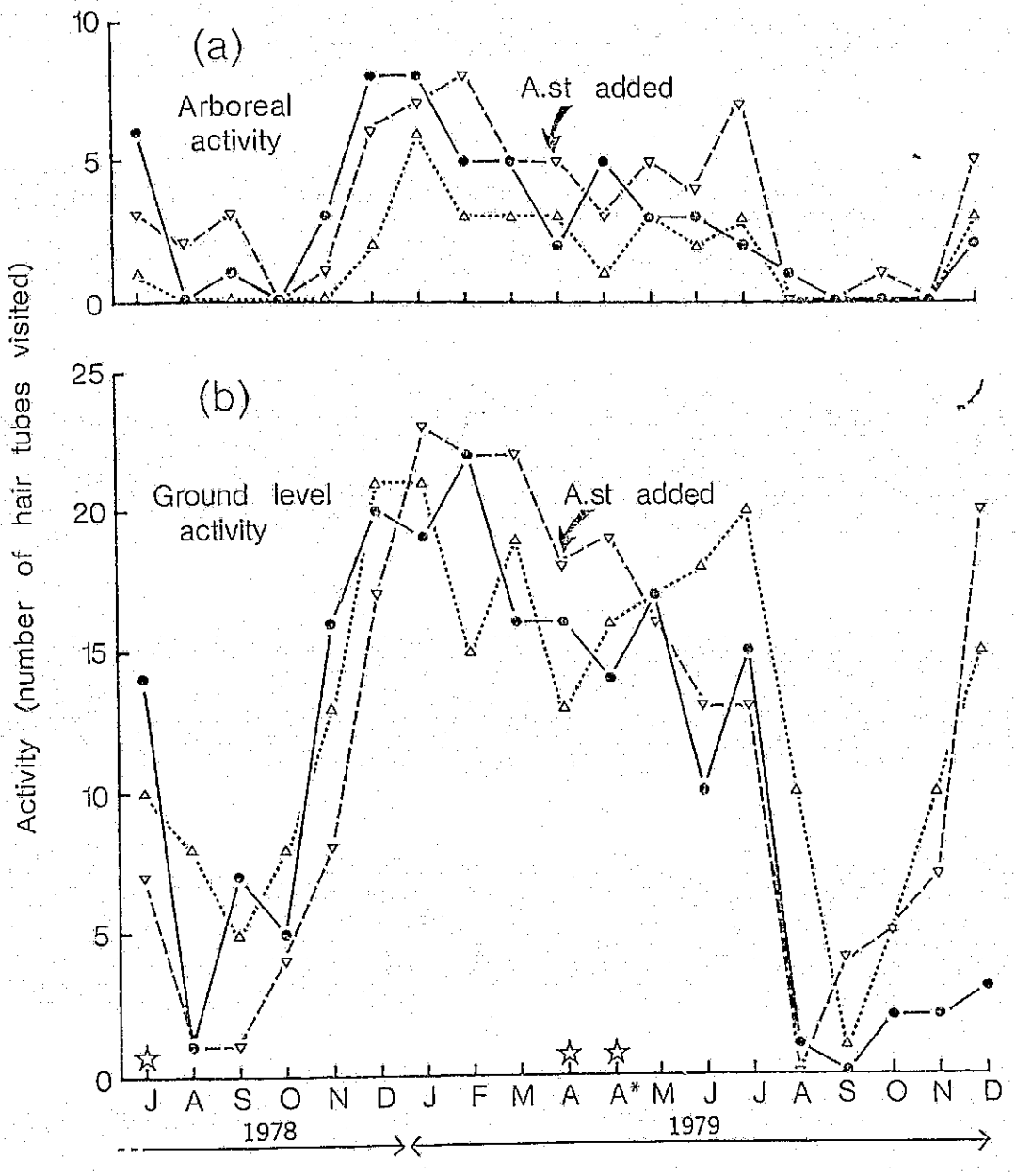
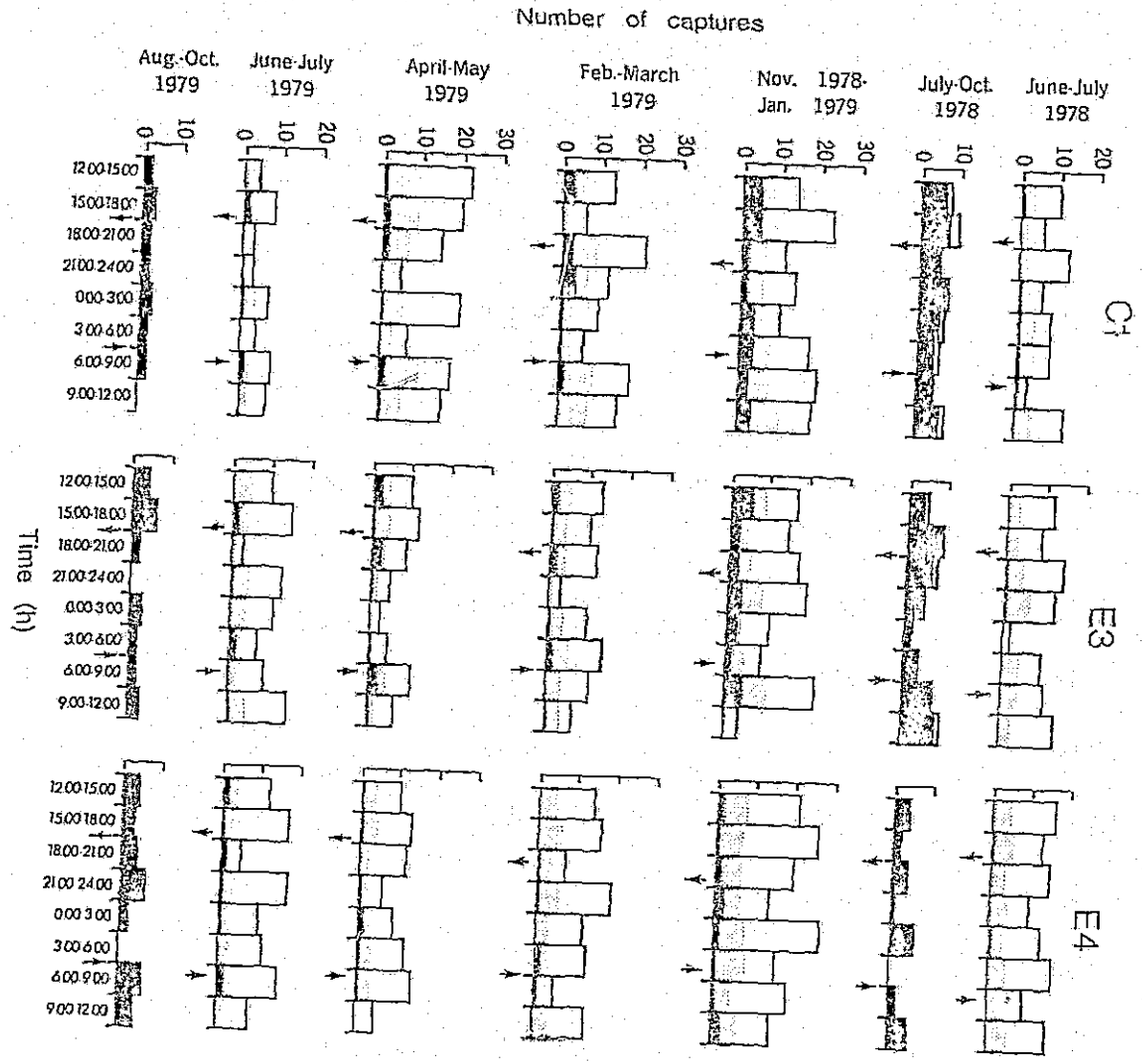

(a)
Arboreal activity
A.st added
10
5
0
(b)
Ground level activity
A.st added
25
20
15
10
5
0
Activity (number of hair tubes visited)
J A S O N D J F M A A* M J J A S O N D
1978
1979

Fig. 2.19 Periodicity of activity of A. swainsonii in enclosures C1, E3 and E4. Captures of males are represented by no shading, females <1 yr old by light shading and females >1 yr old by heavy shading. Inverted arrows represent times of sunset, upright arrows times of sunrise.


Number of captures
Aug.-Oct. 1979
June-July 1979
April-May 1979
Feb.-March 1979
Nov. 1978-Jan. 1979
July-Oct. 1978
June-July 1978
Time (h)
12.00-15.00
15.00-18.00
18.00-21.00
21.00-24.00
0.00-3.00
3.00-6.00
6.00-9.00
9.00-12.00
C1
E3
E4

CHAPTER 3

COMPETITION BETWEEN A. STUARTII AND A. SWAINSONII: THE EFFECTS OF COMPETITOR REDUCTION AND ENHANCEMENT

3.1 INTRODUCTION

The experiments of Chapter 2 were designed to investigate whether competition occurred between A. stuartii and A. swainsonii, and used the crude but effective method of completely removing or reintroducing all individuals of the putative competitor species. The experiments provided strong and consistent evidence of interspecific competition, and showed that A. swainsonii had a disproportionate effect on its smaller congenor. Although, at the outset of my Ph.D. studies, I had planned to replicate the experiments of Chapter 2, these findings suggested that further insight into competition would be obtained by asking different questions about the nature and effects of the process. What, for example, would be the effects on A. stuartii of removing only some A. swainsonii individuals? Would the response of A. stuartii be a function of the numbers of A. swainsonii that were removed, or would the outcome of competition be qualitatively different? What would be the effects of increasing the numbers of A. swainsonii individuals? This chapter addresses these questions by investigating the effects on A. stuartii of reducing and enhancing the numbers of A. swainsonii.

Plant ecologists have long been concerned with the effects of varying competitor population densities (Jackson 1981), and their experiments have yielded much information on the nature of species interactions and the resources for which competition occurs (deWit 1960, Hall 1974a,b, Etherington 1975). Usually, plant species are

grown alone or together in precisely defined ratios, and the quantities of space and other resources that are available to them are strictly prescribed. However, for the animal ecologist the problem of reducing or enhancing competitor numbers is not so straightforward. To create a situation in which, for example, A. stuartii was four times as abundant as A. swainsonii, the numbers of one or both species would have to be artificially fixed. Aside from the practical difficulty of maintaining a precise ratio of 4:1 (or any other ratio), there would be no way of knowing whether numbers were fixed above or below the level at which resources were limiting. In addition, in the absence of such information, it would be unreasonable to expect competition effects to be simple functions of competitor ratios, and this would reduce the chance to make accurate predictions about the magnitude and direction of competition effects.

In Chapter 2, removal experiments were conducted on relatively undisturbed, equilibrium populations of Antechinus. Ideally, species reduction or enhancement experiments should also be conducted on such populations, and have predictable effects. Thus, reduction of the numbers of one species of Antechinus should increase the availability of mutually limiting resources, and reduce the intensity of interspecific competition. In contrast, enhancement of the numbers of one species should intensify the shortage of such resources and exacerbate interspecific competition. In this chapter, the effects of reducing and enhancing the numbers of A. swainsonii on the populations and resource use of A. stuartii are described. Except for time (periodicity of activity), home range area and overlap, the resources used and population parameters are the same as those

considered in Chapter 2. The experiments were performed between January 1980 and November 1981.

3.2 EXPERIMENTAL DESIGN

Ideally, the design for these experiments would have been the same as that used in Chapter 2, except that the numbers of species A would be reduced (or enhanced) and not completely removed. Two factors prevented the use of this design. First, the decimation of the Antechinus population in the control enclosure C1 (and in source area sites) meant that this enclosure had to be abandoned. Second, as trapping in the experimental enclosures continued in 1979, it became obvious that the creeks separating E1 from E2 and E3 from E4 were no longer acting as effective barriers to Antechinus movements. (The numbers of individuals crossing the creeks increased particularly towards the end of 1979 (Tables 2.1 and 2.2), probably because a prolonged dry spell (Fig. 2.2) reduced water flow in the creeks to a level at which crossings could be made). Consequently, enclosures E1 and E2 had to be considered together as a single large enclosure (3.45 ha) and E3 and E4 as another (3.48 ha). No further attempts were made to keep debris out of the creeks flowing through these enclosures.

Simple experiments using only two enclosures are shown in Fig. 3.1, with the rectangles representing enclosures containing both species of Antechinus. In the experimental enclosure in 1980, some A. swainsonii were removed so that its numbers were low relative to those of A. stuartii, whereas in 1981 A. swainsonii was reintroduced to make it the more abundant of the two species. (I stress that no attempt was made to maintain a constant ratio of the numbers of one

species to the other, as implied in Fig. 3.1. I attempted to manipulate the numbers of A. swainsonii so that they were relatively low or relatively high compared to the numbers of A. stuartii). In the control enclosure the numbers of the two species were similar in both years. In 1980 the reduction of A. swainsonii numbers was expected to reduce competition on A. stuartii and produce predictable, expansive shifts in the population parameters and resource use of this species, but in 1981 the increase in A. swainsonii numbers was expected to reverse these shifts. For convenience, enclosures E1 and E2 of Chapter 2 were combined and used as the "new" experimental enclosure, whereas enclosures E3 and E4 were combined and used as the "new" control enclosure. Henceforth, the control and experimental enclosures will be designated C and E respectively, and the suffix 80 or 81 will be used to designate the year. (For example, C80 will refer to the control enclosure in 1980; E80 to the experimental enclosure in 1980 when the numbers of A. stuartii were high relative to those of A. swainsonii).

If niche shifts are observed in A. stuartii in the experimental enclosure, it may be reasonable to infer that they have been caused by changes in the numbers of A. swainsonii, and hence to changes in the amount of interspecific competition. Unlike the design of Chapter 2, however, the inference here cannot be critically tested by returning A. swainsonii numbers to normal, control levels due to the lack of a third enclosure. Nevertheless, confidence may be gained in the interpretation of competition by simultaneously comparing the effects of relatively high, low and "medium" (control) numbers of A. swainsonii on A. stuartii, and by showing that the effects vary in consistent and predictable ways.

3.3 METHODS

3.3.1 Methods for assessment of population parameters and patterns of resource use.

Except where stated below, the field and analytical methods used in the reduction/enhancement experiments were exactly the same as those described in Chapter 2. Grid trapping was conducted for four days a month every month except in January 1980 and 1981 and between July and September in both years. In January, trapping was conducted for four days in the first half of the month and for a further four days in the second half of the month. Between July and September, additional, irregular trapping was conducted for up to seven days in each month to obtain information on the timing of reproductive events. In 1980 two traps were set at every grid trap station, but in 1981 this practice was continued only at trap stations located in dense, creek vegetation. All grid traps were checked twice daily, once near dawn and once near dusk. No pitfall traps were set for Antechinus, ground level hair sampling tubes were not set, no head-body measurements were taken, and no 24-hour trapping was conducted to investigate periodicity of activity.

3.3.2 Treatment of data.

Ostensibly, the experimental design allows a separate comparison to be made of control versus experimental populations in 1980 and in 1981, using appropriate one-tailed, two-sample tests. However, although statistically legitimate, such comparisons do not use all of the biological information that is available. Hence, although it is of interest to compare the effects on A. stuartii of A. swainsonii

reduction versus no reduction (control) in 1980, and the effects of A. swainsonii enhancement versus no enhancement (control) in 1981, it is of still greater interest to compare both controls and experimentals simultaneously. Such a comparison is obviously unbalanced, however, and it introduces the confusing effects of between-year differences in addition to the different enclosure and treatment effects that already exist. Nevertheless, it may be argued that between-year effects could not be detected at all if separate comparisons were made in 1980 and in 1981, and such effects may subsequently be helpful in interpreting particular results. Hence, only 4-sample comparisons (C80, C81, E80 and E81) are considered below.

To assess whether differences existed between populations, Model 1 ANOVAs and G-tests were used, as described in section 2.4.6. Planned comparisons involved four populations, and the appropriate null hypothesis, for A. stuartii, is stated as follows:

$$H_o : \mu\ E80 = \mu\ (C80 \text{ and } C81) = \mu\ E81$$

where μ is the parameter mean of the population.

In normal circumstances appropriate orthogonal comparisons for a two-experimental, two-control design would be i) μ (C1 and C2) vs μ (E1 and E2), ii) μ C1 vs μ C2 and iii) μ E1 vs μ E2, with 3 degrees of freedom (Chew 1976). Since the experiments in E80 and E81 were expected to have different consequences, however, it would be illogical to combine them as in i) above. There are, instead, two biologically interesting (and statistically legitimate) planned tests:

$$\mu\ E80 = \mu\ (C80 \text{ and } C81) \quad \ldots\ldots (1)$$

and

$$\mu\ E81 = \mu\ (C80 \text{ and } C81) \quad \ldots\ldots (2)$$

Unexpected (unplanned) differences between means were detected by the Student-Newman-Keuls (SNK) test.

To summarise the results of ANOVAs and the planned comparison tests, the following notation is used: F_o denotes the F ratio for the overall ANOVA, F_{p1} the F ratio for the planned comparison (1) above, and F_{p2} the F ratio for the planned comparison (2) above. As before, sample means that were not significantly different are underlined, and the numerical values for mean, standard deviation and sample size are shown in the data summary. Equivalent notation is used to distinguish overall and planned G-tests.

3.4 RESULTS

3.4.1 Effectiveness of the reduction and enhancement experiments

At the end of 1979, both species of Antechinus were present in the control and experimental enclosures. In the control enclosure, A. stuartii established itself after its reintroduction in April 1979, and by early 1980, after breeding successfully, the numbers of the two species there were similar (Fig. 3.2). The numbers of the two species remained similar throughout the periods February-July 1980 and 1981, and no removals or additions of A. swainsonii were necessary. The numbers of both species were considerably lower in 1981 than in 1980.

In the experimental enclosure, A. swainsonii also established itself successfully after its reintroduction in April 1979, and in early January 1980 eleven individuals were removed to make its numbers low

in relation to those of A. stuartii (Fig. 3.2). Between February and July 1980, the numbers of A. swainsonii were between 13% and 21% of the numbers of A. stuartii, and no further manipulations of the numbers of the former species were made. In the experimental enclosure in 1981, it was necessary to increase the numbers of A. swainsonii relative to those of A. stuartii. The numbers of A. stuartii in this enclosure declined between 1980 and 1981, and A. swainsonii was increased by adding 6 individuals in early January, 4 in late January, 5 in February, and 4 in March. No further additions were made, and between February and July 1981 the numbers of A. swainsonii were 38-56% greater than those of A. stuartii (Fig. 3.2).

In contrast to the experiments of Chapter 2, reductions and enhancements of A. swainsonii numbers were relatively unaffected by the comings and goings of individuals that were extraneous to the enclosures. No more than five such individuals were recorded on the trap lines in any month, and since they did not upset the ratio of one species to the other, they were not removed. Because the two species breed at different times and the young appear in the trappable population up to two months apart, consistent differences in the numbers of one species to the other could be maintained only between February and July. In the following analyses, comparisons are restricted to this six month period each year.

3.4.2 Effects of the reduction and enhancement of A. swainsonii numbers on the population parameters of A. stuartii

3.4.2.1 Population numbers and composition

The population numbers of A. stuartii fluctuated synchronously in both enclosures in 1980 and 1981 (Fig. 3.3a). Numbers were lowest between September and December each year when only females >1 yr old were present, and highest usually between February and April when juveniles were present.

Comparisons between the enclosures between February and July showed that the population in E80 was consistently larger than any other population, whereas that in E81 was consistently smaller (Fig. 3.3a). The population in E80 was never less than 91% larger than that in E81 (May), and in February it was 183% larger. Between-year differences were also found in the A. stuartii population in the control enclosure, but these varied between only 6% (July) and 38% (February). In 1980 the population in the experimental enclosure was always 5-44% greater than that in the control, and in 1981 the population in the experimental enclosure was always 19-89% less than that in the control. Statistically significant differences were found only in planned (1d.f.) comparisons of (C80 and C81) vs E80 in February ($G = 4.94$, $P < 0.05$), March ($G = 4.31$, $P < 0.05$) and April ($G = 3.88$, $P < 0.05$). Planned male versus female comparisons for these months revealed no significant differences, suggesting that neither sex contributed disproportionately to the relatively large population of E80.

These findings suggest that when the numbers of A. swainsonii were reduced (1980), the population of A. stuartii predictably

increased; when the numbers of A. swainsonii were enhanced, the population of A. stuartii predictably declined. (The decline was not, however, statistically significant). Although A. stuartii populations declined in both enclosures between 1980 and 1981, the decline was much greater in the experimental than in the control enclosure.

3.4.2.2 Survival

Minimum sessional survival rates of A. stuartii again fluctuated more or less synchronously in both years (Fig. 3.3b). Low survival (22-57%) always occurred in August due to the disappearance of all males, but survival rates of 60-100% were recorded for all other months.

Reducing and enhancing the numbers of A. swainsonii had little evident effect on the overall survival of A. stuartii, and no statistically significant overall or planned differences were detected in any month (or combination of months) between February and July of either year. The survival rates of males, females <1yr and females >1yr old were also similar between enclosures in both years (Tables 3.1, 3.2 and 3.3), and again, no significant differences were found. Considering females alone, however, survival in June in C80 was less than in C81 (Fisher exact probability test, $P \sim 0.02$).

The survival of pouch and nestling A. stuartii was uniformly high in both enclosures in both years (Table 3.4a). In contrast, the survival of newly-weaned individuals in E81 was less than in E80 ($G = 4.35$, 1d.f., $P < 0.05$), and also less than in the control enclosure when results for 1980 and 1981 were combined ($G = 3.87$, 1d.f., $P < 0.05$) (Table 3.4b).

Despite between-year differences in survival (e.g. Table 3.4b) these results suggest that newly weaned individuals survive less well when A. swainsonii numbers are high than when they are low. In contrast, manipulation of A. swainsonii numbers had no effect on the survival of A. stuartii pouch or nestling young, or independent individuals between February and July.

3.4.2.3. Trappability

Outside the months September to December, when sample sizes were small, trappability of A. stuartii was usually 90-100% (Fig. 3.3c). Monthly comparisons of all individuals and of males and females failed to detect any statistically significant differences, and suggested that reduction and enhancement of the numbers of A. swainsonii had no effect on A. stuartii trappability.

3.4.2.4 Reproduction

Reproductive events in A. stuartii occurred at about the same time as in previous years, although they may have occurred slightly earlier in 1981 than in 1980 (Table 3.5). However, the differences were of the order of only 3-4 days, and were not associated with manipulations of the numbers of A. swainsonii. (It should be noted, however, that breeding occurred outside of the months February-July, when ratios of the numbers of A. swainsonii to A. stuartii were maintained). All males disappeared by early September each year, and females gave birth in the last 11 days of September after a pregnancy of 4-5 weeks. Young were carried in the pouch for about 5 weeks but continued to be suckled for a further two

months. Independent young began to appear in traps at about three months of age.

3.4.2.5 Movements

Because morning and evening trap rounds were conducted, it was possible to calculate movements between traps that occurred in the daytime and at night. These calculations showed that night-time movements were almost always greater than daytime movements (compare Tables 3.6 and 3.7). The movements of males and females were generally comparable, and there was little evidence that movements increased in either sex throughout the period February to July (Tables 3.6 and 3.7).

Comparisons between the enclosures revealed several statistically significant planned differences in movements (Tables 3.6 and 3.7):

1) The night-time movements of females were less in E80 between February and April and between May and July than in C80 and C81.

2) In contrast, the daytime movements of females between February and April were least in E81.

3) Between May and July, the daytime movements of females, and of males and females together, were less in E80 than in C80 and C81.

In summary, reductions in the numbers of A. swainsonii generally reduced the movements of A. stuartii, especially of females, whereas enhancement had little consistent effect.

3.4.2.6 Body size

Body weight: Between February and July the body weights of male A. stuartii generally increased (Table 3.8), whereas those of females <1yr old remained more or less constant (Table 3.9). Statistically significant planned differences were evident in several months, and may be summarised as follows:

1) Males weighed less in March and May in E80 than in any other enclosure.

2) Males weighed more in June in E81 than in any other enclosure.

3) Females <1yr old weighed less in June in E80 than in any other enclosure.

The results show that reduction of the numbers of A. swainsonii reduced the body weights of male and female A. stuartii in some months, whereas enhancement increased the body weights of male A. stuartii in one month only.

The sample sizes of females >1yr old were small (Table 3.10), and no statistical comparisons were made.

3.4.3 Effects of the reduction and enhancement of A. swainsonii numbers on the resource use of A. stuartii

3.4.3.1 Arboreal habitat

Antechinus stuartii was active in trees throughout the year in both the control and experimental enclosures (Fig. 3.4). Between February and July, there were several statistically significant differences between enclosures. Overall differences were detected in

May (G = 12.69, 3d.f., P < 0.01) and June (G = 9.56, 3d.f., P < 0.05), and were due to the relatively low arboreal activity in the experimental enclosure in 1980 (Fig. 3.4). After combining the months February to April, arboreal activity was less in E80 than in C80 and C81 together (G = 4.25, 1d.f., P < 0.05), but there was no difference in the comparison of E81 vs (C80 and C81) (G = 1.51, 1d.f., P n.s.). After combining the months May to July, arboreal activity was very much less in E80 than in C80 and C81 together (G = 24.11, 1d.f., P < 0.001), but again the planned comparison of E81 vs (C80 and C81) was not significant (G = 0.74, 1d.f., P n.s.).

These results show that the arboreal activity of A. stuartii was reduced when the numbers of A. swainsonii were reduced, but was relatively unaffected when the numbers of A. swainsonii were enhanced.

3.4.3.2 Terrestrial habitat (structural habitat complexity)

As before (see section 2.5.4.2), A. stuartii was captured most frequently at sites offering some structural habitat complexity (Table 3.11). Comparisons of the terrestrial habitat use of A. stuartii between enclosures are shown in Table 3.11, but they may be summarised as follows:

1) February-April. The habitat used by A. stuartii in E80 was structurally more complex than that used in any other enclosure. The comparison of E81 vs (C80 and C81) was not significant. Females >1yr old consistently used sites offering greater S.H.C. than either males or females <1yr old, and the relatively large number of these older females in E80 contributed to the significant sex x enclosure comparison.

2) May-July. There were no sex differences in the use of S.H.C. by A. stuartii within enclosures, but differences existed in the overall use of S.H.C. between enclosures. The between-enclosure comparisons showed that A. stuartii was captured in more complex habitat in E80 than in C80 and C81, but in less complex habitat in E81.

The results show that A. stuartii generally used structurally more complex habitat when the numbers of A. swainsonii were low (E80), but (in the period May-July only) structurally less complex habitat when A. swainsonii numbers were high (E81).

3.4.3.3 Food

Food type: Scat material collected between March and May 1980 and 1981 comprised the remains of 24 types of food (Table 3.12a). Coleoptera, Aranea, Dermaptera and larvae were generally found most frequently, but Amphipoda, Lepidoptera and other types of invertebrates occurred sporadically. The vertebrate remains appeared to be those of skinks (Leiolopisma spp.), whereas the hair was that of A. stuartii. The plant material was identified as the seeds and soft, mauve-staining tissues of Blackberry (Rubus fruiticosus). Berries were ingested largely in March after they had ripened and fallen to the ground.

Comparisons between the enclosures showed that:

1) The types of prey eaten by A. stuartii in E80 differed overall from those eaten in C80 and C81, but there was no difference in the comparison of E81 vs (C80 and C81). Partitioning G showed that A. stuartii in E80 ate

proportionally more Amphipoda ($G_{(1d.f.)} = 5.46$, $P < 0.05$), more larvae ($G_{(1d.f.)} = 10.40$, $P < 0.01$) and less Aranea ($G_{(1d.f.)} = 4.67$, $P < 0.05$) than in C80 and C81 together.

2) Prey type diversity was greatest in E80 and least in E81. This was due largely to the difference in the numbers of prey types represented (21 in E80 and 18 in E81), and apparently not to differences in the evenness with which prey types were represented in the diets (Table 3.12a).

Food size: As in section 2.5.4.3, only a fraction (54-65%) of the fragments identified to type could be assigned to a size class (Table 3.12b). Most prey were 1-12.5 mm long, although a few were ≥20 mm long (Table 3.12b).

Comparisons between the enclosures showed that:

1) Prey sizes differed overall between the enclosures. However, the differences were between C80 and C81 ($G_{(5d.f.)} = 15.35$, $P < 0.01$) and between C81 and E81 ($G_{(5d.f.)} = 14.97$, $P < 0.05$) but not between E80 and E81 ($G_{(5d.f.)} = 8.38$, P n.s.). Partitioning G showed that A. stuartii ate proportionally more prey (especially Aranea and Coleoptera) in the 1-2.4 mm size class in C80 than in C81 ($G_{(1d.f.)} = 4.60$, $P < 0.05$), and more (especially Chilopoda, Diplopoda and larvae) in the 2.5-4.9 mm size class in C81 than in the other enclosures together ($G_{(1d.f.)} = 7.63$, $P < 0.01$).

2) Prey size diversity was greatest in E80 and least in C81. This difference presumably arose because more prey size

classes were represented in the diets of A. stuartii in E80 than in the other enclosures, and because the evenness of representation of prey size classes in C81 was relatively low (Table 3.12b).

In summary, the reduction in the numbers of A. swainsoniii was followed by an increase in the proportion of terrestrial prey (Amphipoda, larvae) eaten by A. stuartii. The diversity of types and sizes of prey in the diet of the smaller species also increased. In contrast, enhancement of the numbers of A. swainsonii had little evident effect on the diet of A. stuartii.

3.5 DISCUSSION

Reductions in the numbers of A. swainsonii were expected to produce shifts in the population parameters and patterns of resource use of A. stuartii that were similar in direction but less in magnitude to those produced by the removal of A. swainsonii (see Chapter 2). In contrast, enhancement of the numbers of A. swainsonii was expected to produce reciprocal shifts. Comparison of Tables 2.23 and 3.13 show that these expectations were largely (but not completely) borne out, and lend strong support to the conclusion of Chapter 2 that A. stuartii is affected adversely by competition from A. swainsonii. Much of the discussion of Chapter 2 is applicable also to the results of the present chapter, so here I only discuss some of the problems associated with the experimental design, unexpected findings, and some of the biological consequences of reducing and increasing competitor numbers.

A restriction of conducting competitor reduction and enhancement experiments on Antechinus is that they can be effective for only

those months (February to July) when juveniles of both species are present and trappable. In other months, only small numbers of pregnant or lactating females are present, and these are difficult to manipulate. This restriction was not particularly serious, however, because it included some of the winter months when interspecific competition was expected to be most intense (Chapter 4). Previous attempts at varying the numbers of one competitor species to another have usually been conducted over periods of only a few days (e.g. Price 1978).

Only two enclosures were available in 1980 and 1981, so only two approaches to manipulating competitor numbers were possible. These were 1) to compare control versus experimental manipulations in the same enclosure at different times, and 2) to compare control versus experimental manipulations in different enclosures at the same time. The first approach controls for between-enclosure differences, whereas the second approach eliminates temporal (seasonal or annual) differences (see Grant 1972b). Since previous experience (Chapter 2) suggested that between-enclosure differences should be minimal, the second approach, controlling for between-year differences, was the one that was used here.

The advantages of using the second approach became apparent between 1980 and 1981, when populations of both species of Antechinus in the control enclosure declined (Fig. 3.2). The decline was accompanied by an increase in the severity of a drought (Fig. 2.2), and by a decrease in the abundance of invertebrate food (Chapter 4). The decline in Antechinus numbers could have influenced the results of the experiments in two ways. First, the frequencies of interspecific contacts in, low density, "rarefied"

populations would be less than in dense ones, and any resultant competitive effects would thus be difficult to detect. Second, such effects would be still more difficult to detect by statistical analyses due to the inevitably small sample sizes obtained from these populations. A further difficulty with interpretation of the results is that, although the population densities of two species and the frequencies of interspecific contacts between their constituent individuals are usually positively correlated (Terman 1978, Glass and Slade 1980), the behaviour of individuals can vary unpredictably at different densities (Lomnicki 1978, Taylor and Taylor 1979, Cohen et al. 1980 and papers therein). The results of the present chapter showed that enhancing the numbers of A. swainsonii generally had less measurable effect on the A. stuartii populations than had the corresponding reductions of A. swainsonii numbers. Because of the overall decline in Antechinus numbers throughout the study, however, it is not clear whether competitor enhancement actually failed to intensify interspecific competition, or whether this simply could not be detected.

Reductions in the numbers of A. swainsonii were followed by a predictable increase in the numbers of A. stuartii, and by predictable shifts in the arboreal activity, habitat use and diet of the latter species. There is, however, one interesting question: Why, contrary to the findings of Chapter 2, did movements of A. stuartii decrease when A. swainsonii numbers were reduced? The most attractive explanation is that removal of some A. swainsonii allowed A. stuartii access to additional terrestrial sources of food, but still curtailed extensive ground-level foraging movements. This explanation is supported by the decreased arboreal activity of A.

stuartii in E80, and by the finding that this species ate more terrestrial invertebrates (Amphipoda, larvae) when A. swainsonii numbers were reduced.

If reducing the numbers of A. swainsonii increased the food available to A. stuartii, why did the mean body weights of the latter species decrease in some months in this situation (section 3.4.2.6)? This thorny problem was tackled in Chapter 2, where I suggested that, contrary to expectation, intraspecific interference effects arising in unusually high density populations could actually reduce food intake. The problem is now considered further in the light of fresh evidence.

While clearing traps in the mornings and evenings, it became obvious that A. stuartii was considerably more active by day in E80 than in any other enclosure, especially in the winter months (Table 3.14). This finding was unexpected, since no shifts in the periodicity of activity of A. stuartii were detected during 24 hour trapping (section 2.5.4.4). Conceivably, in the presence of only a few interspecific competitor individuals, individual foraging efficiency is maximised by becoming partially diurnal and moving less at ground level, whereas in the complete absence of competitor individuals it is maximised by maintaining a normal, nocturnal activity pattern, but moving more at ground level. However, this explanation invokes optimal foraging analyses, which have not been attempted, and also credits A. stuartii with considerable behavioural plasticity.

An alternative explanation for the increase in diurnal activity, for which there is supporting evidence, is that A. stuartii was actually short of food. In addition to the reduced mean body weights of this species in E80, it was noticed that individuals in this

enclosure lost more weight in the course of the four day trapping sessions than in any other enclosure. Moreover, the magnitude of the weight losses in E80 appeared to coincide with levels of diurnal activity. Average weight losses of females captured three or more times in each monthly trapping session in E80 were -0.05g (February), -0.08g (March), -0.56g (April), -1.00g (May), -0.41g (June) and -0.77g (July). These weight losses were correlated with the proportions of daytime captures of females in these months ($r_{(4d.f.)} = -0.84$, $P < 0.05$). Corresponding weight losses of males were +0.07g (February), -0.25g (March), -1.25g (April), -1.57g (May), -0.83g (June) and -0.86g (July), which were almost correlated with the proportions of daytime captures of males in these months ($r_{(4d.f.)} = -0.76$, $P < 0.1$). It is reasonable to suggest that, as individuals lost weight, their need to find food increased and resulted in unusually high daytime activity. It is irrelevant whether trapping provided a true indication of diurnal activity in A. stuartii, or whether such activity increased because trapped individuals were deprived of their natural invertebrate food: because correlations of weight losses and diurnal activity were recorded only in E80, food was presumably less abundant, or less available, in this enclosure than in any other.

So far, the discussion has provided arguments that lead to two quite different conclusions. On the one hand I proposed that reducing the numbers of A. swainsonii should increase the food available to A. stuartii, while on the other I suggested that the decreased body weights and associated increases in diurnal activity were due to a decrease in available food. How are these conclusions

to be reconciled? Other findings (shifts in diet, arboreal activity and terrestrial habitat use) suggest that reduction of the numbers of A. swainsonii does indeed allow A. stuartii access to additional, terrestrial sources of food, while in Chapter 4 it is shown that there were no detectable differences in overall food abundance between the enclosures in 1980 or 1981. Since the numbers of A. stuartii in E80 were considerably greater than in C80 or C81, it seems reasonable to conclude that individual A. stuartii interfered with one another in gaining access to food, even though that food did not appear to be limiting. A point in support of this conclusion is that large average monthly weight losses and increased diurnal activity in A. stuartii occurred only after March, when levels of agonistic behaviour increase and the social structure of the population begins to break down (Chapter 4).

How does the existence of intraspecific interference influence the interpretation of competition between A. stuartii and A. swainsonii? In E81, where the competitive effects of A. swainsonii on A. stuartii were expected to be most intense, the numbers and survival of newly-weaned A. stuartii were relatively low. Daytime movements of females were curtailed between February and April, and the terrestrial habitat used by both sexes between May and July was less complex than that used in C80 and C81. Assuming that intraspecific interference effects were no greater in E81 than in C80 and C81 (this is reasonable in view of the low numbers of A. stuartii in E81), these effects were presumably due to increased competition from the enhanced numbers of A. swainsonii. In contrast, the reciprocal effects observed in E80 when A. swainsonii numbers were reduced were presumably due to decreased interspecific competition.

Since most niche shifts in A. stuartii may be explained by shifts in the intensity of interspecific competition, decreased body weights and increased diurnal activity were probably the only consequences of intraspecific competition. Moreover, since such intraspecific effects were observed only when A. swainsonii was removed or reduced, increased intraspecific interference competition may be seen as a further consequence of alleviating interspecific competition. These conclusions support the tentative conclusions of Chapter 2.

3.6 SUMMARY

An investigation was made of the effects of reducing and enhancing the numbers of A. swainsonii on the population parameters and resource use of A. stuartii. Populations of the two species were observed in two enclosures (control and experimental) between February and July in 1980 and 1981. In the control enclosure, the numbers of both species were similar in both years, whereas in the experimental enclosure the numbers of A. swainsonii were reduced relative to A. stuartii in 1980, but increased in 1981. Reduction in the numbers of A. swainsonii was expected to alleviate the effects of interspecific competition on A. stuartii, whereas enhancement was expected to exacerbate these effects.

When the numbers of A. swainsonii were reduced, the numbers of A. stuartii increased. Individuals generally used structurally more complex habitat and moved less at ground level, and a decline in arboreal activity was associated with an increase in the proportion of terrestrial invertebrates (Amphipoda and larvae) in the diet. These effects were generally consistent with the interpretation that interspecific competition had been reduced, and suggested that the

reduction of A. swainsonii allowed the smaller species access to terrestrial sources of food. An apparently inconsistent effect was that body weights of A. stuartii decreased in some months. There was some evidence that this was due to increased interference among A. stuartii individuals in obtaining access to food, even though food did not appear to be limiting.

When the numbers of A. swainsonii were enhanced, the numbers and survival of A. stuartii decreased (although the decrease in numbers was not statistically significant). Individuals used structurally less complex habitat in some months (May to July), and the daytime movements of females were curtailed between February and April. These effects suggested that competition from A. swainsonii had been increased. The single effect that conflicted with this interpretation was an increase in the mean body weight of male A. stuartii that occurred in June 1981.

Although manipulations of the numbers of A. swainsonii had predictable effects on A. stuartii, the effects of reduction were generally stronger and more consistent than those of enhancement. The investigation of enhancement used relatively small and "rarified" populations of A. stuartii and A. swainsonii, so that frequencies of interspecific contacts, and hence competitive effects on A. stuartii, may have been difficult to detect.

Changes in the intensity of interspecific competition, produced by the reduction and enhancement experiments, had largely predictable effects on population parameters and resource use of A. stuartii, and hence support the conclusions of Chapter 2. Problems that arose in the interpretation of these experiments concerned the nature of the resource for which competition occurs, and this is considered in the next two chapters.

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Table 3.1 Minimum sessional survival (%) of male Antechinus stuartii. Sample sizes are shown in brackets.

	E80	C80	C81	E81
Feb.	83(12)	89(9)	100(4)	100(3)
Mar.	70(10)	67(9)	100(5)	75(4)
Apr.	73(11)	89(9)	60(5)	100(4)
May	100(9)	78(9)	100(5)	83(6)
Jun.	92(12)	75(8)	83(6)	80(5)
Jul.	75(12)	63(8)	57(7)	80(5)

Table 3.2 Minimum sessional survival (%) of female Antechinus stuartii (<1yr old). Sample sizes are shown in brackets.

	E80	C80	C81	E81
Feb.	88(17)	77(13)	78(9)	100(7)
Mar.	83(18)	92(12)	100(9)	86(7)
Apr.	65(17)	91(11)	78(9)	57(7)
May	91(11)	80(10)	100(8)	100(4)
Jun.	90(10)	55(11)	100(8)	75(4)
Jul.	70(10)	100(6)	78(9)	75(4)

Table 3.3. Minimum sessional survival (%) of female Antechinus stuartii (>1yr old). Sample sizes are shown in brackets.

	E80	C80	C81	E81
Feb.	100(5)	100(2)	100(2)	100(2)
Mar.	60(5)	100(2)	50(2)	50(2)
Apr.	33(3)	50(2)	100(1)	100(1)
May	100(1)	100(1)	100(1)	0(1)
Jun.	50(2)	0(1)	100(1)	-
Jul.	100(1)	50(2)	0(1)	-

Table 3.4 Survival of pouch, nestling and newly weaned Antechinus stuartii.

(a) Pouch and nestling young

	Number of pouch young in September 1980 or 1981	Numbers surviving until December (1980) or November (1981)	Overall survival (%)
E80	36	34	94
C80	37	36	97
C81	37	35	95
E81	18	18	100

(b) Newly weaned young

	Number of nestling young in December 1979 or 1980	Numbers surviving until January to April 1980 or 1981	Overall survival (%)
E80	61	40	66
C80	48	34	71
C81	36	19	53
E81	34	14	41

$G_{o(3d.f.)} = 8.90$, $P < 0.05$.

In (a), results for pouch young are derived only from those parous females that survived from September 1980 to December 1980, and those that survived from September 1981 to November 1981. The numbers of pouch young in September each year were obtained by counting young in the pouch, but the numbers of those young surviving until November or December were obtained by counting the numbers of used nipples on their mothers (Woolley 1966).

In (b), the numbers of nestling young in December 1979 and December 1980 were also obtained by counting used nipples on lactating females. The survival of these young as weanlings in late December 1979 and 1980 was assessed by counting the numbers of new juveniles that appeared in each enclosure between January and April of the following year.

Table 3.5. The range in timing of reproductive events in Antechinus stuartii in 1980 and 1981.

Enclosure	Last male captured	Pregnancy	Birth	Placed in nest	End of lactation	First juvenile captured
E80	3 Sept.	18* Aug.- 30 Sept. (N=9)	27-31 Sept. (N=8)	31 Oct.- 3 Nov. (N=5)	4 Jan.	2 Jan.
C80	5 Sept.**	23* Aug.- 27 Sept. (N=8)	23-28 Sept. (N=6)	26 Oct.- 2 Nov. (N=5)	28(?) Jan.	10 Jan.
C81	29 Aug.	26* Aug.- 25 Sept. (N=8)	22-26 Sept. (N=8)	27-31 Oct. (N=7)	-	-
E81	30 Aug.	15* Aug.- 21 Sept. (N=5)	20-22 Sept. (N=2)	24 Oct. (N=1)	-	-

* Estimated from the condition of the hairs surrounding the pouch (Woolley 1960).

** A male that was castrated in a trapping accident in July survived beyond 5 September. He was removed to the laboratory on 24 September. Sample sizes (N) are in brackets.

Table 3.6 Night-time movements of Antechinus stuartii. Values are mean average distances moved (m) ± standard deviation. Sample sizes are in brackets.

		E80	C80	C81	E81	F_o	F_{p1}	F_{p2}	Conclusion
Feb-	♂	44.2±23.4	38.0±15.0	44.1±16.8	48.8±34.8	0.63	0.43	1.12	E80 C80 C81 E81
April		(26)	(21)	(14)	(10)				
	♀	34.7±19.9	43.6±20.2	40.3±17.1	41.7±12.3	2.07	5.13**	0.01	E80 C80 C81 E81
		(62)	(36)	(27)	(24)				
	♂+♀	37.3±21.3	41.5±18.5	41.6±16.9	43.8±21.1	1.14	1.71	0.31	E80 C80 C81 E81
		(88)	(57)	(41)	(34)				
May-	♂	54.9±30.5	41.5±24.1	53.9±28.9	44.0±21.2	1.34	1.49	0.09	E80 C80 C81 E81
July		(30)	(23)	(17)	(11)				
	♀	36.0±19.5	50.1±23.0	36.7±16.1	37.5±17.9	3.12*	2.94*	0.94	E80 C80 C81 E81
		(34)	(26)	(26)	(13)				
	♂+♀	44.9±26.8	46.1±23.7	43.5±23.4	40.5±19.3	0.31	0.00	0.62	E80 C80 C81 E81
		(64)	(49)	(43)	(24)				

Table 3.7. Daytime movements of Antechinus stuartii. Values are mean average distances moved (m) ± standard deviation. Sample sizes are in brackets.

		E80	C80	C81	E81	F_o	F_{p1}	F_{p2}	Conclusion
	♂	31.4±7.0	28.0±18.9	30.3±5.6	40.7±23.5	0.60	0.51	1.72	E80 C80 C81 E81
Feb.-		(9)	(5)	(4)	(3)				
April	♀	36.2±17.4	29.6±15.1	34.1±10.9	17.4±3.1	2.29	0.71	3.61*	E80 C80 C81 E81
		(31)	(7)	(10)	(5)				
	♂+♀	35.1±15.7	28.9±16.0	33.0±9.6	26.1±17.6	1.11	1.10	0.68	E80 C80 C81 E81
		(40)	(12)	(14)	(8)				
	♂	35.0±18.8	36.8±16.4	44.5±21.1	14.0	0.53	0.53	-	-
May-		(21)	(8)	(5)	(1)				
July	♀	28.2±11.6	42.6±28.1	31.6±10.3	32.3±16.4	1.57	2.95*	0.23	E80 C80 C81 E81
		(25)	(7)	(7)	(3)				
	♂+♀	31.3±15.5	39.5±22.0	37.0±16.2	27.8±16.3	1.19	2.92*	1.35	E80 C80 C81 E81
		(46)	(15)	(12)	(4)				

Table 3.8 Body weights of male Antechinus stuartii. Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	E80	C80	C81	E81	F_o	F_{p1}	F_{p2}	Conclusion
Feb.	21.5±2.4 (12)	20.5±1.3 (8)	20.9±1.7 (4)	19.5±2.3 (3)	0.97	1.21	0.73	E80 C80 C81 E81
Mar.	21.5±2.3 (9)	22.8±2.1 (9)	24.1±3.0 (5)	22.9±2.0 (4)	1.40	3.19*	0.10	E80 C80 C81 E81
Apr.	21.9±2.1 (10)	23.7±2.8 (9)	22.5±1.7 (5)	24.8±1.7 (4)	2.03	2.33	1.29	E80 C80 C81 E81
May	22.3±2.1 (9)	24.1±1.6 (8)	24.1±1.7 (5)	25.5±1.5 (5)	3.76*	5.34**	2.33	E80 C80 C81 E81
Jun.	22.7±2.5 (12)	22.3±2.2 (8)	23.5±2.2 (6)	25.4±1.8 (5)	2.25	0.02	4.81**	E80 C80 C81 E81
Jul.	24.7±3.0 (12)	24.2±1.7 (8)	26.5±1.9 (7)	24.7±1.5 (5)	1.44	0.46	0.23	E80 C80 C81 E81

Table 3.9 Body weights of female Antechinus stuartii (<1 yr old). Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	E80	C80	C81	E81	F_o	F_{p1}	F_{p2}	Conclusion
Feb.	16.9±1.3 (17)	16.9±1.2 (11)	17.2±1.3 (9)	16.5±0.4 (7)	0.45	0.02	0.92	E80 C80 C81 E81
Mar.	16.4±1.0 (18)	16.1±1.0 (11)	16.6±1.3 (9)	16.3±0.6 (6)	0.42	0.01	0.00	E80 C80 C81 E81
Apr.	15.4±1.2 (17)	16.3±1.2 (11)	15.7±1.6 (7)	16.9±0.8 (6)	2.72	2.47	2.27	E80 C80 C81 E81
May	16.4±1.6 (11)	16.5±1.1 (10)	17.4±1.5 (7)	17.8±1.3 (4)	1.55	0.78	1.27	E80 C80 C81 E81
Jun.	15.7±1.0 (10)	16.7±1.6 (11)	16.8±1.1 (7)	17.1±0.6 (4)	2.14	4.96**	0.36	E80 C80 C81 E81
Jul.	16.0±1.1 (10)	16.2±0.7 (6)	16.9±1.9 (9)	17.1±0.5 (4)	1.19	1.27	0.51	E80 C80 C81 E81

Table 3.10 Body weights of female Antechinus stuartii (>1 yr old). Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	E80	C80	C81	E81
Feb.	22.4±1.7 (5)	23.5 (2)	25.0 (1)	24.5 (2)
Mar.	20.9±1.3 (5)	23.5 (2)	21.8 (2)	20.5 (2)
Apr.	21.0±1.3 (3)	23.0 (2)	22.0 (1)	24.0 (1)
May	18.5 (1)	24.0 (1)	24.0 (1)	25.0 (1)
Jun.	19.5 (2)	20.0 (1)	24.0 (1)	-
Jul.	22.0 (1)	20.0 (2)	21.0 (1)	-

Table 3.11 Frequency of capture of Antechinus stuartii at sites of different structural habitat complexity (S.H.C.). The number of captures (N), mean S.H.C. ($\bar{x}$) and standard deviation (s.d.) are given.

February-April

	sex/age class	Structural Habitat Complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
E80	♂	(2)	3	8	7	7	25	17	14	13	8	1	105	8.51	2.24
	♀<1yr	(5)	7	9	29	25	58	41	20	11	14	3	222	8.10	2.10
	♀>1yr	(1)	2	2	14	4	6	15	11	7	3	(5)	70	8.63	2.41
C80	♂	(2)	4	6	9	18	16	11	8	4	5	1	84	7.81	2.20
	♀<1yr	(6)	8	13	20	24	14	10	10	3	0	(3)	111	7.00	2.22
	♀>1yr	0	1	0	0	5	3	3	3	1	0	0	16	8.19	1.72
C81	♂	0	6	4	5	7	6	4	3	4	2	(1)	42	7.57	2.52
	♀<1yr	2	1	3	10	22	18	16	3	5	3	0	83	7.81	1.82
	♀>1yr	0	0	0	2	3	4	1	2	2	1	0	15	8.53	1.88
E81	♂	1	1	2	8	12	5	4	5	4	2	0	44	7.80	2.12
	♀<1yr	0	2	6	14	16	10	9	5	2	2	1	67	7.52	1.93
	♀>1yr	0	1	0	1	6	2	3	4	1	1	0	19	8.32	1.95

Summary[1]

SHC x E x S, $G_{o(116\ d.f.)} = 199.04^{***}$

SHC x E, $G_{o(30\ d.f.)} = 70.71^{***}$

E80 vs (C80+C81), $G_{p1(10\ d.f.)} = 42.26^{***}$

E81 vs (C80+C81), $G_{p2(10\ d.f.)} = 8.03$

SHC x S, $G_{o(20\ d.f.)} = 38.53^{**}$

E x S, $G_{o(6\ d.f.)} = 21.07^{**}$

Table 3.11 (cont.)

May-July

	sex/age class	Structural Habitat Complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
	♂	(3)	6	10	25	10	39	23	14	20	4	3	157	8.08	2.29
E80	♀	(5)	5	8	19	5	24	28	36	30	7	7	174	8.81	2.37
C80	♂	(2)	2	6	14	11	17	9	5	4	13	1	84	8.15	2.45
	♀	(3)	4	2	15	17	17	8	10	7	6	1	90	7.93	2.29
C81	♂	(4)	2	7	7	10	9	8	3	4	3	1	58	7.48	2.47
	♀	2	3	3	10	18	19	14	11	6	9	1	96	8.27	2.19
E81	♂	4	3	2	5	4	4	8	6	3	1	1	41	7.66	2.67
	♀	(3)	1	4	9	4	11	10	7	3	0	0	52	7.62	2.10

Summary[1]

SHC x E x S, $G_{o(73\ d.f.)} = 131.28^{***}$

SHC x E, $G_{o(30\ d.f.)} = 78.13^{***}$

E80 vs (C80+C81) $G_{p1(10\ d.f.)} = 57.76^{***}$

E81 vs (C80+C81) $G_{p2(10\ d.f.)} = 21.24^{*}$

SHC x S, $G_{o(10\ d.f.)} = 15.09$

E x S, $G_{o(3\ d.f.)} = 4.95$

[1] The G statistic was used to test the joint independence of S.H.C., sex/age class (S) and enclosure (E). If dependence was found, G was partitioned to examine which pairs of criteria were associated.

A few captures occurred in S.H.C. categories 1, 2, 14 and 15. They were grouped with captures in category 3 or 13 and are shown in brackets. Morning and evening captures are pooled.

Table 3.12. The dietary diversity of Antechinus stuartii

(a) Prey type diversity

Prey type	E80 N = 28	C80 N = 20	C81 N = 24	E81 N = 25
Oligochaeta	(4	1	2	0)
Isopoda	(4	2	0	0)
Amphipoda	12	5	1	4
Chilopoda	1	3	5	6
Diplopoda	2	2	4	1
Aranea	14	12	26	18
Acarina	0	2	2	4
Collembola	7	2	3	4
Coleoptera	18	15	26	29
Isoptera	(1	0	2	0)
Dermaptera	17	11	6	5
Lepidoptera	1	2	3	10
Diptera	(2	3	1	0)
Formicoidea	4	2	6	2
Other Hymenoptera	1	1	0	2)
Blattodea	3	2	5	3
Hemiptera	(3	2	0	0)
Orthoptera	(1	2	3	1)
Thysanoptera	(0	1	0	0)
Larvae	24	4	9	7
Other inverts	3	2	5	6
Hair	(0	0	0	2)
Vertebrates	(4	0	4	1)
Plant	6	5	3	1
Total no. prey items	132	81	116	106
No. prey types represented	21	21	19	18
Evenness J	0.85	0.88	0.84	0.83
Diversity H	2.36	2.34	2.24	2.16
G_o (d.f.)		$78.92_{(39)}$***		
G_{p1} (d.f.)	$34.94_{(13)}$***			
G_{p2} (d.f.)	$16.58_{(13)}$			

Table 3.12 (cont.)

(b) Prey size diversity

Prey size class (mm)	E80 N = 28	C80 N = 20	C81 N = 24	E81 N = 25
0.0-0.9	4	5	2	9
1.0-2.4	12	16	8	18
2.5-4.9	23	10	26	14
5.0-7.4	20	7	14	10
7.5-9.9	10	8	4	9
10.0-12.4	6	2	5	4
12.5-14.9	(1	0	2	4)
15.0-17.4	(2	3	0	0)
17.5-19.9	(2	0	0	1)
≥20.0	(3	1	2	0)
Total no. prey items	83	52	63	69
No. prey size classes represented	10	8	8	8
Evenness J	0.83	0.88	0.79	0.90
Diversity H	1.75	1.62	1.49	1.70
$G_{o(d.f.)}$		$25.78_{(15)}$*		
$G_{p1(d.f.)}$		$2.42_{(5)}$		
$G_{p2(d.f.)}$		$5.45_{(5)}$		

Samples for C80 and E80 were collected in March-May 1980, whereas samples for C81 and E81 were collected in March-May 1981. G-tests were performed on the raw frequency data, excluding values in brackets. Data for males and females were pooled.

Table 3.13 *Summary of the effects of reducing and enhancing the numbers of A. swainsonii on the population parameters and resource use of A. stuartii*

	Effects of reduction			Effects of enhancement		
	♂	♀	Both	♂	♀	Both
Population parameters						
Numbers	–	–	√	–	–	–
Survival	–	–	–	–	–	√
Trappability	–	–	–	–	–	–
Reproduction	–	–	–	–	–	–
Movements	–	√*	√*	–	√	–
Body weight	√*	√*		√*	–	
Resources						
Habitat (arboreal)			√√			–
Habitat (terrestrial)	√√	√√	√√	√	√	√
Food type			√√			–
Food size			–			–

All results (except reproduction) refer to comparisons during the period February–July in 1980 and 1981. √ denotes that statistically significant effects occurred in some sampling sessions only; √√ that effects occurred in all sampling sessions; – that no statistically significant effects were detected at any time. All effects were consistent with the interpretation of interspecific competition, except where marked *.

Table 3.14. Diurnal activity of A. stuartii. Frequencies of daytime captures are expressed as a percentage (%) of the total number of all captures (N) for each month. Males and females are shown separately.

		E80	C80	C81	E81
		% (N)	% (N)	% (N)	% (N)
	♂	7 (30)	7 (28)	18 (11)	18 (11)
Feb.	♀<1yr	14 (59)	6 (32)	8 (26)	8 (24)
	♀>1yr	23 (26)	14 (7)	0 (3)	13 (8)
	♂	22 (37)	10 (31)	13 (15)	25 (16)
Mar.	♀<1yr	14 (74)	12 (41)	19 (31)	9 (22)
	♀>1yr	21 (24)	0 (5)	13 (8)	0 (7)
	♂	29 (38)	12 (25)	6 (16)	18 (17)
Apr.	♀<1yr	35 (89)	5 (38)	15 (26)	5 (21)
	♀>1yr	40 (20)	0 (4)	25 (4)	0 (4)
	♂	32 (38)	15 (26)	6 (16)	0 (10)
May	♀	34 (67)	6 (36)	14 (29)	5 (19)
	♂	38 (58)	12 (33)	14 (21)	0 (15)
Jun.	♀	30 (53)	10 (30)	10 (31)	6 (16)
	♂	31 (61)	4 (25)	14 (21)	6 (16)
Jul.	♀	26 (54)	8 (24)	8 (36)	12 (17)

Fig. 3.1. Experiments designed to investigate the effects of reducing and increasing competition on A. stuartii (A.st) from A. swainsonii (A.sw). All steps are described in detail in the text. Rectangles (CONTROL and EXPT.) represent enclosures. Solid arrows within enclosures represent an expansive shift in population parameters or patterns of resource use of A. stuartii when A. swainsonii numbers are reduced, the broken arrow a return shift when A. swainsonii numbers are enhanced.

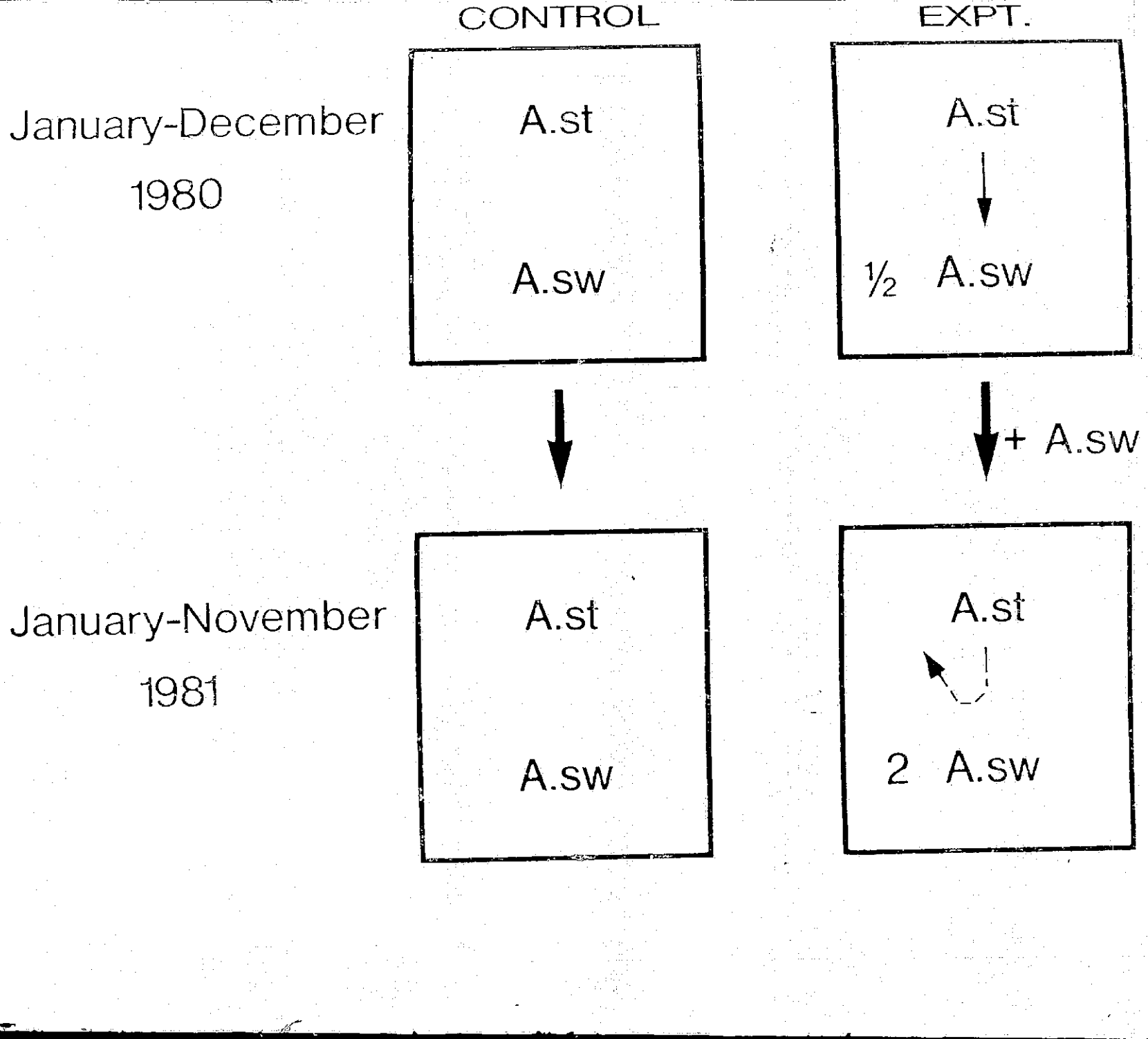

CONTROL
EXPT.
January-December
1980
A.st
A.sw
A.st
½ A.sw
+ A.sw
January-November
1981
A.st
A.sw
A.st
2 A.sw

Fig. 3.2. The minimum numbers of A. stuartii and A. swainsonii known to be alive in the control and experimental enclosures in 1980 and 1981. The numbers of A. swainsonii were adjusted in the experimental enclosure in both years (see text).

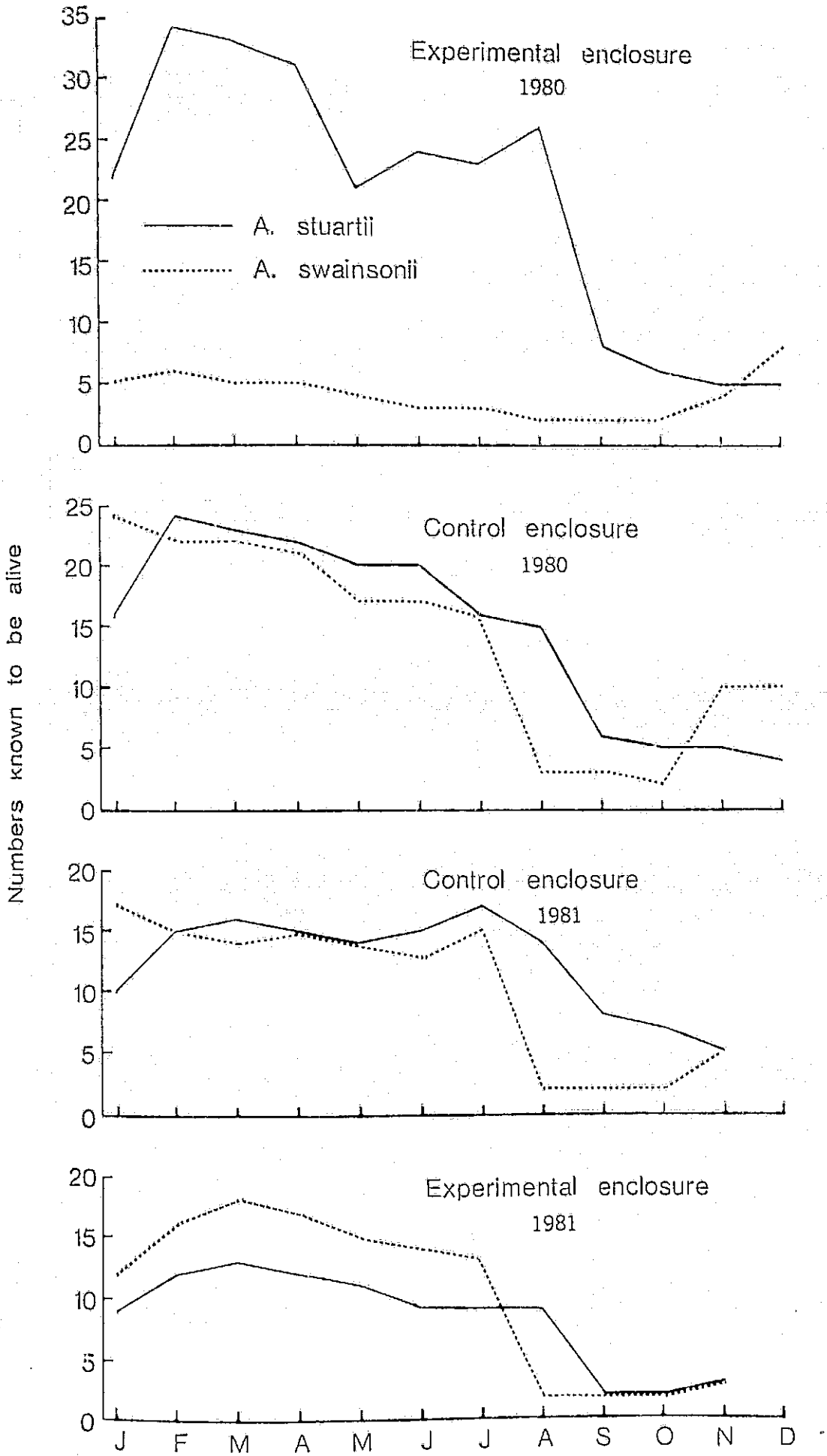

Experimental enclosure
1980
A. stuartii
A. swainsonii
Control enclosure
1980
Control enclosure
1981
Experimental enclosure
1981
Numbers known to be alive
0
5
10
15
20
25
30
35
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 3.3. Population parameters of A. stuartii (a) minimum numbers known to be alive, (b) minimum sessional survival of individuals known to be alive, (c) trappability of individuals known to be alive.

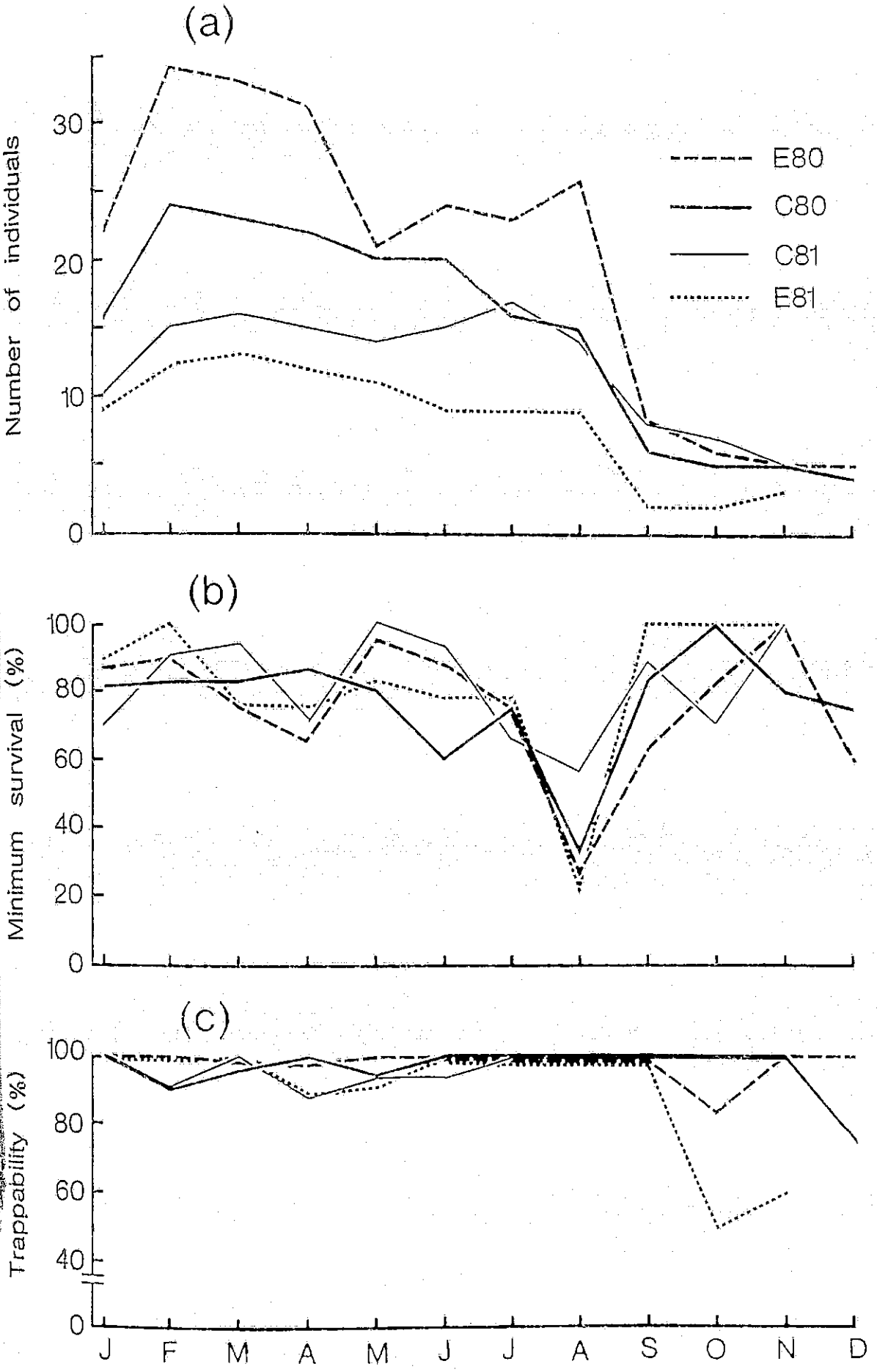
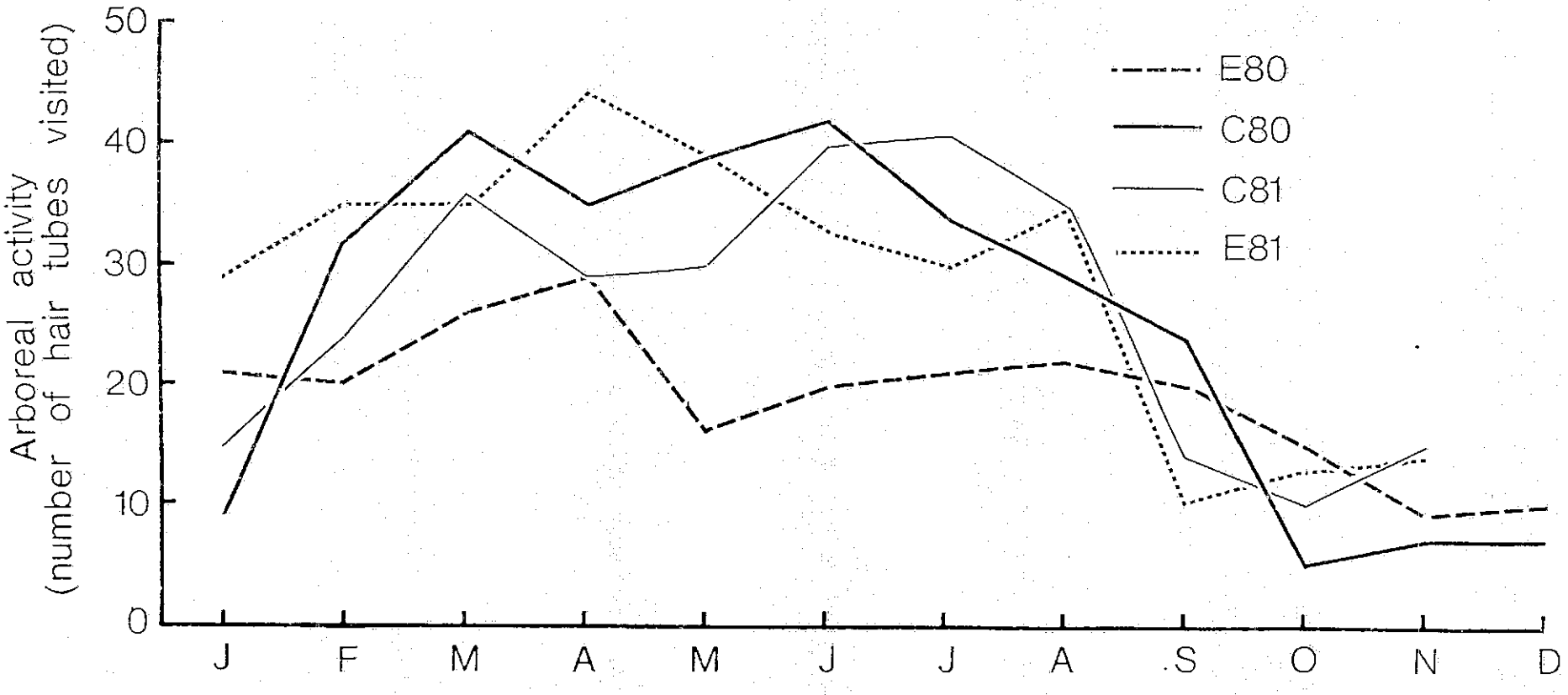

(a)
Number of individuals
30
20
10
0
E80
C80
C81
E81
(b)
Minimum survival (%)
100
80
60
40
20
0
(c)
Trappability (%)
100
80
60
40
0
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 3.4. Arboreal activity of A. stuartii.


Arboreal activity
(number of hair tubes visited)
50
40
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D
E80
C80
C81
E81

CHAPTER 4

THE RESOURCE BASE

4.1 INTRODUCTION

Although strong evidence for competition between A. stuartii and A. swainsonii has been presented in chapters 2 and 3, the manipulation experiments have provided little insight into the nature or identity of those resources for which competition occurs. However, there are several clues that an important scarce resource might be invertebrate food. Thus, following the removal or reduction of A. swainsonii, the dietary diversity of A. stuartii expanded, and the proportion of large, typically terrestrial forest litter invertebrates (e.g. larvae and Amphipoda) in the diet increased (sections 2.5.4.3 and 3.4.3.3). Casual observations also suggested that invertebrates were less abundant, or less conspicuous, in winter: at this time, females occupy more or less exclusive home ranges, or territories (section 2.5.3.6), and individuals can spend a relatively large amount of time foraging by day, as well as by night, to maintain their body weights (section 3.5). Moreover, Lee et al., Wainer 1976 and others have proposed that mating in Antechinus is timed so that lactation and the weaning of young coincide with increased insect activity in spring and summer; this again implies that seasonal peaks and shortfalls may occur in food abundance.

This chapter describes an investigation of what food was available to both species of Antechinus in the enclosures throughout the entire 3½ year period of study, and attempts to determine whether seasonal changes occurred in either the abundance or availability of this food.

4.2 METHODS

Invertebrates were collected systematically by sticky strip sampling, pitfall sampling and litter sampling, and casually by turning logs and rocks, looking under loose or decorticating bark, and beating vegetation. These methods were designed to sample invertebrates in each of the enclosures in habitats where Antechinus was known to forage. For consistency within this chapter, the enclosures are termed C1, E1, E2 E3 and E4 throughout (see Chapter 2). However, it will be remembered that, in 1980 and 1981, enclosures E1 and E2 were considered together as one enclosure, and E3 and E4 were considered together as another enclosure.

4.2.1. Sticky strip sampling

Braithwaite (1979) obtained an index of general insect abundance by using Aeroxon sticky strips. This method was also adopted here: at a site in each enclosure, two strips were suspended 1-2 m above ground, hanging loose from an Acacia or Cassinia branch. In addition, two further strips were wound around the trunks of nearby Ribbon Gum trees, one about 1 m above ground on old, residual and accumulated bark, and the other 2-3 m above ground on smooth bark. All strips were replaced at the end of each month. All invertebrates (except mites) on each strip were counted: the mean for the two hanging strips at each site was used to compare with Braithwaite's (1979) findings, but the results for the two tree-bark strips are presented separately. In 1978 and 1979, four strips (two hanging, two on trees) were used in each of the five enclosures, but thereafter, in 1980 and 1981, four strips were used in each of E1-E4, but not in C1.

4.2.2. Pitfall trap sampling

Pitfall traps were glass jars (opening diameter 7.0 cm), sunk flush to ground level, and provided with 2-3 cm of 5% formalin as preservative. To prevent the capture of small mammals, the opening of each trap was covered with 1 cm chicken wire mesh. All traps were left open and cleared at the end of each month; preserved invertebrates were removed and stored in 70% ethanol. Five pitfall traps were established in each of the five enclosures in late June 1978, and maintained until December 1979. In 1980 and 1981, five pitfalls were operated in each of E1-E4, but those in the control area were removed.

In each enclosure, pitfall traps were set 5-7 m apart in a line adjacent to the sticky strip sites, and run from the creek up to near the perimeter of the enclosures on the lower slopes of the valley. Pitfall traps were set singly along the lines, each in a different habitat. These were a) At the base of a mature Ribbon Gum (Eucalyptus viminalis) tree; b) under Water Fern (Blechnum nudum; c) under a rotting log (> 30 cm diameter and > 3 m long); d) in open ground; and e) on a dry slope above the valley floor. From trapping records, these habitats were known to be visited by both species of Antechinus. Arachnida captured in the pitfall traps were deposited with Mr. R. Moran (CSIRO, Division of Plant Industry, Canberra) for detailed identification, but most of the remaining invertebrates were deposited with the Australian National Insect Collection, Canberra.

4.2.3. Litter sampling

Four samples of litter and topsoil were taken in each enclosure at approximately three monthly intervals. To ensure that the volume of each sample was relatively constant (about 7900 cm^3), a steel quadrat (31.5 cm by 31.5 cm and 8 cm deep) was sunk into the ground, and the contents dug out with a trowel. Samples were collected on dry mornings and placed into large plastic bags in the field, and returned to the laboratory for processing the same day. The samples were placed separately into Berlese funnels and subjected to an increasing heat regime over 5-6 days. Invertebrates were driven out of the litter and preserved in picric acid, before later transfer to 70% ethanol.

Four samples of litter and topsoil were taken in each enclosure in four of the five habitat types sampled by pitfall trapping. (Due to the open, stony composition of the slopes and the general lack of litter, no attempt was made to obtain samples from this habitat). All litter samples were collected within 10 m of pitfall traps in the respective habitats. Sampling was conducted from October 1978 to January 1981, in October (Spring), January/February (Summer), April (Autumn) and July (Winter). Unfortunately, it was not feasible to obtain monthly samples of litter, since the collection and extraction procedures were extremely laborious and time-consuming. Extracted litter invertebrates were donated either to Mr. R. Moran or to the Australian National Insect Collection.

4.2.4. Casual sampling

Several potentially important groups of invertebrates were consistently under-represented in the systematic monthly collections

described above. These groups generally live in particular, local habitats (although they are potentially available to Antechinus), and they were recorded or collected casually each month. The most important of these habitats are logs, under rocks, under old, residual bark at the base of Ribbon Gum trees, on fern fronds and angiosperm leaves, and on creeks and creek banks. These habitats provide homes for a wide range of larvae, termites, beetles, cockroaches and other invertebrates. Detailed estimates of diversity and abundance could not be obtained from casual sampling of invertebrates, and observations are discussed in general terms only.

4.2.5. Alternative sources of food, and the dispersion of food

In addition to the systematic and casual sampling procedures described above, some observations were made of gross seasonal changes in some plant species in each of the enclosures. Such changes may influence the food available to Antechinus in two ways: first, by directly providing alternative sources of foods, such as fruits (section 2.5.4.3 and 2.5.6.3) and flowers (Statham 1982a); and second by altering the dispersion, abundance and availability of invertebrate microhabitats, and hence, indirectly, of invertebrates themselves. Observations were made of the decortication of Ribbon Gum bark, the spring growth and autumn death of Water Ferns, and of the fruiting times of certain species of shrubs (Table 4.1). Observations were quantified monthly by recording phenological changes of individually marked plants (Table 4.1).

4.2.6. Treatment of data

In many studies where an attempt has been made to examine the food available to insectivores, only the biomass of such food has been measured (e.g. Morton 1978, Statham 1982a, Dunham 1980). Biomass is easy to measure, and it may provide some indication of seasonal changes in the gross amount of available food. Unfortunately, estimates of biomass alone fail to take account of seasonal differences in the composition, palatability and energy content of food, or to recognise that predators may prefer to eat prey of a certain type or size. In this study, the biomass of available food was not estimated. Instead, all specimens obtained by pitfall and litter sampling were counted and identified (usually to the level of Order). Although laborious, this procedure allowed estimates to be made of the numerical abundance and diversity of invertebrates available to Antechinus, and facilitated statistical comparison of invertebrate type and size distributions between seasons and also between the enclosures.

Estimates of the numerical abundance of invertebrates were obtained by counting all individuals (except mites < 0.5 mm) collected on sticky strips and from pitfall and litter samples. Estimates of invertebrate type and size diversity were obtained only from pitfall and litter samples, as many sticky-trapped invertebrates dissolved into the glue and could not be further identified. Brillouin's (1956) index H (section 2.4.5) was used as a measure of diversity throughout. This index is particularly appropriate if collections of invertebrates are not made randomly (pitfall samples are biassed towards freely-moving invertebrates, and litter samples towards more sessile invertebrates; Plowman 1981), and if all individuals in the collection are identified and counted (Poole 1974, Pielou 1975).

Brillouin's index has been criticised by Hurlbert (1971) on the ground that it lacks biological relevance, and by Peet (1974) on the grounds that it may be unduly biassed by the differences in the sample sizes of collections. However, the non-random sampling procedures adopted here (pitfall and litter sampling) fail to satisfy the conditions required by alternative indices, such as the commonly-used Shannon-Weaver index. The Brillouin index is used consistently here as a comparative measure of diversity, and it is consistent also with the method used to estimate the dietary diversity of Antechinus in section 2.4.5.

Forty-six different types of invertebrates (listed in Appendix 5) were identified by reference to CSIRO (1970), (1974), Womersley (1939), Main (1976) and McColl (1977). In addition, all litter invertebrates and all invertebrates collected in pitfall traps in 1979 (some months only) and 1980 were measured from the tip of the head to the tip of the abdomen, and placed into one of 10 size classes (Appendix 6). The sizes of invertebrates recognised here are those used in the analysis of dietary diversity of Antechinus (sections 2.5.4.3, 2.5.6.3 and 3.4.3.3). However, some of the more abundant types of invertebrates, such as Coleoptera, Collembola and Hemiptera, have been subdivided into smaller groups than were used in the dietary analysis (Appendix 5). Some invertebrates - such as carabid and lycid beetles, snails and crayfish - as well as lizards - were found commonly in pitfall traps, but appeared to be eaten infrequently by Antechinus (sections 2.5.4.3, 2.5.6.3 and 3.4.3.3, see also Statham 1982a). These groups were therefore discarded, and abundance, prey type and prey size diversity were calculated only from those groups that were eaten or probably eaten by Antechinus.

Because Brillouin's index measures the diversity of a fully censused collection, it has no standard error (Poole 1974). Prey type and prey size diversity are therefore shown graphically. Differences in the distributions of prey types and prey sizes between study areas were tested by Kendall's coefficient of concordance, W (Siegel 1956). This statistic has been used specifically to compare the abundance distributions of invertebrates from two (or more) samples (Ghent 1963, Pielou 1975) and has been shown to be robust by Bullock (1971). Rare invertebrates, represented by a single individual in a comparison of several samples, were omitted from further analysis (Ghent 1963). No attempt was made to statistically compare absolute differences in the abundances of different invertebrate groups within or between study areas. Such methods are available (e.g. multivariate analysis of variance), but their assumptions are often restrictive and the results difficult to interpret (A.J. Campbell, personal communication).

4.3 RESULTS

4.3.1. Sticky strips

The numbers of invertebrates collected on sticky strips are shown in Fig. 4.1. In all study areas, invertebrates (70-100% flying insects) were most abundant in summer and least abundant in winter. There were no obvious differences in the distributions of abundances of these invertebrates either between enclosures, or between hanging and tree-bark strips at a site in any one enclosure (Table 4.2). In terms of absolute abundance, sticky strips on the rough bark near the base of Ribbon Gums usually collected more invertebrates than strips placed higher up on the smooth bark. The rough-bark strips

collected insects alighting on the outside of the strip, as well as insects that moved in the interstices of the bark that were caught on the inside surface of the strip. These findings provide evidence that some invertebrates, particularly flying insects, show very marked seasonal changes in abundance, and that these changes occur synchronously in each of the enclosures.

4.3.2. Pitfall sampling

A total of 72,036 invertebrates were captured in pitfall traps in this study; of these, 21735 (30%) were Collembola. Collembola were the most numerous invertebrates captured in pitfall traps in most months although Coleoptera also occasionally predominated (Fig. 4.2). Other invertebrates, such as Arachnida (especially Aranea), Dermaptera, Hymenoptera, Diptera and Hemiptera were abundant only in spring and summer. Amphipoda and larvae were usually less abundant components of the fauna, but they were trapped consistently in low numbers throughout the year (Fig. 4.2, see also Dickman et al., in press).

In view of the large numbers of Collembola in the pitfall traps and the fact that they were not eaten frequently by either species of Antechinus (sections 2.5.4.3, 2.5.6.3 and 3.4.3.3), the components of prey type diversity (numbers of individuals, numbers of types of prey, and evenness) have been calculated with, and without, these invertebrates (Appendices 5a,b,c,d,e). However, perusal of these appendices suggests that Collembola do not seriously bias estimates of prey type diversity, and the comments below apply irrespective of whether these invertebrates are considered as part of the overall pitfall fauna.

Figure 4.3 shows that prey type diversity peaked in summer (November-February), but was usually lowest in winter (June-August) each year. These differences appear to be due to differences in the total numbers of prey captured and the numbers of prey types represented (both of which were higher in summer), rather than to seasonal differences in evenness (Appendix 5). Trends in diversity were broadly similar in the five habitats. Prey type diversity generally decreased from 1978 to 1981 (Fig. 4.2). Inspection of the raw data for invertebrates in each habitat (Appendices 5a,b,c,d,e) suggested that this was probably due to a marked decrease in the numbers of invertebrates captured. The decline in prey abundance and diversity towards the end of the study may have been due to drought.

Comparisons between the enclosures (Appendix 5) show that, for some months, there was statistically significant concordance in the abundance distributions of prey. In every habitat, this was particularly evident in summer, but less so in winter. The lack of concordance at this time may be explained in two ways. First, flooding of the pitfall traps occurred more often in winter than in summer. This presumably washed out already preserved insects, and subsequently rendered the trap inoperative. On other occasions, rainwater diluted the preservative so that trapped insects began to rot. This apparently attracted large numbers of predacious beetles or their larvae. In turn, this greatly reduced the evenness of representation of all prey types, and hence, diversity. Since some pitfall traps were more prone to flooding than others, concordance in the wet winter months was often low. Second, very few prey items were captured in pitfall traps in winter, and this may have unduly influenced the test statistic. If, for example, one pitfall captured 1

beetle, 2 spiders and 3 ants, and a second captured 1 ant, 2 beetles and 3 spiders, there would be little concordance in the ranked abundances of these prey, and the test statistic W would yield a value of only 0.25. It is difficult to be certain that such low numbers represent true differences in prey abundance, or simply chance events. It seems reasonable to suggest that the abundance distributions of prey are concordant between the enclosures for much of the year, but in winter the appropriate statistical evidence is difficult to obtain.

Fig. 4.4 shows the sizes of pitfall trapped prey. In all months, prey less 2.5 mm long predominated, and the overwhelming majority of prey was always less than 7.5 mm long. Most very small prey were Collembola, Hymenoptera (especially Formicoidea) and Diptera, whereas longer prey (≥ 7.5 mm long) were usually Oligochaeta, Amphipoda, Chilopoda, Diplopoda, Dermaptera, Orthoptera and larvae. In all habitats (except perhaps under logs), size diversity was highest in summer and lowest in winter (Fig. 4.3). As with changes in prey type diversity, these differences appear to arise largely from differences in the total numbers of prey captured and the numbers of size classes represented (both of which were higher in summer), rather than from differences in evenness (Appendix 6).

Comparisons between the enclosures (Appendix 6) show that there was statistically significant concordance in prey size distributions in all habitats every month.

4.3.3. Litter sampling

A total of 48330 invertebrate prey items was collected from litter samples. In contrast to the results for pitfall trapping, the most

abundant litter invertebrates were usually larvae and Hymenoptera (especially Formicoidea); only 3513 Collembola were collected, representing just 7% of the total litter fauna (Fig. 4.2 and Appendix 7). Coleoptera, Arachnida (especially Aranea and Pseudoscorpiones) and Hemiptera tended to be well represented throughout the year, but other types of invertebrates appeared to be seasonal or were represented by low numbers (Fig. 4.2).

Changes in the diversity of litter invertebrates are shown in Fig. 4.5, and the components of diversity in Appendix 7. Figure 4.5 shows that the diversity of prey types in litter was relatively constant throughout the year, particularly for samples taken from under logs or from Ribbon Gum litter. In contrast to the findings for pitfall samples (section 4.3.2.), the total numbers of individuals and the numbers of prey types represented from litter were not much lower in winter than in summer. Low diversity values appeared to be associated with low evenness values (Appendix 7): in such samples, a single type of prey (e.g. larvae) usually contributed more individuals to the sample than all others combined.

Comparisons of prey abundance distributions between the enclosures show that there was statistically significant concordance in all sample months in all habitats (Appendix 7).

The sizes of prey in litter samples are shown in Fig. 4.4. Overall, most prey were less than 7.5 mm long, with prey in the 2.5-4.9 mm size class usually predominating (Fig. 4.4). Most of the prey less than 5 mm long were larvae, Collembola, Formicoidea and Arachnida (especially Pseudoscorpiones), but longer prey (≥7.5 mm) were usually Amphipoda, Chilopoda, Diplopoda, Coleoptera and other larvae.

The prey size diversity of litter invertebrates was relatively constant throughout the year in the four habitats from which samples were drawn (Fig. 4.5). The number of prey size classes represented in winter samples (usually 5-8) was lower than in summer samples (usually 6-10), but in contrast to the pitfall trap results, the distribution of individuals in each size class appeared to be more even in winter than in summer (Appendix 8). Unusually low values for prey size diversity (for example in "open habitat" at E4 in February 1980, Appendix 8d) were associated largely with low evenness values.

There were no differences in the prey size distributions in similar habitats between the enclosures, and coefficients of concordance were statistically highly significant in all sample months (Appendix 8).

4.3.4. Casual sampling

The invertebrate fauna under old, residual bark, logs and rocks was present at all times of the year. No attempt was made to quantify seasonal changes in abundance or diversity, but little difficulty was experienced in finding the invertebrates of these habitats at any time. In contrast, the invertebrates of fern fronds and leaves and the creek and its banks appeared to be abundant only in spring and summer. Except for some small spiders (Family Toxopidae) on the undersides of fronds of the Water Fern, it was difficult to find even single specimens of the invertebrates of these habitats in winter. The patterns of abundance of this latter group of invertebrates appeared to be qualitatively similar to the pitfall trap findings, whereas the more constant representation of invertebrates under old, accumulated bark, logs and rocks appeared to be qualitatively more similar to the litter sample findings.

4.3.5. Alternative sources of food, and the dispersion of food

Each species of fruiting plant (Table 4.1) fruited at almost exactly the same time in each enclosure. In all years, Rubus triphyllus fruited from early January to early February, R. fruticosus from early February to mid March, and Coprosma hirtella from mid February to late March. Changes in the dispersion patterns of some invertebrates were correlated with phenological changes in the Water Ferns and Ribbon Gums. The Water Ferns produced young fronds from late September to early December each year, and die back of the fronds occurred between March/April and June. Some types of prey (e.g. Heteroptera, Opiliones, some Aranea and some Coleoptera) were found only on the growing fronds in late spring and early summer, but in winter only toxopid spiders lived among the dead fronds.

Perhaps the most important seasonal change in the dispersion of invertebrate food was associated with the decortication, or peeling, of Ribbon Gum bark. In late winter each year in all enclosures, the grey outer layers of overwintered bark loosened and detached from the soft, creamy wood underneath, and provided an extensive but protected microhabitat for invertebrates. In spring, many types of invertebrates use this microhabitat, possibly having migrated upwards from overwintering haunts in the permanent, old, accumulated bark at the bases of the trees. Some, such as elaterid beetles, some cockroaches (Family Blaberidae), Dermaptera and huntsmen spiders (Family Sparassidae) are flattened dorso-ventrally and apparently specialised for this habitat (Hamilton 1978). Others, such as some Heteroptera nymphs, and many species of beetles and spiders appear to use the bark space opportunistically and are also found elsewhere. In November and December the bark splits and begins to peel (Fig.

4.6a). As peeling continues through January/March each year, the invertebrates that lived under the bark migrate to the old, accumulated bark at the bases of the trees, or to the ground. Large numbers of invertebrates were captured on sticky strips at this time (Fig. 4.6b). In February and March, relatively large numbers of earwigs, weevils and other invertebrates were captured in pitfall traps situated under the trees, and the diversities of types and sizes of prey at this time were correspondingly high (Fig. 4.6c,d). Very few invertebrates were captured on the freshly-peeled trunks of Ribbon Gums (Fig. 4.6b), but some appear to overwinter in the accumulated bark at the bases of the trees (section 4.3.4.).

4.4 DISCUSSION

At the beginning of this chapter it was suggested that food was an important limiting resource for Antechinus. To investigate this suggestion, invertebrates were sampled in each of the enclosures over a period of 3½ years. In general, pitfall-trapped invertebrates peaked in abundance and diversity in summer and declined in winter, whereas sessile invertebrates, buried in the forest litter, were relatively constant throughout the year. Seasonal fluctuations in the abundance of pitfall fauna have been demonstrated by other authors (e.g. Neumann 1978, 1979), but the constancy of the litter fauna was somewhat surprising. Leonard (1976) stated that litter invertebrates peak in winter and decline in summer, but he presented no data to support this assertion. Conversely, in a detailed analysis of the litter and soil fauna of rainforest and tall open-forest in Queensland, Plowman (1979) found that peak invertebrate abundances occurred in summer. In view of the conflicting findings of the present study

with others, the reliability of the present data base will be briefly assessed before further conclusions are drawn.

The major problem in the present study was that systematic sampling for invertebrates was conducted on a small scale. Only five pitfall traps were operated in each enclosure each month, and only four litter samples were taken from each enclosure every three months. Unfortunately, it was not possible to increase the numbers of samples collected or to sample in other parts of the enclosures; over 120 000 invertebrates were collected using a "small scale" sampling programme, and the counting and identification of these specimens alone was an extremely laborious task for this investigator and numerous "volunteers". However, in view of the very high degree of concordance in the type, size and abundance distributions of prey sampled from similar habitats between the enclosures, it seems reasonable to suggest that small scale sampling was sufficient to detect representative portions of the total prey population. In addition, the floristic and structural similarities of each of the enclosures may have limited further the possibility of unevenness of faunal representation, and hence increase confidence in the results.

A second problem in determining the prey available to free-living predators, particularly insectivores, is that the prey live in a very wide range of microhabitats. Although an attempt was made to systematically or casually record some of these prey, many were probably overlooked. (One such example was a transient influx of jewel beetles (Family Buprestidae) on spring-flowering wattles that was noticed only in the final year of the study). However, failure to census transient prey items and other local or ephemeral sources of

food, such as carrion, and nectar and manna from Eucalyptus (Smith 1980), may not be very important, since they probably contribute little to overall trends in food abundance. It seems reasonable to conclude that the sampling methods used in the present study provided at least an index of invertebrate prey, and hence that trends in the levels of food abundance are reliable.

Freely-moving invertebrates, sampled casually and by sticky strips and pitfall traps, were abundant and diverse in summer, but not in winter (see also Braithwaite 1979). In contrast, sessile invertebrates, which were sampled most effectively by sifting forest litter and by looking under logs, rocks and tree bark, were represented quite constantly at all times of the year, with only slight drops in abundance and diversity in winter. Antechinus stuartii appears to be better adapted than A. swainsonii for finding and catching freely-moving invertebrates (e.g. Dermaptera, some Coleoptera, Diptera), and such prey are well represented in its diet (sections 2.5.4.3 and 3.4.33). In contrast, A. swainsonii appears to be better adapted to digging out the sessile invertebrates in forest litter (e.g. larvae, Diplopoda), and these prey are frequently represented in its diet (section 2.5.6.3). Given these findings, it is reasonable to expect that A. stuartii (but not A. swainsonii) faces considerable seasonal fluctuations in the abundance, type and size diversity of its food. Further, in view of the very low numbers of freely-moving invertebrates in winter, and the lack of possible alternative food sources at this time (for example manna (Smith 1980), and fruits (section 4.3.5) it is reasonable to suggest that A. stuartii may be food limited in winter.

Antechinus stuartii does not, of course, have an immutable preference for freely-moving invertebrates, and it is usually considered to be an opportunistic predator (section 2.6, Hall 1980b). This is not surprising: in an environment where food resources fluctuate seasonally, dietary specialisation may be difficult to achieve, and natural selection may instead favour dietary generalism (Fretwell 1972). It is therefore relevant to inquire whether A. stuartii faces a real shortage of food in winter, or whether it is able to take advantage of the more constant source of food in the forest litter. In Chapter 2 this was clearly demonstrated: after A. swainsonii was removed, A. stuartii became more terrestrial (Section 2.5.4.1) and its dietary intake of typical forest litter invertebrates such as larvae and Amphipoda, increased markedly (Section 2.5.4.3). Thus, A. stuartii may indeed be food limited in winter, but the shortage is likely to be more severe in the presence than in the absence of A. swainsonii, since this species apparently denies its smaller congenor access to the litter fauna. In contrast, A. swainsonii does not appear to be food-limited at any time of the year, although juvenile females may nevertheless achieve larger body weights in the absence than in the presence of A. stuartii (Section 2.5.5.7).

These combined findings suggest that food shortage and consequent interspecific competition are most severe in winter. But, the winter decline in invertebrate food may have other, less obvious effects. In the enclosures, A. stuartii usually constructs nests above ground in hollows in Ribbon Gum trees. Until about March each year, mothers and some of their independent young continue to use the same nest, and they sometimes forage together as a loose group (Dickman 1982b). Group foraging presumably benefits individuals

while food resources are relatively abundant and clumped under the bark of trees, but by the time all invertebrates have migrated to the ground at the end of bark peeling, the advantages of foraging in a group would disappear. Thus, with invertebrate food "scattered" on the forest floor, foraging returns are presumably higher for lone individuals than for individuals in groups (Krebs and Davies 1978, but cf. Taylor 1977), and after March, the family "hunting group" breaks up and individuals disperse (Dickman 1982b).

Conceivably, the break-up of the family foraging unit in March could subsequently lead to increased interspecific competition. Since the foraging area traversed in a given time by a group of individuals (one "large predator") will almost certainly be less than that traversed by a much larger number of independent, solitary individuals, the frequency of interspecific contacts after March may increase markedly. If the frequency of such encounters can be taken as a measure of the intensity of competition (see Chapter 3, also Terman 1974, 1978), A. stuartii would then be expected to compete most strongly with A. swainsonii after March and throughout the winter months. Hence, competition for A. stuartii would be exacerbated both by dwindling food resources in winter, and by a change in the dispersion of food from clumped to dispersed.

Communal nesting and foraging, and subsequent break-ups of family groups, evidently occur in populations of A. stuartii that do not inhabit Ribbon Gum forest (Braithwaite 1973, 1979, D.H. King, personal communication). However, bark peeling is a common phenomenon in many other species of Eucalyptus (e.g. Gill 1980, E.W. Pook, personal communication). It would be of great interest to investigate seasonality in the bark fauna of these species using

specialist emergence traps (Glen 1976), and to compare this with demographic and social events in Antechinus. The bark fauna of some eucalypts which do not shed their bark (e.g. E. andrewsii) are relatively constant throughout the year (Lawrie 1974). Conceivably, in forests where all or most of the trees do not shed their bark, demographic and social events in Antechinus are less attuned to shifts in the dispersal of food, and interspecific competition for this resource is less intense.

4.5 SUMMARY

An investigation has been made of the invertebrate fauna of the enclosures used in the Antechinus manipulation experiments. Once a month in each enclosure, invertebrates were sampled in five habitat types by sticky strip trapping and pitfall trapping, and by looking under rocks, logs, tree bark and fern fronds. Every three months, further sampling was conducted in four habitat types by sifting forest soil and litter.

The invertebrates sampled by the pitfall and sticky strip trapping peaked in abundance in summer (December to February) and declined in winter (June to August). Whereas the sticky strips captured mostly flying insects, the pitfall traps captured a wide range of freely-moving, largely terrestrial invertebrates. Forty-six types of invertebrates were obtained during pitfall sampling over 3½ years, but, of the 72,036 individuals captured, 30% were Collembola. Amphipoda and larvae were consistently represented in the pitfall traps throughout the year, but Arachnida, Dermaptera, Hymenoptera, Diptera, Hemiptera and Coleoptera peaked in abundance in spring and summer. In all months, invertebrates less than 2.5 mm long were

most numerous, and relatively few invertebrates exceeded 7.5 mm. The diversity of types and sizes of these prey fluctuated between peaks in summer and troughs in winter. The prey type and prey size distributions were very similar in all habitats between the enclosures.

The invertebrates sampled by sifting the forest soil and litter were relatively constant in abundance throughout the year. Forty types of invertebrates were recognised (four Orders of winged insects, phasmids and turbellaria (flatworms) were absent) and, of the 48,330 individuals captured, the most abundant were larvae and ants. Coleoptera, Arachnida and Hemiptera were well represented throughout the year; other invertebrates were less abundant. Although most litter invertebrates were less than 7.5 mm long, most fell into the 2.5-4.9 mm size class. The diversities of types and sizes of these prey differed little between the enclosures, and were only slightly less in winter than in summer.

Since A. stuartii mostly exploits freely-moving prey, it was suggested that this species may face a shortage of food in winter, and also competition from A. swainsonii in gaining access to the more constant source of food in the forest litter. A break-up in the social structure of the A. stuartii population in March coincides with the dispersal of invertebrates from under the bark of Ribbon Gum trees to the forest floor. After March, and through the winter months, individual A. stuartii probably forage alone on this scattered food; this may increase interspecific encounters, and hence exacerbate interspecific competition.

Taken together, these findings suggest strongly that food may be the resource for which A. stuartii and A. swainsonii compete. A critical test of this suggestion is presented in the next chapter.

Table 4.1. Phenological observations of plant species that may provide food (fruits) for Antechinus, or influence the dispersion of invertebrate food.

Plant species	Observation*	No. of marked individuals per enclosure				
		C1	E1	E2	E3	E4
Eucalyptus viminalis	Decorticating?	12	6	6	6	6
Blechnum nudum	Frond growth? (Spring)	8	8	8	8	8
	Frond death? (Autumn)	8	8	8	8	8
Coprosma hirtella	Fruiting?	5	5	5	5	5
Rubus fruticosus	Fruiting?	4	6	4	4	5
Rubus triphyllus	Fruiting?	3	3	4	4	3

* scored as yes or no for each marked plant each month.

Table 4.2 Comparison of abundance distributions of sticky-trapped invertebrates between a) all enclosures and b) hanging and tree-bark strips in one enclosure.

a)

	1978 and 1979			1980 and 1981		
Sticky strip	W	$\chi^2_{(d.f.)}$	P	W	$\chi^2_{(d.f.)}$	P
Hanging	0.86	$64.4_{(15)}$	<0.001	0.90	$79.6_{(22)}$	<0.001
On rough bark	0.83	$62.5_{(15)}$	<0.001	0.85	$75.0_{(22)}$	<0.001
On smooth bark	0.70	$52.5_{(15)}$	<0.001	0.72	$63.7_{(22)}$	<0.001

b)

Enclosure	W	$\chi^2_{(d.f.)}$	P	W	$\chi^2_{(d.f.)}$	P
C1	0.84	$37.6_{(15)}$	<0.01	-	-	-
E1	0.81	$36.4_{(15)}$	<0.01	0.78	$51.2_{(22)}$	<0.001
E2	0.82	$37.1_{(15)}$	<0.01	0.86	$56.4_{(22)}$	<0.001
E3	0.78	$35.2_{(15)}$	<0.01	0.77	$50.6_{(22)}$	<0.001
E4	0.85	$38.4_{(15)}$	<0.001	0.85	$55.9_{(22)}$	<0.001

Fig. 4.1 Invertebrate abundance on sticky strips. In (a)-(f), solid circles represent the numbers of invertebrates captured in C1. In (a), (c) and (e), open inverted triangles represent the numbers captured in E1, and open upright triangles represent the numbers captured in E2. In (b), (d) and (f), open inverted triangles represent the numbers of invertebrates captured in E3, and open upright triangles the numbers captured in E4.

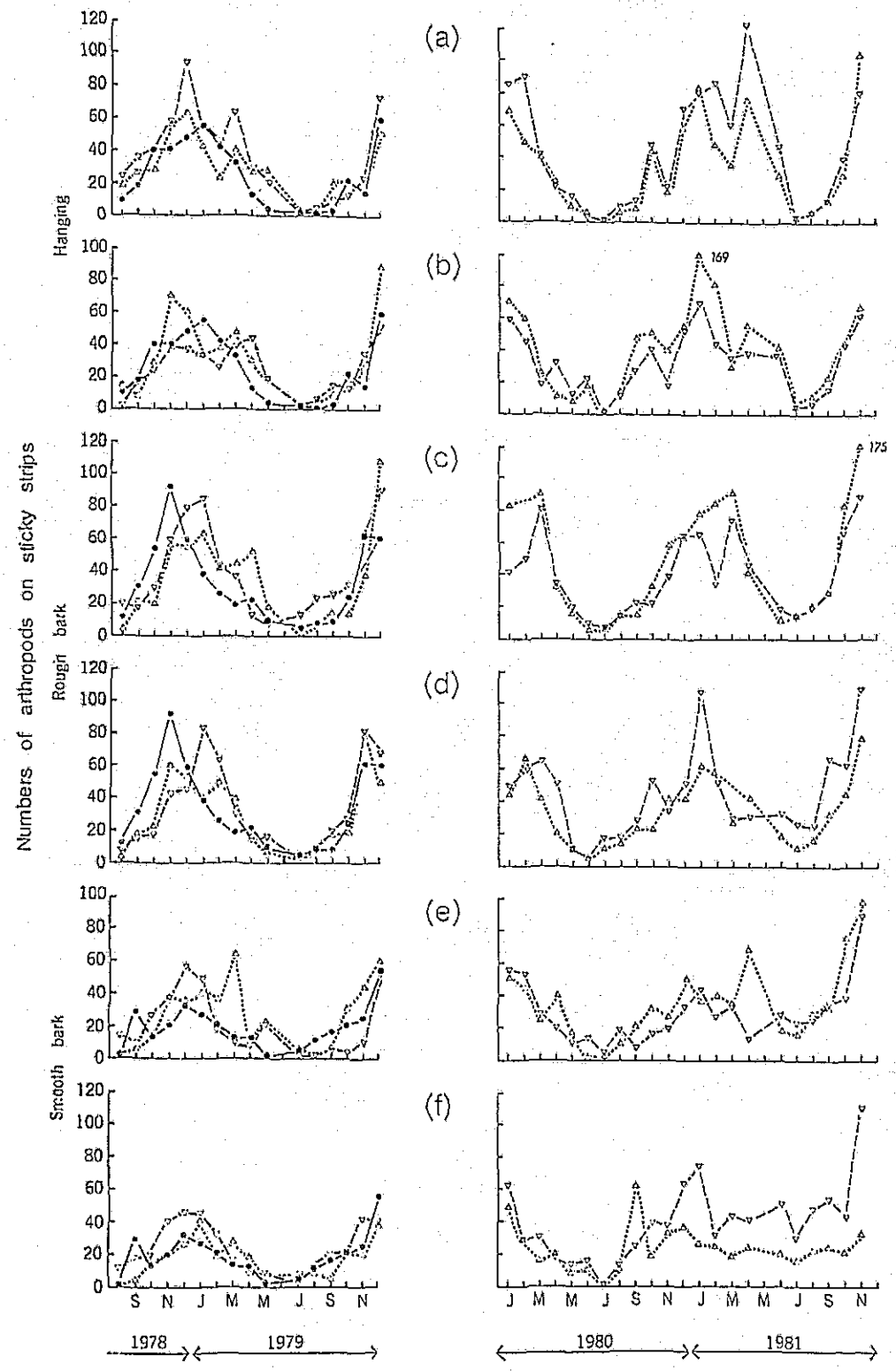

Numbers of arthropods on sticky strips
Hanging
Rough bark
Smooth bark
(a)
(b)
(c)
(d)
(e)
(f)
169
175
S N J M M J S N
J M M J S N J M M J S N
1978
1979
1980
1981

Fig. 4.2 The types of prey in pitfall trap and litter samples in 1979. In the months illustrated, all prey sampled in pitfall traps were combined, as were all prey sampled in the litter. To allow comparison of the graphs, the abundance of each prey type each month has been expressed as a proportion of the most abundant type. Proportions of 0.02 or less are shown by a star.

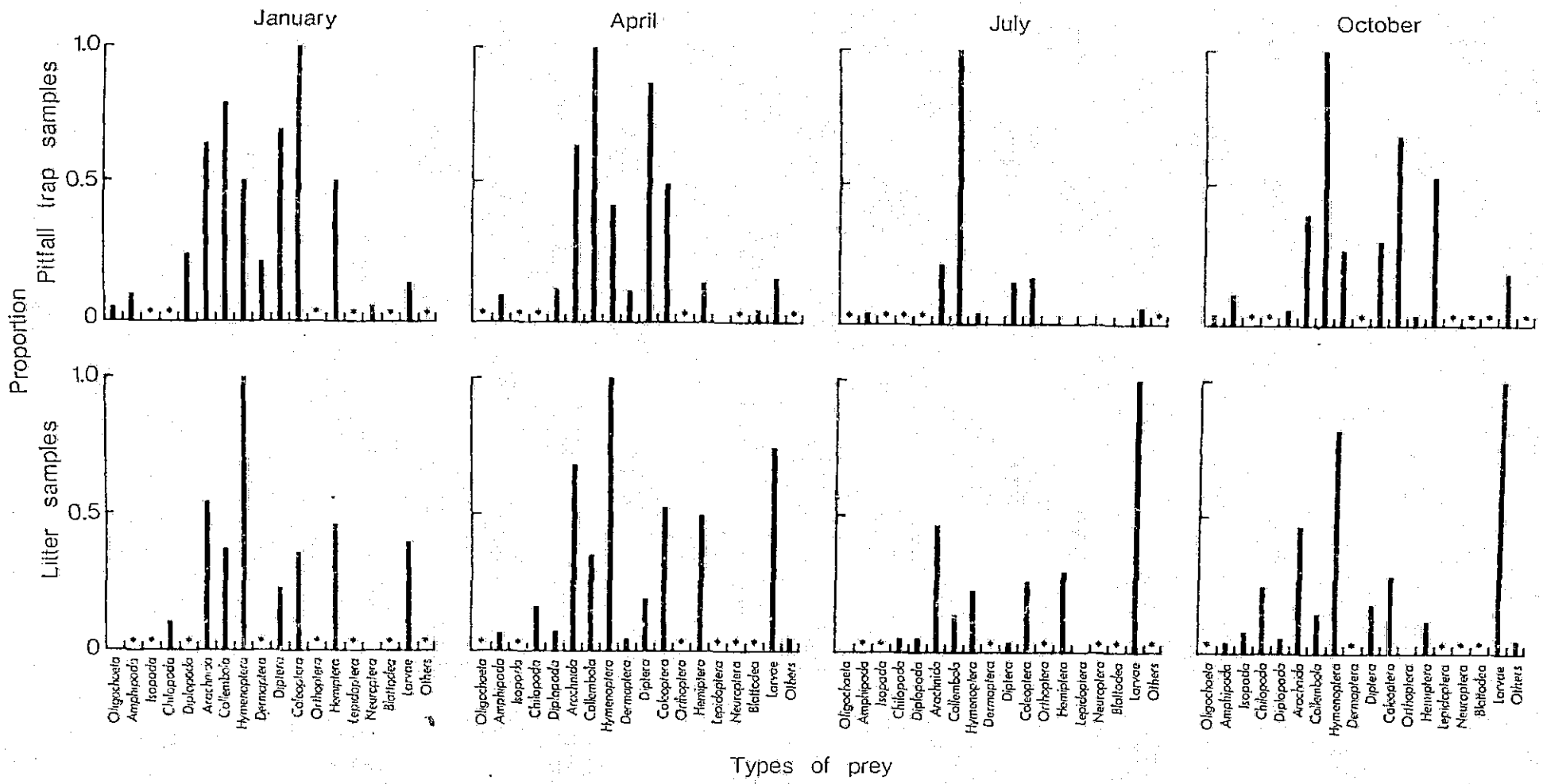

January
April
July
October
Proportion
Pitfall trap samples
Litter samples
1.0
0.5
0
Oligochaeta
Amphipoda
Isopoda
Chilopoda
Diplopoda
Arachnida
Collembola
Hymenoptera
Dermaptera
Diptera
Coleoptera
Orthoptera
Hemiptera
Lepidoptera
Neuroptera
Blattodea
Larvae
Others
Types of prey

Fig. 4.3 The type and size diversity of prey in pitfall trap samples. Solid circles represent average diversity values for pitfall samples from all the enclosures combined, while the bar through the circle represents the range in diversity for the individual pitfall samples. (Detailed data are given in Appendices 5 and 6).

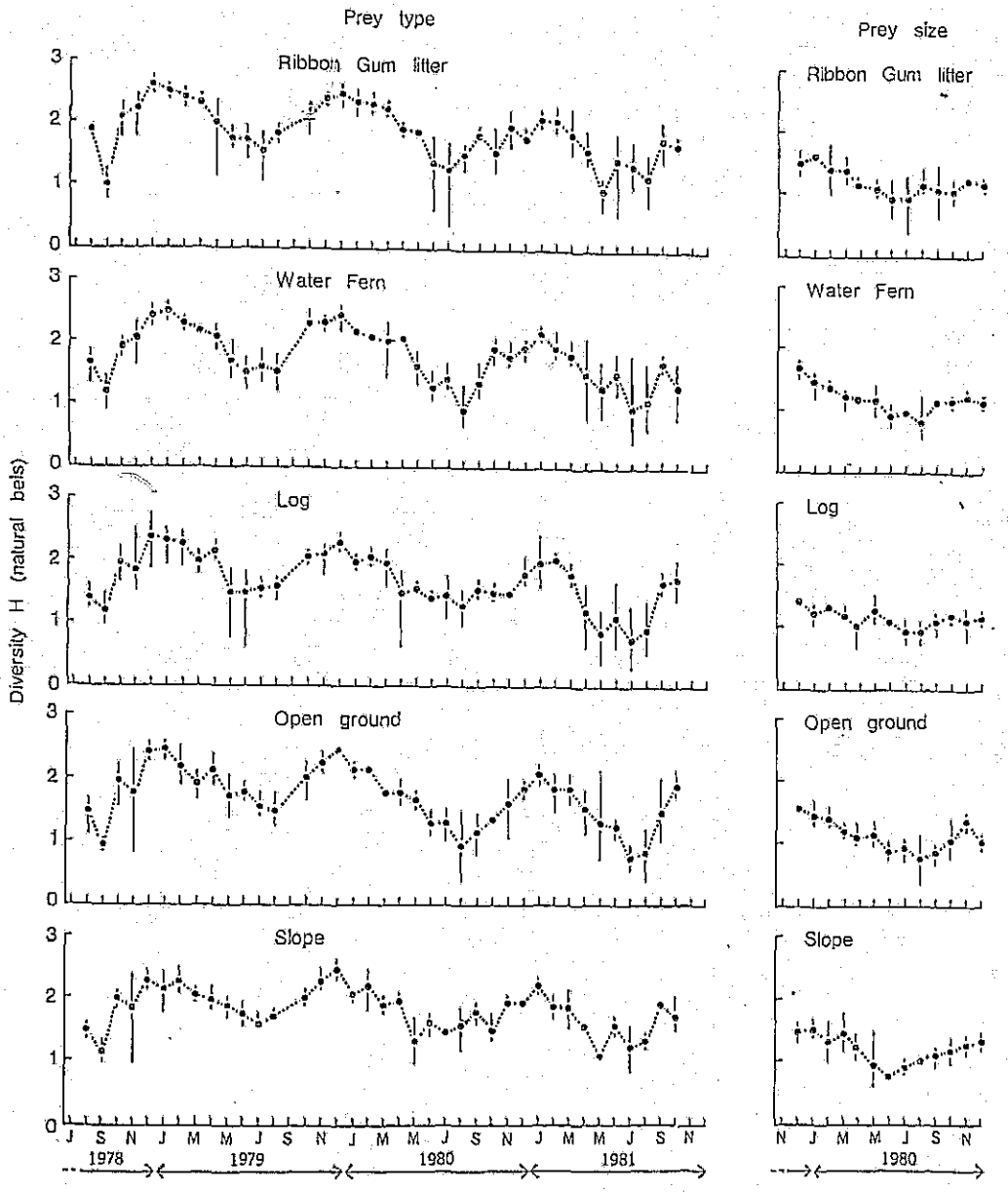

Prey type
Prey size
Ribbon Gum litter
Water Fern
Log
Open ground
Slope
Diversity H (natural bels)
0
1
2
3
J S N J M M J S N J M M J S N J M M J S N
1978
1979
1980
1981
N J M M J S N
1980

Fig. 4.4 The sizes of prey in pitfall trap and litter samples in 1979. In the months illustrated, all prey sampled in pitfall traps were combined, as were all prey sampled in the litter. To allow comparison of the graphs, the abundance of each prey size class each month has been expressed as a proportion of the most abundant size class.

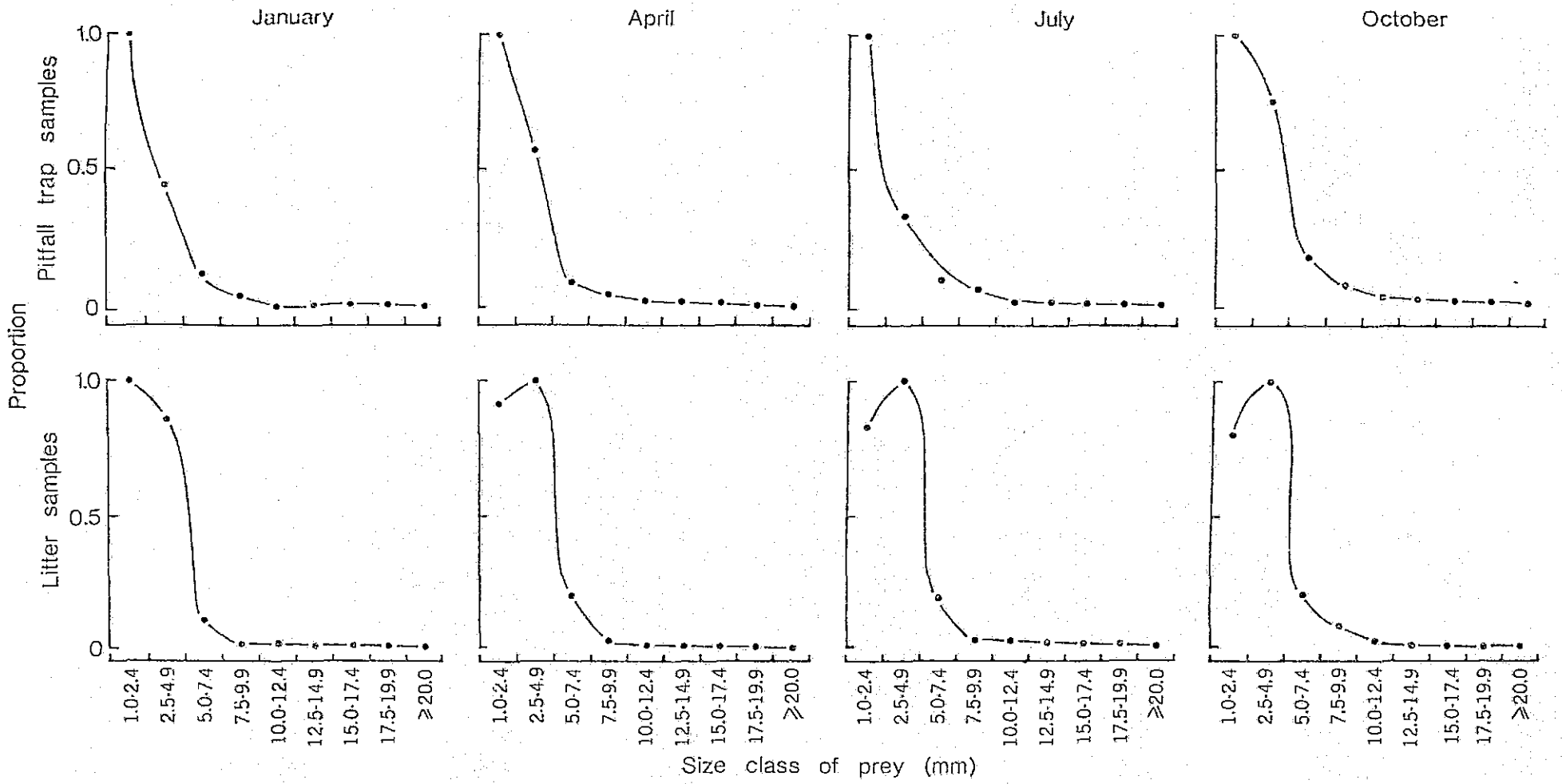
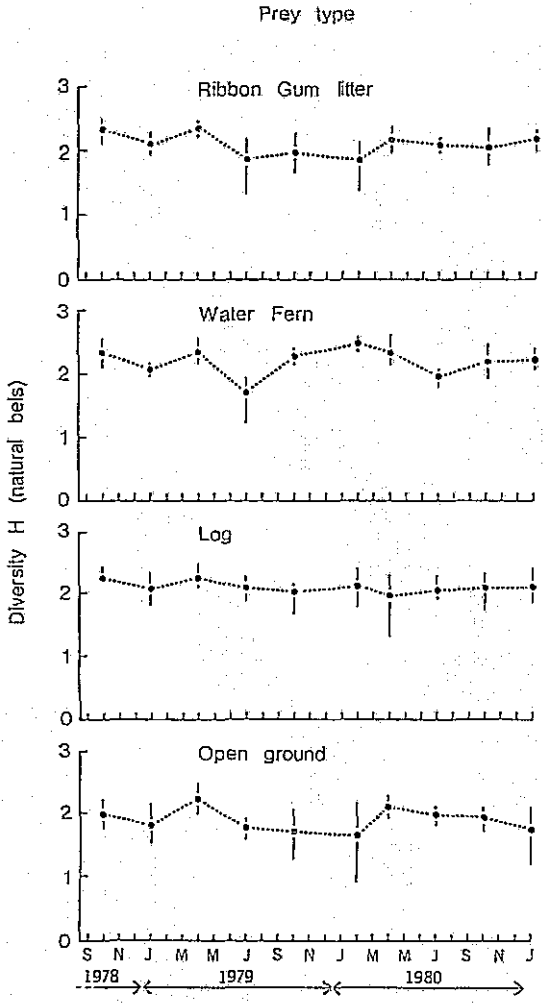

January
April
July
October
Proportion
Pitfall trap samples
Litter samples
1.0
0.5
0
1.0-2.4
2.5-4.9
5.0-7.4
7.5-9.9
10.0-12.4
12.5-14.9
15.0-17.4
17.5-19.9
≥20.0
Size class of prey (mm)

Fig. 4.5 The type and size diversity of prey in litter samples. Solid circles represent average diversity values for litter samples from all the enclosures combined, while the bar through the circle represents the range in diversity for the individual litter samples. (Detailed data are given in Appendices 7 and 8).


Prey type
Ribbon Gum litter
Water Fern
Log
Open ground
Diversity H (natural bels)
0
1
2
3
S N J M M J S N J M M J S N J
1978
1979
1980

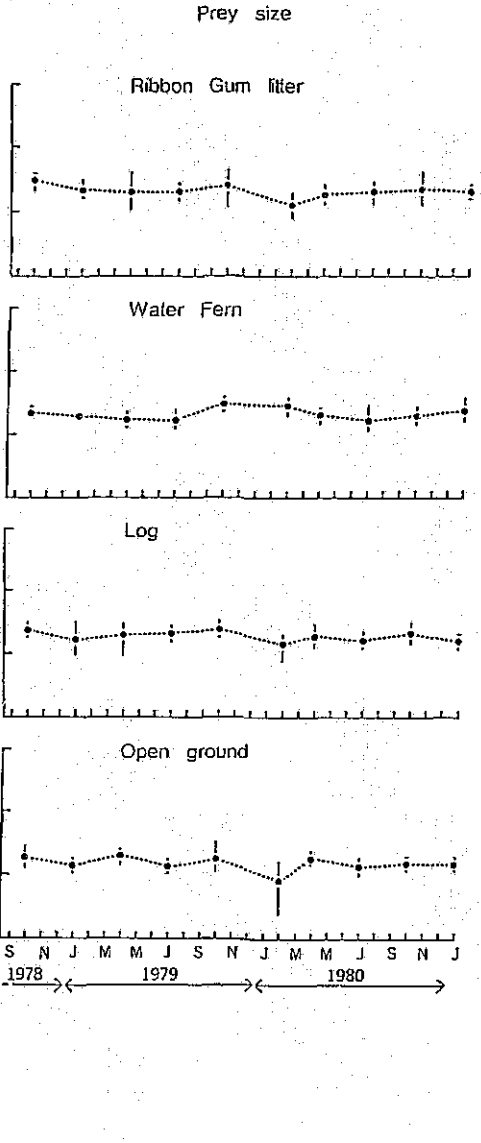

Prey size
Ribbon Gum litter
Water Fern
Log
Open ground
S N J M M J S N J M M J S N J
1978
1979
1980

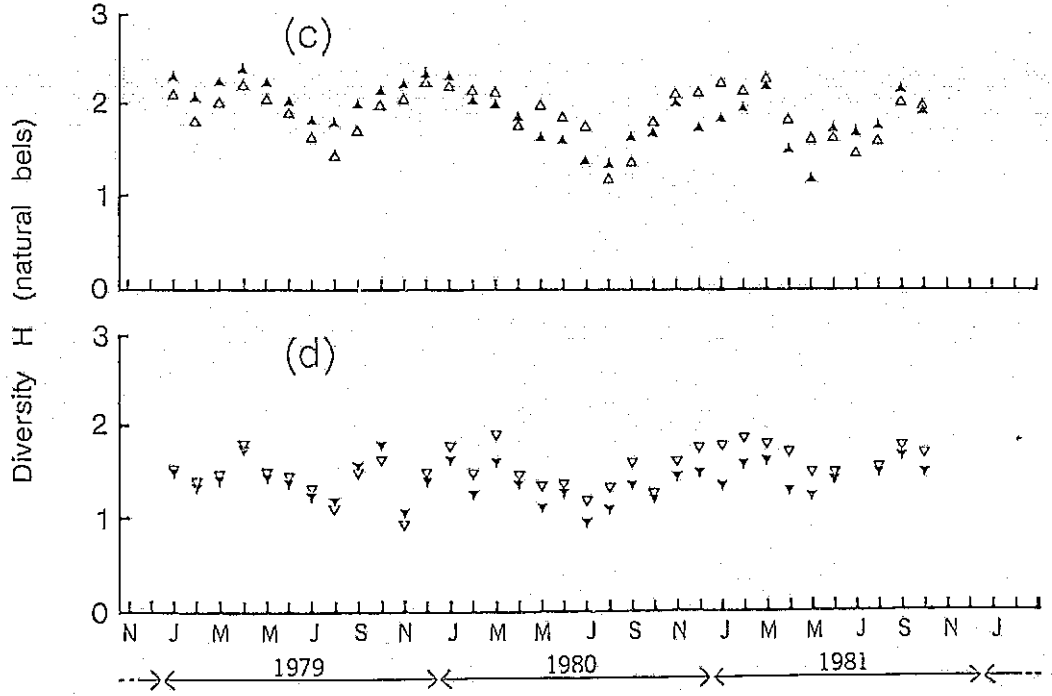
Fig. 4.6 Changes in the invertebrate prey associated with bark peeling in Ribbon Gum trees.

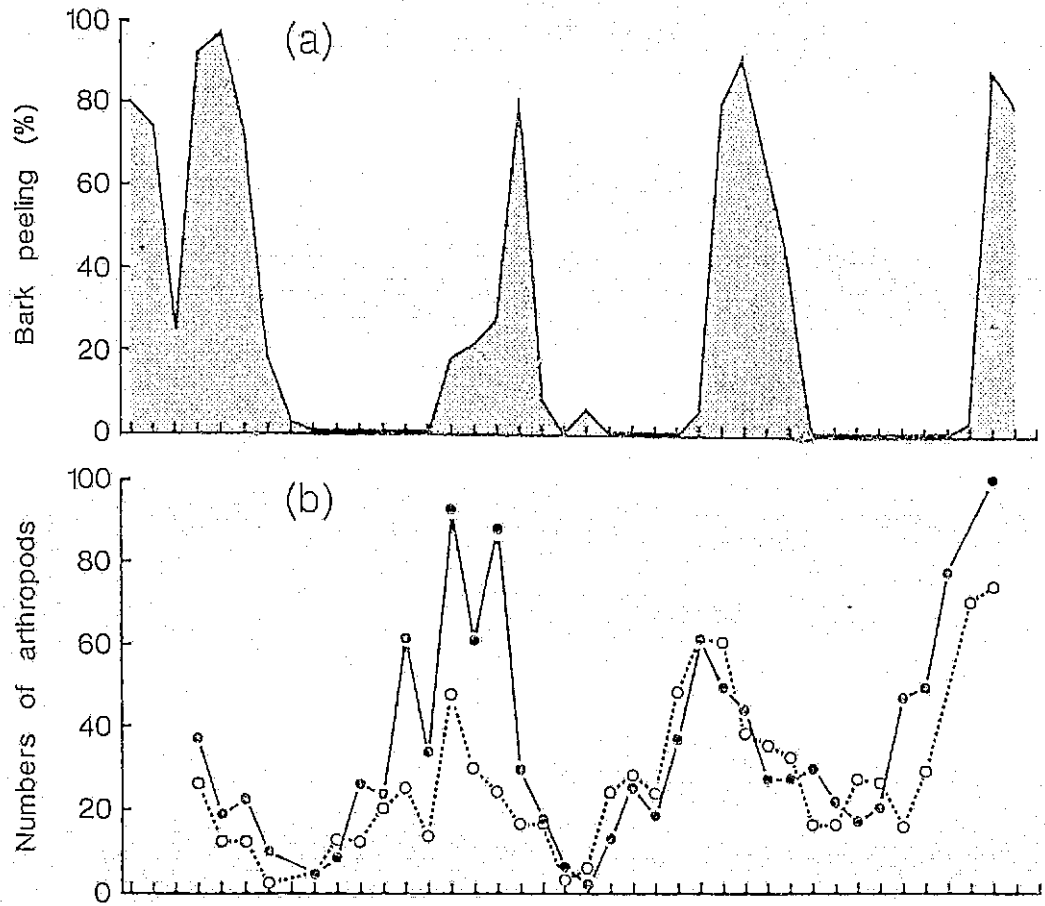
(a) Percentage of trees peeling.

(b) The solid line represents the numbers of invertebrate prey captured on a sticky strip wound around the rough bark at the base of a Ribbon Gum tree; the dotted line represents the numbers captured on a sticky strip wound around the smooth bark higher up (3m) on the same tree.

(c) Diversity of types of prey captured in pitfall traps at the base of a Ribbon Gum tree. Solid triangles represent the total prey diversity, open triangles the diversity with Collembola omitted.

(d) Diversity of size classes of prey captured in pitfall traps at the base of a Ribbon Gum tree. Solid triangles represent the total prey diversity, open triangles the diversity with Collembola omitted.


Diversity H (natural bels)
(c)
(d)
3
2
1
0
N J M M J S N J M M J S N J M M J S N J
1979
1980
1981


(a)
Bark peeling (%)
100
80
60
40
20
0
(b)
Numbers of arthropods
100
80
60
40
20
0

CHAPTER 5

FOOD: THE SCARCE RESOURCE?

5.1 INTRODUCTION

In Chapter 4 it was shown that invertebrates in the forest litter remain relatively constant in abundance and diversity throughout the year, whereas invertebrates that move freely on the surface of the litter and in the trees decline markedly in winter. Antechinus stuartii feeds largely on freely moving invertebrates, and hence is likely to face a seasonal shortage of food. Why doesn't A. stuartii simply broaden its diet and forage in the forest litter? In Chapters 2 and 3 it was suggested that this species is denied access to the relatively abundant litter fauna by A. swainsonii. If A. swainsonii is removed, not only does A. stuartii become less arboreal, but its diet shifts to include more typically terrestrial forest litter fauna such as Amphipoda and larvae.

These findings suggest the hypothesis that the two species of Antechinus compete for food, and further that the effects of such competition are greater on A. stuartii than on A. swainsonii. To test this hypothesis, it was desirable to provide supplementary food to populations of A. stuartii, but not to those of A. swainsonii. If food was not, after all, a scarce resource (the null hypothesis), supplementary food would be expected to have no effect on A. stuartii. If, on the other hand, food was the scarce resource for which competition occurred, supplementary food would be expected to alleviate competition and cause shifts in the population parameters and patterns of resource use of A. stuartii that were similar to those produced when A. swainsonii was removed (sections 2.5.3 and 2.5.4).

This chapter describes an experimental attempt to test the hypothesis that there is competition for food by providing supplementary food only to populations of A. stuartii. Although, as in previous chapters it was considered desirable to conduct experiments on enclosed or semi-enclosed populations, further enclosures could not be found. It was therefore necessary to conduct experiments in similar-sized areas of similar habitat, and to compare population parameters and patterns of resource use between these. Except for food, time (periodicity of activity) and overlaps in home ranges, the resources and population parameters considered in the present chapter are the same as those considered in Chapter 2.

5.2 EXPERIMENTAL DESIGN

Simple experiments designed to investigate the effects of supplementary food on populations of A. stuartii are shown in Fig. 5.1. Each of the rectangles (EXPT. 1, EXPT. 2 and CONTROL) represents a study area containing a population of A. stuartii. (Note that A. swainsonii is also present, although it is extraneous to the simple design described here, for reasons that become apparent below). In the first step, conducted between September and December 1980, populations were trapped to ensure that each contained similar numbers of breeding females and their young. In the second step, conducted between January and May 1981, food was added monthly to A. stuartii populations in two study areas (EXPT. 1 or E1, and EXPT. 2 or E2) but not to those in the third, control study area (C1). If populations of A. stuartii in E1 and E2 exhibited an expansive shift in population parameters or patterns of resource use, but those in C1 did not, it would be reasonable to infer that the added food has produced this effect. In the third step, conducted

between June and November 1981, this inference would be critically tested. Supplementary feeding would be discontinued in E1, and a reciprocal shift in population parameters or patterns of resource use would confirm that shifts in A. stuartii populations were due to manipulations of their food supply.

This design is analogous to that presented in section 2.2, but differs in that falsification of the null hypothesis may imply acceptance of not one alternative hypothesis, but two. The first hypothesis is obviously that supplementary feeding has effects on populations of A. stuartii. The second hypothesis is that supplementary feeding reduces competition with A. swainsonii. This hypothesis cannot be derived from the design of Fig. 5.1 alone, but it follows logically from the findings of Chapter 2. That is, if expansive shifts in the population parameters and patterns of resource use of A. stuartii are caused only by the reduction of competition, and the same or similar effects are produced by adding food, the added food must perforce also serve to reduce competition. If the provision of a scarce resource such as food (Chapter 4) alleviates competition, it is reasonable to conclude further that this is at least one resource for which competition occurs. In this design, it is essential that the numbers of A. swainsonii are not manipulated, because it would be impossible to separate the responses of A. stuartii to this action from their responses to the supplementary food.

5.3 STUDY AREAS[1]

The study areas used in the supplementary feeding experiments occur in localities that had been used previously in source area trapping (section 2.4.1.3). These areas are similar floristically to the enclosures described earlier, but the forest structure and understorey vegetation surrounding the creeks are generally more open. From earlier trapping in 1978 and 1979, it was known that populations of both species of Antechinus occurred mostly along the creeks in these areas. In contrast to the study areas used in the previous experiments (chapters 2 and 3) however, the present study areas were not enclosed, as there were movements into and out of the areas. In addition, densities of the two species in the study areas were relatively low. These areas were among those raided in 1979 (section 2.5.5) and it is possible that the numbers of A. swainsonii, in particular, were still recovering when the programme of supplementary feeding began.

The study areas are each 3.06 ha, and are 850-925 m above sea level. The nearest weather stations are those at Lees and Blundell Creeks; hence rainfall and temperature regimes may be expected to be very similar to those of the enclosures described in Chapter 2.

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[1] Although I have designated the study areas used in the supplementary feeding experiments C1, E1 and E2, it should be remembered that these are not the same as the enclosures that were so designated in earlier chapters. I have used the same terminology only for methodological consistency.

5.4 METHODS

5.4.1 Provision of supplementary food

Because of the practical difficulties of manipulating the abundance of invertebrate prey for A. stuartii, a more readily acceptable form of food had to be found. A simple alternative was the mixture that was used to bait traps throughout this study, since this was eaten by both species of Antechinus with no evident adverse effects. Unfortunately, although the bait contains protein, sugars, carbohydrates and fat (in the peanut butter), it was not known whether the proportions of these components in the mixture were in any way representative of their occurrence in the natural diet. Nor was it known whether A. stuartii was likely to face a shortage of any one component, such as protein, above the others.

To remedy these problems, a dried, proprietary cat food (Harper's Cat Chow) containing added minerals and vitamins was crumbled up and added to the bait mixture. This had two further advantages. It was readily eaten by Antechinus in captivity (personal observations), and, unless moistened, it did not go mouldy for up to five weeks. Approximate proportions (by weight) of the mixture were: oats, 20 parts; honey, 4 parts; peanut butter, 2-2½ parts; cat chow, ½-1 part.

The natural diet of A. stuartii is comprised largely of invertebrates, but also includes plant remains (sections 2.5.4.3 and 3.4.3.3, Statham 1982a) and possibly nectar (Recher 1981). Thus, although the composition and characteristics of bait differ markedly from invertebrate food, the ability of A. stuartii to make opportunistic use of plants and plant derivatives suggested that the bait may be an acceptable dietary supplement.

How much supplementary food should be provided? Because the precise energy content of bait and the particular dietary requirements of A. stuartii were unknown, this question was difficult to answer. However, the energy contents of the bait constituents are known: Honey contains 13.0 kJ g^{-1}, oats 18.5 kJ g^{-1}, peanut butter 24.9 kJ g^{-1}, and cat chow 13.8 kJ g^{-1}, so that 1g of bait mixture contains 18.1 kJ. Statham (1982a), citing unpublished work by I. Hume, stated that the daily net energy requirement for maintenance, growth and some activity of a 35g A. stuartii was 84 kJ, or the equivalent of 4.64g of bait. The digestible energy available in bait is unknown. If, however, a rather conservative guess of 50% digestibility is made, and it is remembered that in the present study A. stuartii averaged body weights of 20-25g, the provision of 6g of bait was probably sufficient to satisfy the daily energy requirements of the average individual.

In the laboratory, it is easy to ensure that 6g of food is available to each individual, but in the field such certain knowledge is difficult to obtain. The numbers and whereabouts of A. stuartii individuals eating supplementary food are seldom precisely known, and information on spoilage and theft by other species is almost completely lacking. In an attempt to address such problems, bait was provided in the field in clean, dry, waterproof 1 litre cardboard cartons. (These were generously donated by the Bega Milk Co-op, Canberra, A.C.T.). Bait was placed at the bottom of each carton, furthest from the entrance hole (3 cm diameter) at the top of the carton. To reduce the chances of visitations by the more terrestrial A. swainsonii and R. fuscipes, cartons were tied with wire about 2m above ground on the trunks or limbs of trees, with the entrance

pointing slightly downwards to prevent entry of rain. Double sided sticky tape was placed around the entrances to the cartons, and loose hairs were later removed from the tapes to check the identities of mammalian species using the bait.

Thirty-two cartons were set out randomly in trees in each of the three study areas, but bait was provided only in those in E1 (until May 1981) and in E2. (The empty cartons in C1 were set out as controls, so that the only difference in treatments between the study areas was the provision of bait). Once a month, one day after grid trapping had finished in E1 and E2, bait was replenished and sticky tapes were changed. The minimum quantity of food (grams) provided each month was calculated by multiplying 6x the MNA for that month for that study area x 30 days. These quantities were then divided by 32 and the resultant weights of food were provided in each carton. Additional food was provided in February (10%), April (30%), May (20%) and June (10%) to offset losses of food to other species.

Evidence that A. stuartii actually ate the supplementary food was obtained in February and April 1981. In these months, one to four days after supplementary food had been replenished, unbaited traps were set at night in sites where I expected A. stuartii to be captured. These were cleared the following morning, and the faecal material of captured individuals was examined for traces of the soft, yellow bait. Such traces were found in individuals captured in both study areas in February (two out of five individuals captured) and in April (two out of nine individuals captured), showing that at least some animals had eaten the supplementary food.

5.4.2. Methods for assessment of population parameters and patterns of resource use.

Live trapping with Elliott type B folding metal traps was used to assess the effects of supplementary feeding on population parameters and use of terrestrial habitat by A. stuartii. In each study area, trap stations were located on a rectangular - shaped grid comprising four lines of 35 traps. Trap stations were 20m apart (± 3m) on the long axes and 15m apart (± 2m) on the short axes of the rectangle. Traps were set and baited as described in section 2.4.1, and left in position for three consecutive days each month. In view of the heavy trapping programme that was still in progress in the enclosures (Chapter 3), I was unable to clear traps more than once daily. No line traps were set. Animals were weighed only at the time of first capture in any month, and no scat material was collected. Animal handling procedures were otherwise the same as those described in section 2.4.2.

To assess the arboreal activity of A. stuartii, 25 hair sampling tubes were attached to tree trunks or branches 2½-4m above ground in each of the three study areas. None was placed at ground level. Sticky tape was replaced at the end of each monthly trapping session, and hairs were identified to species.

Analysis, interpretation and treatment of data were conducted as before (sections 2.4.4., 2.4.5. and 2.4.6.). The following planned comparisons, again stated as null hypotheses, are derived from Fig. 5.1:

	A. stuartii
January-May 1981	H_o: $\mu C1 = \mu$ (E1 and E2)
June-November 1981	H_o: μ (C1 and E1) = μ E2

where μ is the parameter mean of the population.

No null hypothesis is necessary for the period September-December 1980. During this period, trapping was conducted only to ensure that the three study areas contained similar numbers of A. stuartii.

5.5 RESULTS

Between September and December 1980, four parous female A. stuartii were known to be alive in each of the study areas. The numbers of pouch young carried by these females were counted (but not sexed) in October 1980. In C1 there were 36 young (10, 10, 8 and 8), in E1 34 (10, 9, 9 and 6) and in E2 36 (10, 10, 10 and 6). Although no estimates of other population parameters or patterns of resource use were made, these findings suggested that population levels between the study areas were similar. Only the results of food supplementation (January-November 1981) are considered below.

5.5.1 Effects of supplementary feeding on population parameters and patterns of resource use of A. stuartii

5.5.1.1 Population numbers and composition

In all three study areas, numbers were relatively low in January, as juveniles were not readily trapped, and between September and November, when only parous females were present (Fig. 5.2, top; Fig. 5.3). Numbers were highest between March

and May and also in August (Fig. 5.2, top). Between January and April females comprised 63-88% of the populations in each study area, but as the time of mating approached in August, males became relatively more abundant (Fig. 5.3).

Comparisons between enclosures showed that the population in E2 was larger than that in C1 in every month except January. Except in this month and from September to November when sample sizes were small, the population in E2 was never less than 21% larger than that in C1; in July it was 71% larger. The populations in E1 and E2 were similar until May, when supplementary feeding in E1 was discontinued. By June, the population in E1 had declined 48% from its May level, whereas those in C1 and E2 changed by only -6% (C1) and +5% (E2) over the same period (Fig. 5.2, top). Between June and November, the population numbers in C1 and E1 were similar.

Despite the above trends, no statistically significant differences in overall populations sizes, or of the numbers of males and females, were found between the study areas. Taking as an example the 16 individuals known to be alive in C1 in February and May, it is relevant to point out that populations in E1 and E2 would each have to have increased 94% (to 31 individuals) to have been different from C1 at the 5% level of statistical significance. Since only 34 and 36 pouch young were counted respectively in E1 and E2 the previous October, such increases would require exceptionally high survival (86-91%) of the young.

5.5.1.2 Survival

Minimum monthly survival of A. stuartii in the three study areas fluctuated seasonally (Fig. 5.2, middle), but was lowest in August

due to male die-off (Table 5.1). Fluctuations in survival in C1 and E1 between September and November were associated with small sample sizes of females (Table 5.2).

Comparisons between study areas showed that survival was generally greater in E2 than in C1. Survival in E1 was also greater than in C1 until April. In May, however, survival in E1 fell dramatically, and thereafter was generally less than in E2 (Fig. 5.2, middle). Except in August and when sample sizes were small, the survival rates of males and females were generally similar (Tables 5.1 and 5.2). Statistically significant differences in survival were recorded in two months: In April survival in E1 and E2 combined was greater than in C1 ($G_{(1d.f.)} = 3.98$, $P < 0.05$), and in May survival in E1 was less than in C1 and E2 ($G_{(2d.f.)} = 9.36$, $P < 0.01$). Poor survival of females in E1 contributed most to the latter result (for females $G_{(2d.f.)} = 7.72$, $P < 0.05$); there was no statistically significant difference in the survival of males between the study areas.

Of the pouch young known to be alive in October 1980, 56% (20/36) in C1, 74% (25/34) in E1, and 65% (22/34) in E2 were captured as independent juveniles between January and April of the following year. There were no differences in the survival of these young between the study areas ($G_{(2d.f.)} = 2.49$, n.s.).

5.5.1.3 Trappability

Except for the months September to November, when populations were comprised solely of parous females, trappability was never less than 80% (Fig. 5.2, bottom). There were no statistically significant differences in the trappability of males and females prior to

September, and no differences in trappability between the study areas at any time.

5.5.1.4 Reproduction

Because trapping was conducted for only three days a month, precise information on the timing of reproductive events was not obtained. Nevertheless, all males disappeared between the final day of trapping in August (29th) and the first day of trapping in September (18th). In the three study areas, all females gave birth between 20 September and 17 October, and placed young in nests between 22 October and 23 November. From measurements of the crown-rump lengths of the pouch young in October, all births were estimated to have occurred between 20 September and 3 October (unpublished findings). These findings suggested that reproductive events in these study areas occurred synchronously, and also at the same time as equivalent events in the enclosures (see sections 2.5.3.4 and 3.4.2.4). Hence there was no evidence that supplementary food influenced the timing of breeding of A. stuartii.

5.5.1.5 Movements

In C1 and E1, movements of male A. stuartii generally increased from January to August (Fig. 5.4, top). In contrast, movements of females of the 1980 year class and males in E2 were relatively constant throughout the year (Fig. 5.4). Comparisons of movements between the study areas are summarised in Table 5.3 and show that:

1. Between January and March, Av.D. values of males and females were remarkably similar in all study areas. Variances were also very similar, and no statistically significant differences in movements were found.

2. In April and May, Av.D. values for males and females combined were larger in C1 than in E1 and E2.
3. Between June and August, after supplementary feeding was discontinued in E1, movements were greater in this study area and in C1 than in E2. This difference was more evident in females than in males.
4. Between September and November, movements of females were the same in the three study areas.

The findings provided some evidence that supplementary food reduced the movements of A. stuartii. Reduction was greatest during the winter months and was most evident in females.

5.5.1.6 Home range

Home ranges were calculated for three groups of months only; hence detailed seasonal trends in home range size are difficult to find. Nevertheless, between January and May, home ranges of males and females <1 yr and >1 yr old were generally comparable, but between June and August, as the time of mating approached, the home ranges of males were consistently larger than those of females (Table 5.4). There was no evidence that home range sizes in the control or experimental study areas differed at any time (Table 5.4).

5.5.1.7 Body size

Body weight: Mean body weights of male A. stuartii increased from January to August (Fig. 5.5a). Mean body weights of females of the 1980 year class increased from January to March, remained relatively constant until August, and increased to a peak in October when they carried young in their pouches (Fig. 5.5b). Sample sizes

of females of the 1979 year class were small, but their mean body weights generally declined from January until June before increasing again to a peak in September (Fig. 5.5c). What were the effects of providing supplementary food to A. stuartii?

Males. There were no statistically significant differences in the body weights of males before June. However, males were heavier in E2 than in C1 and E1 combined in June (F_p = 15.68, $P < 0.001$) and in August (F_p = 4.45, $P < 0.05$).

Females. The body weights of females <1 yr old (1980 year class) were greater in E1 and E2 than in C1 in March (F_p = 7.82, $P < 0.01$) and in May (F_p = 8.86, $P < 0.01$). However, after supplementary feeding was discontinued in E1 in May, body weights were less in this study area and in C1 than in E2 in July (F_p = 22.62, $P < 0.001$) and in August (F_p = 6.73, $P < 0.05$). Differences in the body weights of females <1 yr and also >1 yr old were observed in other months (Fig. 5.5 b and c) but sample sizes were too small to make statistical comparisons.

Head-body length: The mean head-body lengths of males and females of the 1980 year class increased from January to August, with no prolonged lulls in growth (Fig. 5.6a and b).

The effects of providing supplementary food are summarised as follows:

Males. There were no statistically significant planned differences in the mean head-body lengths of males between the study areas in any month. However, an overall difference was found among means in July (F_o = 9.22, $P < 0.01$), and a posteriori testing showed that the mean for E1 was greater than that for C1 (SNK test, q = 5.93, $P < 0.01$).

Females. Between January and May there were no planned differences in the mean head-body lengths of females between the study areas. However mean head-body lengths in E2 were larger than in C1 and E1 in June (F_p = 15.92, $P < 0.01$) and in August (F_p = 6.55, $P < 0.05$).

These findings show that, in some months, A. stuartii was heavier and longer when provided with supplementary food. These differences tended to be greatest in the winter months.

5.5.1.8 Arboreal habitat

Antechinus stuartii visited arboreal hair sampling tubes in all months in all study areas (Fig. 5.7). Arboreal activity was generally greatest between January and August, when males and females were present, and least between September and November when females alone were present.

The provision of supplementary food appeared to have some effect on the arboreal activity of A. stuartii, but there were no statistically significant monthly differences in the numbers of hair tubes that were visited. (A difference was found in October ($G_{(2d.f.)}$ = 6.95, $P < 0.05$), but this was associated with small sample sizes). There were, however, some interesting trends (Fig. 5.7). Between January and August the numbers of hair sampling tubes visited each month in E2 were equal to or greater than the numbers visited in both C1 and E1; between January and May the difference was significant ($G_{(1d.f.)}$ = 4.05, $P < 0.05$). When supplementary feeding was discontinued in E1 in May, the arboreal activity of A. stuartii in this study area fell by 47% over the next

two months (Fig. 5.7). In July, the reduced arboreal activity was almost, but not quite, significantly less than in E2 ($G_{(1d.f.)} = 3.52$, $P < 0.1$, > 0.05). The numbers of hair sampling tubes visited in E1 increased sharply between July and August, possibly due to increased activity of males before mating. These findings show that A. stuartii was generally more arboreal when provided with supplementary food, and that arboreal activity declined (not quite significantly) when supplementary feeding was discontinued.

5.5.1.9 Terrestrial habitat (structural habitat complexity)

Although a few captures of A. stuartii occurred in open and in very complex habitat, most occurred at sites offering moderate cover (Table 5.5). Unlike the enclosures, the proportional representation of sites of different S.H.C. differed between the study areas ($G_{(28d.f.)} = 43.16$, $P < 0.05$). This was because, in E1, the grid encompassed relatively more open habitat than in either of the other two study areas. However, many traps that were set in open habitat failed to capture Antechinus. When such unsuccessful trap sites were omitted from consideration, no difference was found in the proportions of sites of different S.H.C. ($G_{(28d.f.)} = 34.29$, P n.s.); hence it was also possible to directly compare the frequencies of captures of A. stuartii between the study areas.

Comparisons between the study areas are shown in Table 5.5, and suggest that there was no significant effect of providing supplementary food on the terrestrial habitat used by A. stuartii. There were, however, two other statistically significant comparisons (Table 5.5). Between January and March in each of the study areas,

males and females <1 yr old together tended to use more open habitat than females >1 yr old ($G_{(10d.f.)} = 42.42$, $P < 0.001$). Partitioning G showed that this effect was stronger in C1 ($G_{(10d.f.)} = 25.46$, $P < 0.01$) than in either E1 ($G_{(10d.f.)} = 18.31$, $P = 0.05$) or E2 ($G_{(10d.f.)} = 14.58$, n.s.). Between June and August, there were proportionately more males than females in C1 than in E1 and E2 ($G_{(1d.f.)} = 9.12$, $P < 0.01$).

A summary of the effects of supplementary feeding on A. stuartii is presented in Table 5.6.

5.5.2 The numbers of A. swainsonii

Between January and July, populations of A. swainsonii fluctuated more or less synchronously in each study area, and were comprised of males, females <1 yr old and females >1 yr old. During these months, the maximum number of individuals known to be alive in C1 was 16 (February) and the minimum was 10 (June). The respective maxima and minima in E1 were 12 (February and July) and 8 (June), and in E2 19 (January) and 13 (May). After July, and before juveniles became trappable in November, populations in each study area were comprised of only 1-3 pregnant or parous females.

5.6 DISCUSSION

Food has been implicated as a factor influencing the numbers (Bendell 1959, Smith 1971, Freeland and Winter 1975), reproduction (Symth 1968, Andrzejewski 1975), survival (Watts 1969), distribution (Flowerdew 1976b) and activity patterns (Grodzinski 1962) of natural populations of small mammals, and is probably the ultimate resource

for which competition occurs (Grant 1978). However, providing supplementary food to test hypotheses concerning population dynamics and competition is seldom a simple undertaking, and in the present study, several difficulties were encountered with the practical design of the feeding experiments and the interpretation of results.

Perhaps the most aggravating practical problem was theft of the supplementary food by species other than A. stuartii. Traces of hair from Brushtail Possums (Trichosurus vulpecula) and Ringtail Possums (Pseudocheirus peregrinus), Eastern Pygmy-possums (Cercartetus nanus), Pygmy Gliders (Acrobates pygmaeus), Fluffy Gliders (Petaurus australis) and Greater Gliders (Petauroides volans), as well as from Bush Rats (Rattus fuscipes), were found at the food cartons in both study areas where food was provided. Although no more than 16% of food cartons were visited by these species in any one month, food was also taken by other, less obvious thieves, such as ants.

In addition to theft of the food itself, some species of mammals evidently found the food cartons palatable, and either chewed pieces out of them (allowing rain to enter) or tore them loose from the tree. However, such disturbance was infrequent (no more than 9% of cartons were so affected in any study area in any month), and damaged cartons were replaced monthly when food was replenished.

Overall food losses to theft, spoilage and other disturbances were difficult to assess, but probably did not exceed 25-30% in any study area in any month. However, these estimated losses were partly offset by the provision of additional supplementary food in some months (section 5.4.1), and should not have significantly reduced the overall amount of supplementary food that was available to A.

stuartii. Usually, 10-25% of cartons contained some residual food when food was replenished each month.

A further "problem" with the supplementary feeding experiments may be mentioned. In 1981, population densities of A. stuartii (and A. swainsonii) in the study areas were some 3-4 times less than when trapping began in them in 1978. The decline in density appeared to be due not simply to the earlier removal of animals for the manipulation experiments (Chapter 2) or to the unexpected human interference (section 2.5.5), but also to the general decline in invertebrate food that accompanied the drought in 1981 (Chapter 4). To overcome the problem of low animal densities, the sizes of the study areas and the numbers of traps used were increased to the maximum that I could handle. Even so, the minimum numbers of animals known to be alive were relatively low; consequently differences in population parameters and patterns of resource use between the study areas had to be relatively large to be different at the 5% level of significance.

Notwithstanding these difficulties, it was apparent that supplementary feeding produced some effects that implied reduction of competition, whereas other effects implied initially that competition still occurred. Evidence for reduction of competition was that the numbers and survival of A. stuartii increased when provided with supplementary food (although differences in numbers were not statistically significant), and decreased when supplementary feeding was discontinued. These effects were the same as those produced by the removal of A. swainsonii (sections 2.5.3.1 and 2.5.3.2). Other effects of providing supplementary food to A. stuartii were to increase body size and arboreal activity, and to decrease movements.

These effects were in the opposite direction to those observed when A. swainsonii was removed. In addition, supplementary feeding had no effect on the home ranges or terrestrial habitat use of A. stuartii, whereas manipulations of the numbers of A. swainsonii strongly affected these parameters (sections 2.5.3.6 and 2.5.4.2). To what extent, then, did supplementary feeding alleviate competition?

Because the study areas were not isolated, it is possible that increased numbers in the supplemented areas were due to individuals moving in from surrounding habitats. However, this is unlikely because juvenile A. stuartii, especially females, tend to remain in or near the maternal home range for several months after weaning (Wood 1970, Dickman et al. 1983), that is, until mid March or April in the present study. Hence, movements of individuals into or out of the study areas were unlikely to have been extensive prior to this time, and new individuals probably contributed little to the population peaks that occurred in the study areas in March and April (Fig. 5.2). Between May and July, more new individuals were captured in C1 (nine) and E1 (eleven) than in E2 (five). Hence, even if some or all of these individuals moved into the study areas from outside, clearly the influxes were least in the supplemented areas. Thus it is reasonable to conclude that the increases in numbers in the supplemented study areas were due not to incoming individuals, but to the enhanced survival of residents.

In Chapter 2, the decrease in body weights of A. stuartii after A. swainsonii had been removed was attributed to increased intraspecific interference competition. Such interference occurred mostly after breeding in A. stuartii, when population densities were

unusually high. However, since densities in the present study areas were relatively low, even in the populations receiving supplementary food, strong intraspecific interference was not to be expected. Thus, the increase in body size when provided with supplementary food indicated that A. stuartii was indeed food limited, and further, that the food alleviated competition with A. swainsonii.

Although unexpected, the increases in arboreal activity and decreases in movements of A. stuartii when provided with supplementary food do not invalidate the argument that competition occurs for this resource. Instead, these effects are better explained by one further point. This is that placing food in the trees not only altered the abundance of this resource, but also its dispersion. In Chapter 2, it was suggested that the removal of A. swainsonii allowed A. stuartii access to an additional source of invertebrate food that occurred in the soil and litter layers of the forest. To exploit this food, A. stuartii inevitably had to forage at ground level, causing its ground level movements to increase and its arboreal activity to decrease. In contrast, since supplementary food was available only in trees in the present experiments, the decrease in ground level movements and increase in arboreal activity of A. stuartii in the supplemented areas were probably a direct consequence of its exploitation of this resource. Although with hindsight supplementary food should not have been placed only in trees, when the experiment began the difficulties of providing it at ground level and safeguarding it from raids by rats, A. swainsonii, ants and lizards appeared to be of greatest importance. Thus, although the responses of A. stuartii to the supplementary food were different from those that were initially expected, the results nevertheless suggest that this species took

advantage of the food, and so reduced competition with its larger congenor.

Closer inspection of the results revealed two trends that support this conclusion. First, the effects of providing supplementary food were generally most obvious in winter. Differences in the numbers of A. stuartii between the supplemented and non-supplemented study areas tended to be greatest in winter (Fig. 5.2), and statistically significant differences in movements between the study areas occurred only between April and August (Table 5.3). In addition, body weight differences occurred only after February, and were generally most pronounced between June and August (Fig. 5.5). Since supplementary feeding was most effective in winter when interspecific competition was probably most intense, this again suggests that food is the object of competition.

The second trend was that juvenile females responded to the provision of supplementary food more strongly than either males or parous females. Juvenile female survival declined sharply in E1 when supplementary feeding was discontinued there in May, and the reduction in female movements in E2 between June and August was more pronounced than the corresponding decrease in the movements of males. Supplementary feeding also had more consistent effects on the body weights of juvenile females than males, and statistically significant planned differences in head-body lengths between the study areas were found only among females. Since juvenile females generally responded more strongly than males or parous females to the reduction of interspecific competition (Chapters 2 and 3), and since they also responded most strongly to the provision of supplementary food, food is again implicated as the scarce resource for which competition occurs.

One final point may influence the interpretation of results in this chapter, and this is the possible action of interspecific interference competition. Interference effects can occur irrespective of whether resources are actually limiting (section 1.1.1.), so that if A. swainsonii "interfered" with A. stuartii at ground level, provision of supplementary food would not be expected to alleviate all the effects of competition. Unfortunately, the supplementary feeding experiments were not designed to accommodate possible interference effects, as I did not, at the time, appreciate the possible consequences of this form of competition. (A partial assessment of interference effects could have been made by providing A. stuartii with supplementary food and then manipulating the numbers of A. swainsonii, but such extensive additional experiments were beyond the scope of the project). Although interference complicates the issue, it does not outweigh the positive evidence that supplementary feeding reduced interspecific competition on A. stuartii, and hence does not seriously challenge the conclusion that food is an object of competition. The subject of interference competition is discussed further in Chapter 6.

5.7 SUMMARY

This chapter describes an experimental attempt to test the hypothesis that A. stuartii and A. swainsonii compete for food. Three study areas were established in September 1980, and trapped until December of that year to ensure that each contained similar numbers of both species. Because it was expected that A. stuartii would suffer more than A. swainsonii when food was short, supplementary food was provided to populations of this species in two study areas, but not to the population in the third, control, study

area. The supplementary food was a mixture of oats, honey, peanut butter and proprietary dried cat chow, placed in cartons in trees so that it was available only to A. stuartii. It was reasoned that, if food was indeed the resource for which competition occurred, its provision would alleviate competition and hence produce shifts in the population parameters and patterns of resource use of A. stuartii that were similar to those produced by the removal of A. swainsonii (Chapter 2).

Supplementary feeding produced two effects that suggested alleviation of competition: an increase in numbers of A. stuartii (albeit not a statistically significant increase) and an increase in survival. The body weights and body lengths of A. stuartii also increased in some months. However, supplementary feeding also produced increases in the arboreal activity and decreases in the ground level movements of A. stuartii that were opposite to the effects produced by the removal of A. swainsonii, and it had no effect on home range sizes or terrestrial habitat use. These unexpected findings were probably due to the placement of supplementary food in trees and perhaps also to interference from A. swainsonii; however, they were not considered sufficient to warrant rejection of the food competition hypothesis. Two further trends supported the hypothesis. First, the effect of providing supplementary food was greatest in winter when A. stuartii is most likely to suffer competition for food; second, juvenile females, which responded more strongly than males or parous females to the removal of A. swainsonii, also responded most strongly to the provision of supplementary food.

The discussion described some of the difficulties of conducting supplementary feeding experiments, and concluded with an appraisal of the problems caused by possible interference competition. This subject is considered further in Chapter 6.

Table 5.1 Minimum sessional survival (%) of male Antechinus stuartii. Sample sizes are shown in brackets.

	C1	E1	E2
	Food added to E1 and E2		
Jan.	100(2)	100(2)	0(1)
Feb.	75(4)	67(3)	83(6)
Mar.	60(5)	89(9)	75(8)
Apr.	60(5)	88(8)	100(9)
May	71(7)	60(10)	89(9)
	Food added to E2, discontinued to E1		
Jun.	75(8)	83(6)	91(11)
Jul.	75(8)	89(9)	82(11)
Aug.	0(12)	0(11)	0(14)

Table 5.2 Minimum sessional survival (%) of female Antechinus stuartii. Sample sizes are shown in brackets.

	C1		E1		E2	
	<1 yr	>1 yr	<1 yr	>1 yr	<1 yr	>1 yr
			Food added to E1 and E2			
Jan.	75(4)	75(4)	100(1)	100(3)	100(3)	100(4)
Feb.	78(9)	100(3)	100(5)	67(3)	100(8)	75(4)
Mar.	91(11)	33(3)	87(15)	100(2)	92(12)	100(3)
Apr.	73(11)	50(2)	92(13)	100(2)	100(12)	33(3)
May	75(8)	100(1)	46(13)	50(2)	92(12)	100(1)
			Food added to E2, discontinued to E1			
Jun.	83(6)	100(1)	83(6)	100(1)	100(11)	100(1)
Jul.	80(5)	100(1)	75(8)	0(1)	100(11)	100(2)
Aug.	40(5)	0(1)	78(9)	-(0)	58(12)	50(2)
Sep.	-(0)	100(2)	-(0)	63(8)	-(0)	88(8)
Oct.	-(0)	50(2)	-(0)	80(5)	-(0)	100(7)
Nov.	-(0)	100(2)	-(0)	75(4)	-(0)	100(7)

Table 5.3. Movements of Antechinus stuartii. Values are mean average distances moved (m) ± standard deviation. Sample sizes are in brackets.

		C1	E1	E2	F_o	F_p	Conclusion
		Food added to E1 and E2					
	♂	35.0±17.4 (9)	37.2±17.1 (11)	44.6±17.0 (13)	0.99	0.86	C1 E1 E2
Jan.-March	♀<1yr	33.7±18.8 (19)	37.7±21.1 (18)	41.4±26.2 (21)	0.58	0.89	C1 E1 E2
	♀>1yr	50.8±20.7 (9)	38.1±16.2 (8)	44.5±22.3 (11)	0.83	1.20	C1 E1 E2
	♂+♀	38.2±19.8 (37)	37.6±18.5 (37)	43.1±22.5 (45)	0.89	0.36	C1 E1 E2
	♂	52.4±18.8 (10)	38.1±20.9 (17)	38.8±18.3 (17)	2.01	4.00	C1 E1 E2
April-May	♀<1yr	46.1±24.0 (14)	37.5±21.9 (22)	32.8±14.0 (23)	1.97	3.31	C1 E1 E2
	♀>1yr	36.7±10.4 (3)	41.0±18.5 (4)	42.3±13.6 (4)	0.13	0.24	C1 E1 E2
	♂+♀	47.4±21.1 (27)	38.0±20.8 (43)	35.9±15.8 (44)	3.19*	6.12*	C1 E1 E2
		Food added to E2, discontinued to E1					
	♂	63.0±35.7 (29)	56.6±26.6 (24)	46.6±33.3 (34)	2.04	3.58	C1 E1 E2
June-Aug.	♀	45.6±14.6 (21)	43.1±18.0 (27)	33.7±21.4 (46)	3.62*	7.03**	C1 E1 E2
	♂+♀	55.7±29.9 (50)	49.4±23.2 (51)	39.2±27.7 (80)	6.06**	10.79**	C1 E1 E2
Sept.-Nov.	♀	39.5±13.8 (6)	33.7±13.6 (15)	35.7±18.7 (17)	0.28	0.01	C1 E1 E2

For January-May, females <1yr and >1yr old are considered separately; for other months they are considered together.

Table 5.4. Home ranges of Antechinus stuartii. Values are mean minimum areas (m^2) ± standard deviation. Sample sizes are in brackets.

		C1	E1	E2	F_o	F_p	Conclusion
		Food added to E1 and E2					
	♂	2475±1227 (5)	2206±1318 (7)	1917±715 (6)	0.34	0.46	C1 E1 E2
Jan.-May	♀<1yr	1862±726 (7)	2355±1668 (10)	2078±1361 (9)	0.28	0.36	C1 E1 E2
	♀>1yr	2428±838 (3)	1883±870 (2)	1890±925 (3)	0.35	0.71	C1 E1 E2
	♂+♀	2180±922 (15)	2250±1426 (19)	1993±1063 (18)	0.23	0.02	C1 E1 E2
		Food added to E2, discontinued to E1					
	♂	2511±953 (5)	2209±605 (5)	3289±1377 (6)	1.54	2.89	C1 E1 E2
June-Aug.	♀	2028±466 (5)	1830±524 (5)	1906±913 (11)	0.09	0.00	C1 E1 E2
	♂+♀	2269±751 (10)	2020±560 (10)	2394±1256 (17)	0.45	0.58	C1 E1 E2
Sept.-Nov.	♀	1714±267 (2)	2251±686 (4)	2597±1146 (5)	0.68	0.89	C1 E1 E2

For January-May, females <1yr and >1yr old are considered separately; for other months they are considered together.

Table 5.5. Frequency of capture of Antechinus stuartii at sites of different structural habitat complexity (S.H.C.). The number of captures (N), mean S.H.C. ($\bar{x}$) and standard deviation (s.d.) are given.

January-March

sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
♂	(2)	2	5	1	6	2	5	2	1	0	1	27	7.11	2.50
C1 ♀<1yr	(3)	6	2	9	14	10	2	3	2	1	0	52	6.87	2.08
♀>1yr	0	0	3	4	3	0	3	6	4	1	1	25	8.64	2.41
♂	0	4	2	3	7	7	4	1	2	1	0	31	7.39	2.09
E1 ♀<1yr	(1)	5	4	7	11	13	5	2	2	1	0	51	7.16	1.95
♀>1yr	0	1	0	2	4	1	3	4	3	1	1	20	8.85	2.30
♂	1	0	5	7	6	9	3	1	1	1	0	34	7.18	1.85
E2 ♀<1yr	(2)	3	8	8	11	10	4	6	3	1	0	56	7.21	2.13
♀>1yr	(1)	1	2	4	4	3	3	7	2	0	(2)	29	8.21	2.51

Summary[1]

SHC x A x S,	G_o (84d.f.) = 101.88
SHC x A,	G_o^o (20d.f.) = 17.07
C1 vs (E1 + E2),	G_o^o (10d.f.) = 4.99 ***
SHC x S,	G_o^p (20d.f.) = 49.41
A x S,	G_o^o (4d.f.) = 1.17

April-May

sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
♂	0	2	0	2	5	5	6	4	2	1	0	27	8.26	1.95
C1 ♀<1yr	(2)	0	1	6	9	8	5	2	3	3	1	40	8.03	2.29
♀>1yr	0	1	0	0	2	2	1	0	1	1	0	8	8.25	2.49
♂	0	0	1	1	9	16	8	3	2	1	2	43	8.47	1.67
E1 ♀<1yr	1	4	2	8	7	17	13	7	0	0	4	63	7.95	2.15
♀>1yr	0	0	2	1	0	0	1	1	3	2	0	10	9.20	2.82
♂	(2)	2	4	2	8	10	10	1	5	1	(1)	46	7.87	2.28
E2 ♀<1yr	3	3	7	6	11	9	8	8	1	2	0	58	7.38	2.22
♀>1yr	0	1	1	1	0	2	0	3	0	0	2	10	8.70	3.09

Summary[1]

SHC x A x S,	G_o (52d.f.) = 60.93
SHC x A,	G_o^o (20d.f.) = 22.30
C1 vs (E1 + E2),	G_o^o (10d.f.) = 11.48
SHC x S,	G_o^p (10d.f.) = 13.75
A x S,	G_o^o (2d.f.) = 0.44

Table 5.5 (cont'd.)

June-August

sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
♂	3	9	4	4	9	17	13	16	3	1	(3)	82	7.91	2.42
C1 ♀<1yr	1	0	4	2	6	8	9	6	4	2	1	43	8.44	2.14
♀>1yr	0	0	1	1	0	2	6	0	0	1	0	11	8.45	1.81
♂	(1)	5	6	9	14	14	6	7	4	2	2	70	7.64	2.26
E1 ♀<1yr	(2)	4	4	6	12	21	10	7	1	6	(1)	74	7.92	2.20
♀>1yr	0	0	0	0	0	1	2	0	0	0	(2)	5	10.40	2.41
♂	(5)	6	3	11	19	16	13	7	4	7	1	92	7.71	2.38
E2 ♀<1yr	3	5	10	8	13	13	18	14	12	4	(4)	104	8.23	2.47
♀>1yr	0	1	0	1	2	2	2	3	0	2	1	14	8.93	2.50

Summary[1]		
	SHC x A x S,	G_o (52d.f.) = 65.44
	SHC x A,	G_o^o (20d.f.) = 21.29
	(C1 + E1) vs E2,	G_o^o (10d.f.) = 8.64
	SHC x S,	G_p^o (10d.f.) = 12.75**
	A x S,	G_o^o (2d.f.) = 9.42

September-November

sex/age class	Structural habitat complexity 3	4	5	6	7	8	9	10	11	12	13	N	$\bar{x}$	s.d.
C1 ♀	0	1	2	1	0	4	4	1	0	1	1	15	8.20	2.48
E1 ♀	0	0	2	1	4	9	6	7	4	2	(2)	37	9.03	1.96
E2 ♀	0	2	2	0	4	8	13	10	2	4	3	48	9.08	2.10

Summary[1]		
	SHC x A (or S)	G_o (18d.f.) = 17.25
	(C1 + E1) vs E2,	G_p^o (9d.f.) = 6.27

[1] The G statistic was used to test the joint independence of S.H.C., sex/age class (S) and study area (A). If dependence was found, G was partitioned to examine which pairs of criteria were associated. A few captures occurred in S.H.C. categories 1, 2, 14 and 15. These were grouped with captures in category 3 or 13 and are shown in brackets. (Category 3 was omitted from calculations of G in the period September-November). For January-March, females <1 yr and >1 yr old were considered separately in G tests; for other months they were considered together.

Table 5.6 Summary of the effects of supplementary feeding and its discontinuation on the population parameters and resource use of A. stuartii.

	Effects of providing supplementary food			Effects of discontinuing supplementary food		
	♂	♀	Both	♂	♀	Both
Population parameters						
Numbers	-	-	-	-	-	-
Survival	-	-	√	-	√	√
Trappability	-	-	-	-	-	-
Reproduction	-	-	-	-	-	-
Movements	-	-	√	-	√	√
Home range	-	-	-	-	-	-
Body weight	-	√		√	√	
Body length	-	-		√*	√	
Resources						
Habitat (arboreal)			√			-
Habitat (terrestrial)	-	-	-	-	-	-

√ denotes that effects occurred in some sampling sessions; - that no statistically significant effects detected at any time. Effects were detected by planned comparisons (supplemented versus non-supplemented), except where marked *.

Fig. 5.1. Experiments designed to investigate the effects of supplementary feeding and competition on A. stuartii (A. st). All steps are described in detail in the text. Rectangles (EXPT. 1 and EXPT. 2 and CONTROL) represent study areas. Solid arrows represent an expansive shift in population parameters or patterns of resource use in A. stuartii in response to supplementary feeding, the broken arrow a return shift when supplementary feeding is discontinued. Between September and December 1980 (rectangles drawn with broken lines), the population numbers of A. stuartii and A. swainsonii (A. sw) were monitored. The effects of providing supplementary food were assessed by comparing populations in the three study areas in the periods January to May 1981 and June to November 1981 (rectangles drawn with solid lines).

EXPT. 1

September-December
1980

A. st

A. sw

January-May
1981

A. st

A. sw

Food added

June-November
1981

A. st

A. sw

No food added

EXPT. 2	CONTROL
A. st A. sw	A. st A. sw
A. st  A. sw Food added	A. st A. sw (No food added)
A. st  A. sw Food added	A. st A. sw (No food added)

Fig. 5.2. Population parameters of A. stuartii in three study areas. Top, minimum numbers known to be alive; middle, minimum sessional survival of individuals known to be alive; bottom, trappability of individuals known to be alive.

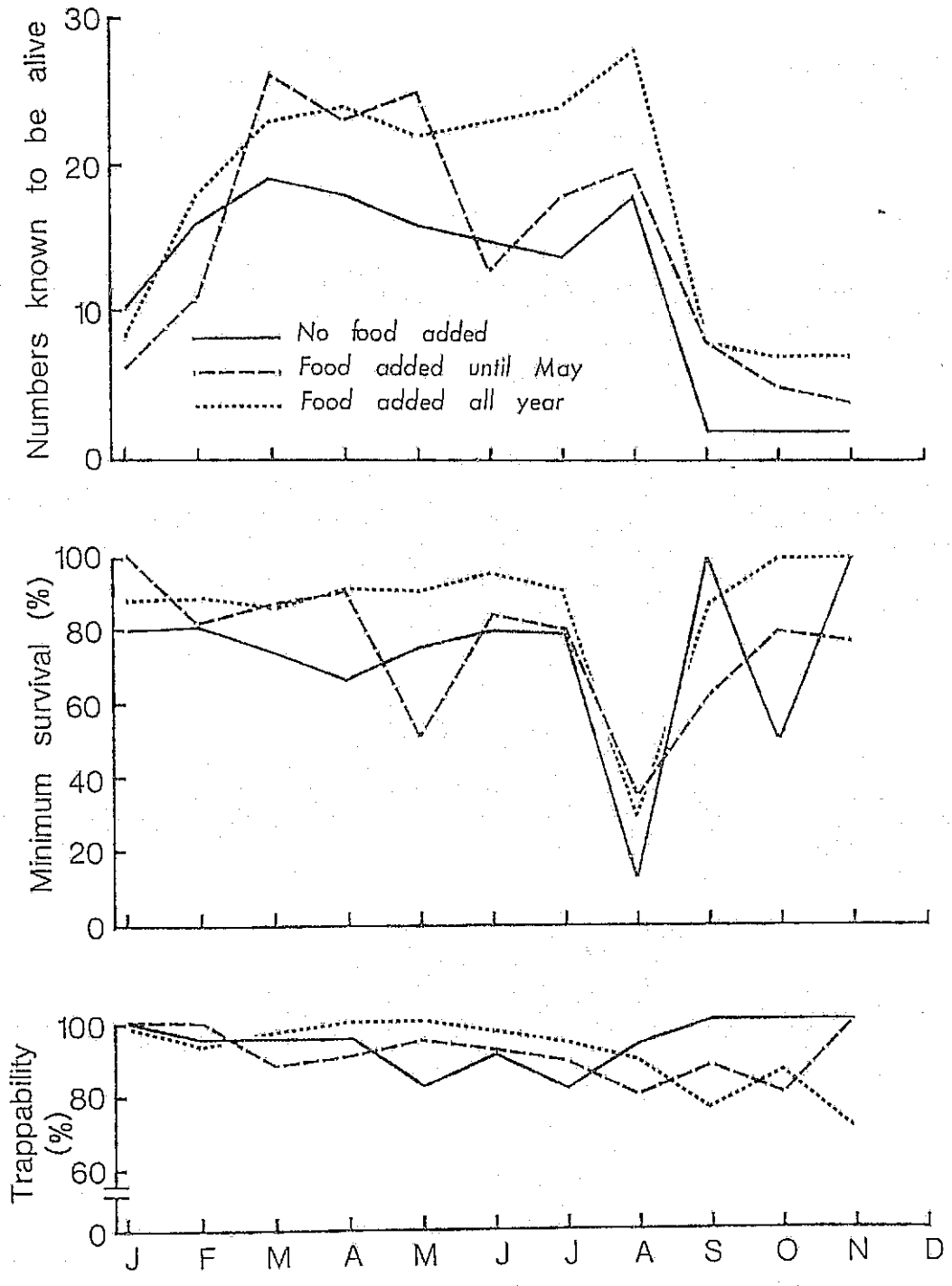

Numbers known to be alive
30
20
10
0
No food added
Food added until May
Food added all year
Minimum survival (%)
100
80
60
40
20
0
Trappability (%)
100
80
60
0
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.3. Population composition of A. stuartii in three study areas. Different female year classes are represented by solid and stippled shading, the male (1980) year class by no shading.

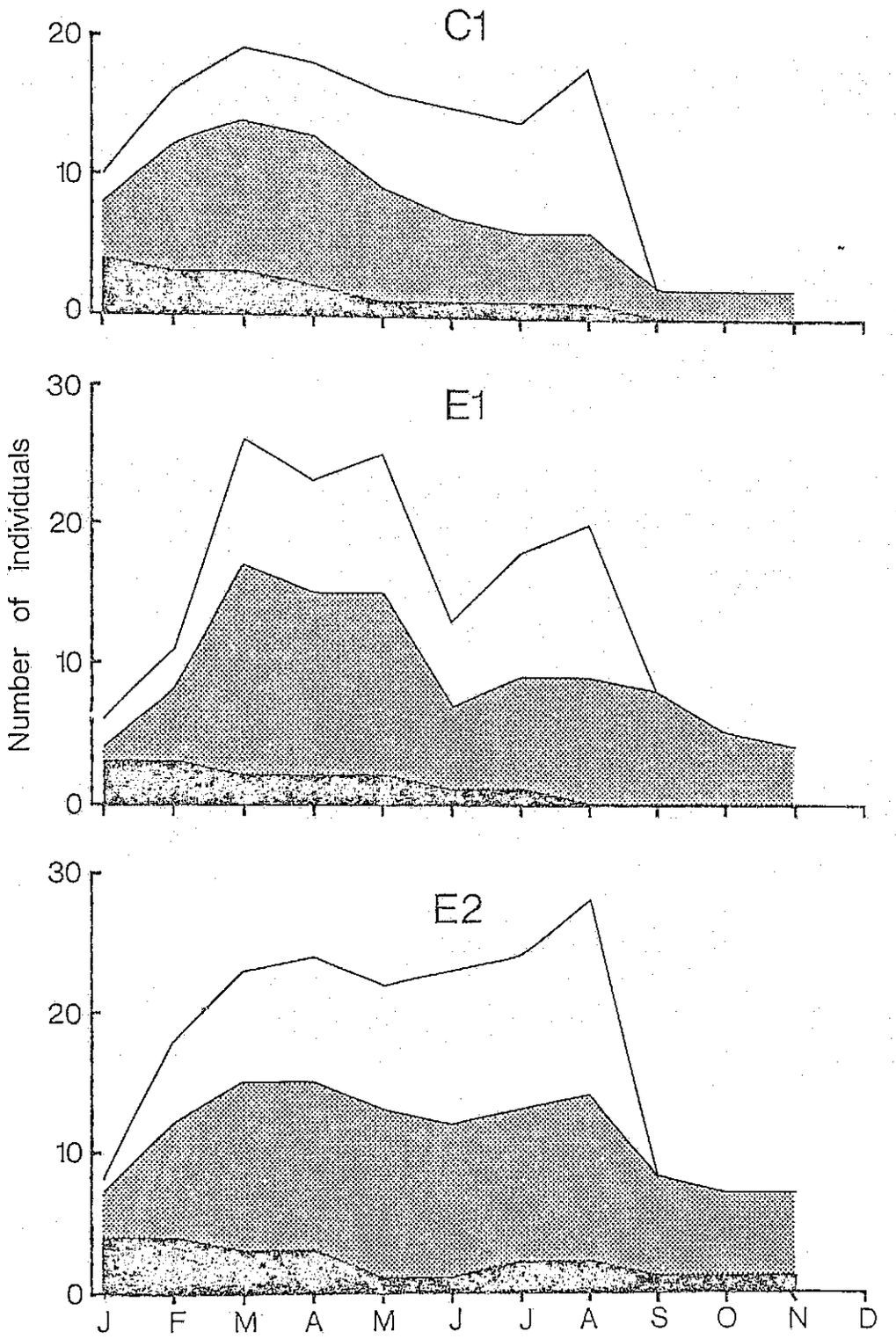

C1
E1
E2
Number of individuals
20
10
0
30
20
10
0
30
20
10
0
J F M A M J J A S O N D

Fig. 5.4. Mean average distances moved by A. stuartii in three study areas. Top, males; bottom, females (1980 year class only). A and A^* represent the first and second trapping sessions, respectively, in August 1981.

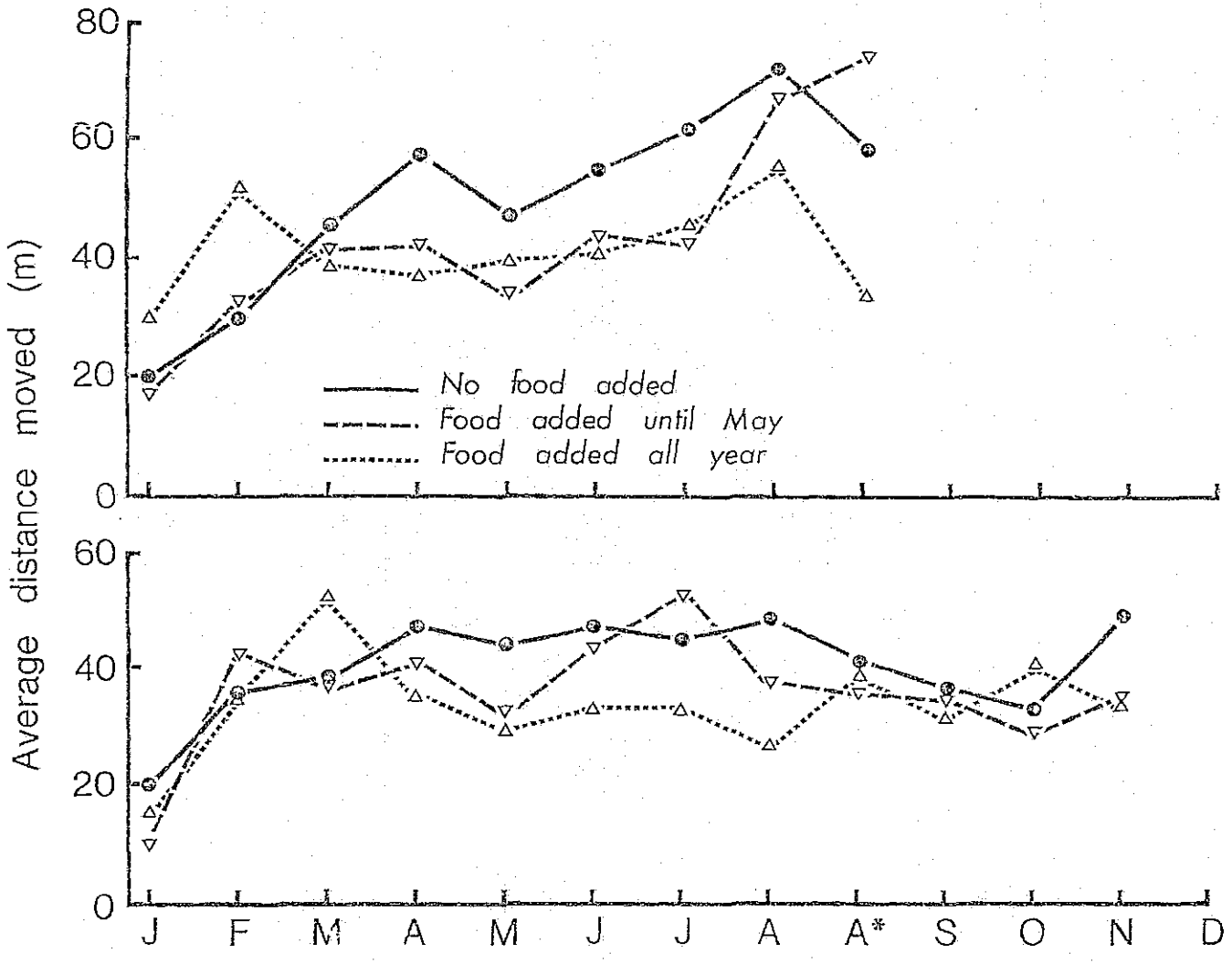

Average distance moved (m)
80
60
40
20
0
No food added
Food added until May
Food added all year
60
40
20
0
J
F
M
A
M
J
J
A
A*
S
O
N
D

Fig. 5.5. Body weights of A. stuartii in three study areas. (a) males, (b) females (1980 year class), (c) females (1979 year class). Symbols (solid circles or open triangles) represent mean body weights, while vertical lines represent standard deviations about the means.

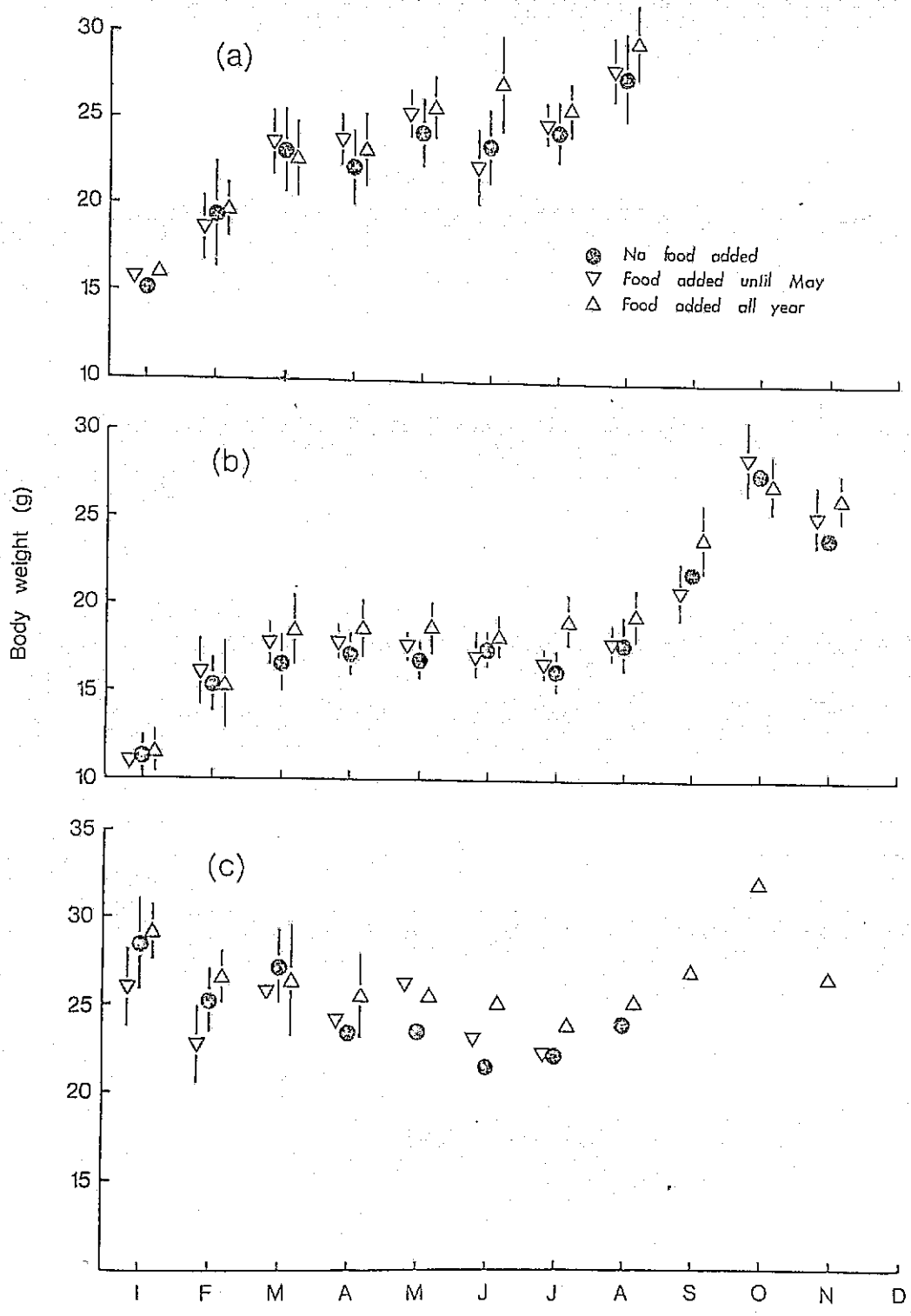
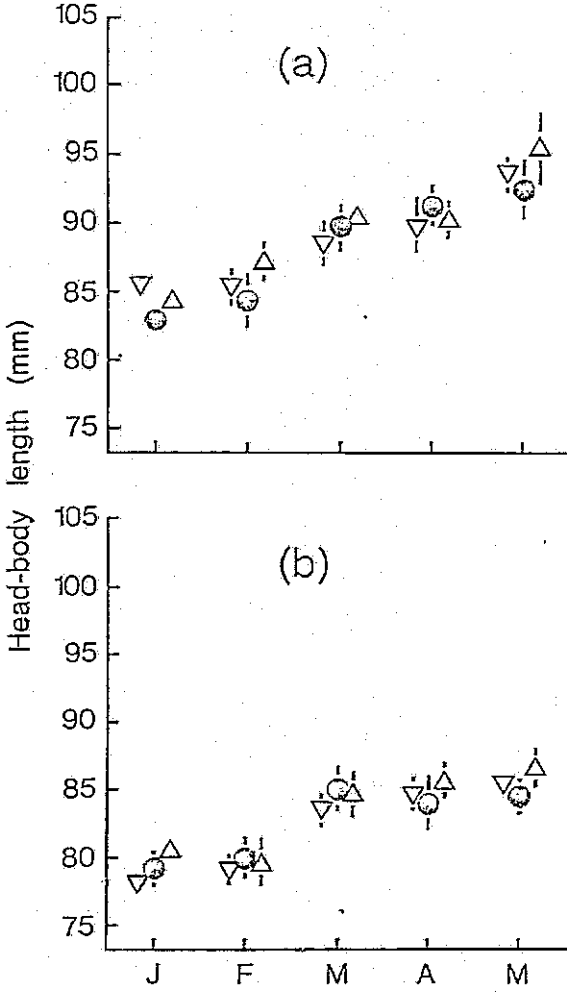

(a)
(b)
(c)
No food added
Food added until May
Food added all year
Body weight (g)
30
25
20
15
10
35
I
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.6. Head-body lengths of A. stuartii in three study areas. (a) males; (b) females (1980 year class). Symbols (solid circles or open triangles) represent mean head-body lengths, while vertical lines represent standard deviations about the means.


(a)
(b)
Head-body length (mm)
105
100
95
90
85
80
75
J
F
M
A
M

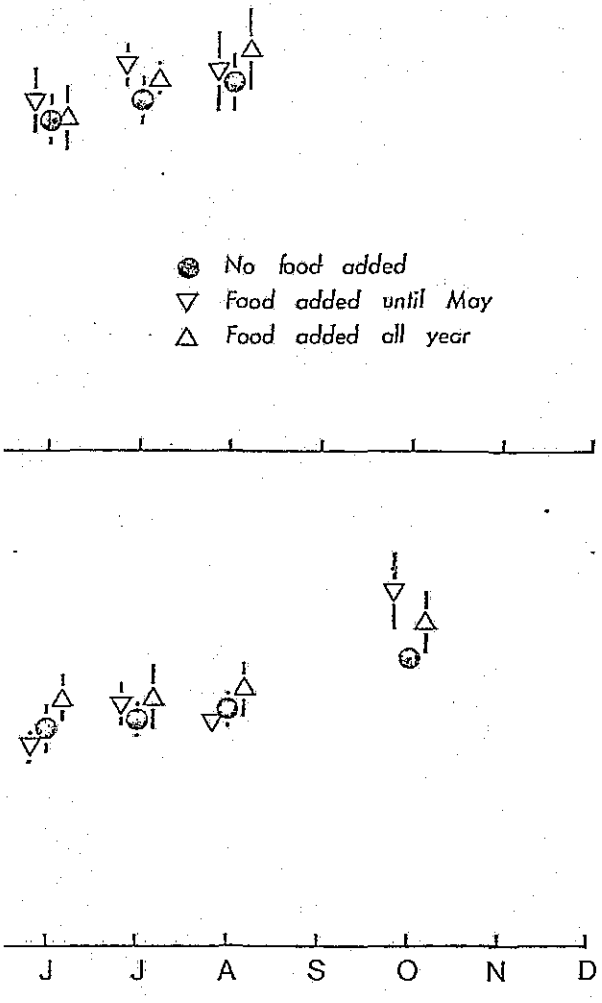
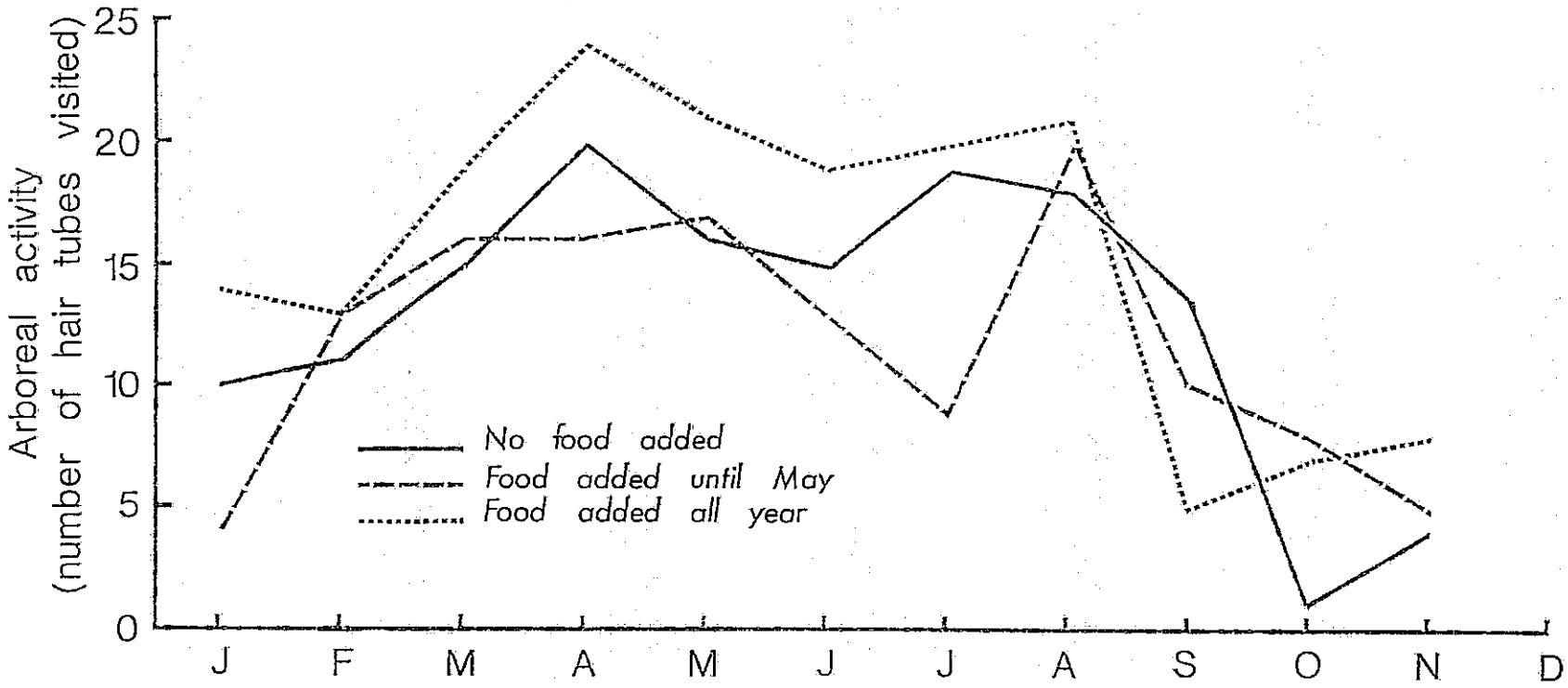

No food added
Food added until May
Food added all year
J
J
A
S
O
N
D

Fig. 5.7. Arboreal activity of A. stuartii in three study areas, measured by numbers of visits to hair sampling tubes each month.


Arboreal activity
(number of hair tubes visited)
25
20
15
10
5
0
No food added
Food added until May
Food added all year
J
F
M
A
M
J
J
A
S
O
N
D

CHAPTER 6

THE MECHANISM OF COMPETITION

6.1 INTRODUCTION

Two important mechanisms of competition have been distinguished, and these are referred to below as "interference" and "exploitation". Park (1954) used interference in reference to situations where individuals directly affect other individuals as by fighting, and exploitation in reference to situations where individuals affect other individuals by using their resources. Miller (1967) sharpened the definitions of interference and exploitation as follows: "Interference refers to any activity which either directly or indirectly limits a competitor's access to a necessary resource or requirement", whereas "Exploitation is the utilization of a resource once access to it has been achieved." Fighting (Park 1954), territoriality (Orians and Willson 1964, Dow 1977) and allelopathy (Gill 1972, Etherington 1975) are often cited as examples of interference competition. In contrast, exploitation competition is difficult to observe and measure, and it may be quantified only by precise measurements of interspecific differences in rates of foraging or harvesting of a limited resource (Schoener 1974a). Examples of exploitation competition are given by Bakker (1961) Jaeger (1972) (but cf. Hairston 1980) and Reynoldson (1966).

Miller (1969) concluded that interference is a "more highly evolved" strategy than exploitation, and listed a number of criteria that were characteristic of both mechanisms. Case and Gilpin (1974) discussed the conditions in which both forms of competition could be expected to occur, and argued further that interference competition was the most widespread form in nature. As Miller (1967) pointed out, however, under certain conditions both forms of competition may

occur, and both may restrict the densities or distributions of competing species.

A further important generalisation is that the particular mechanism of competition that is involved in an intraspecific relationship is often qualitatively similar to the mechanism that operates between species (Hinde 1956, Miller 1969). Where such similarity exists, intraspecific competition is usually more intense than interspecific competition (Wilson 1971, 1975).

Many studies of mammals have implicated the operation of interference rather than exploitation competition. Direct interference competition has been inferred from observations of interspecific intolerant behaviour a) in the field between different species of chipmunks (Eutamias spp.) (Brown 1971, Heller 1971, Meredith 1977), pocket gophers (Thomomys spp.) (Vaughan and Hansen 1964), and possums (Trichosurus spp.) (Biggins 1979), and b) in the laboratory between different species of woodrats (Neotoma spp.) (Howe 1978), voles (Microtus spp.) (Randall 1978, Murie 1971a), and rats (Rattus spp.) (Barnett and Spencer 1951); as well as between voles (Microtus californicus) and mice (Mus musculus) (DeLong 1966), voles (M. pennsylvanicus and Clethrionomys gapperi) and deermice (Peromyscus spp.) (Murie 1971b, Getz 1969), deermice (P. maniculatus) and mice (M. musculus) (King 1957), voles (Microtus spp.) and cotton rats (Sigmodon hispidus) (Terman 1974, Terman and Johnson 1971), and rats and antechinuses (Braithwaite 1973, Kenner 1972). Many other references are given in Grant (1972b).

Interference competition among species of small mammals need not necessarily result from direct intolerant interactions, but it may result also from indirect interactions, mediated by odours. For

example, Daly et al. (1980) recorded differences in the numbers of captures of several species of rodents in traps containing conspecific odours compared with traps containing the odours of other species, and suggested that interspecific odours were sought or avoided according to the reproductive status of the respondent. In addition, Randall (1981) found some avoidance by kangaroo rats (Dipodomys spp.) of Gerbil odour, and Moore (1965) showed that the deermouse Peromyscus maniculatus preferred its own odour to that of its congenor P. polionotus. Many other studies have shown that species of small mammals are able to discriminate the odour of their own species from that of other species (for example Bowers and Alexander 1967, Hawes 1976, Stoddart 1980).

In the present study, evidence has suggested that interference is the most important mechanism of competition between A. stuartii and A. swainsonii. Thus, A. swainsonii denies its smaller congenor access to terrestrial sources of food, and some competition probably still occurs even when the scarce food resource is supplemented (Chapter 5). Moreover, intraspecific interference has already been implicated in high density populations of A. stuartii (see discussions in Chapters 2 and 3), so that this form of competition between the two species of Antechinus should not be surprising. The design of the research described in this chapter was not to provide critical evidence for one mechanism of competition or the other, but rather to identify the kinds of interference interactions that occur between the two species. Three questions are addressed: 1) Do direct interactions occur between the two species?; 2) do indirect (olfactory) interactions occur between the two species?; and 3) how long does it take one species (A. stuartii) to perceive changes in the numbers of the other species (A. swainsonii)?

6.2 METHODS

The methods used to investigate each of the three questions above are described separately.

6.2.1. Direct interactions

In an attempt to observe direct interspecific interactions in the field, systematic watches (1-3½ hours a night for 1-3 nights each month) were made of two nests of A. stuartii at the control study area from October 1978 to November 1979. Animals were observed from dusk onward under red or white torchlight from a distance of 2½-4m. The two nests were in Ribbon Gum trees, separated from each other by about 95m. Both nest trees were near the creek and were surrounded by deep litter and ferns, where A. swainsonii were also known to occur. Pieces of ham or decapitated cockroaches were scattered about to temporarily attract individuals of both species to the bases of the trees, where my field of view was unobstructed. Other than scattering food, no attempt was made to experimentally "induce" interspecific interactions (for example, by locking up individuals of one species in a wire mesh cage and placing them in the known range of individuals of the other species) since I hoped to watch "natural" encounters. The presence of the investigator sitting on a log in relatively close proximity to a nest and to the scattered food did not appear to unduly influence the activity of Antechinus, although some curious individuals evidently regarded the investigator as a new object to be urinated upon. All observations were recorded in a notebook, and every effort was made to remain silent and still throughout each watch.

6.2.2. Indirect interactions

Antechinus stuartii deposit scats and urine in the vicinity of their nests (Golding 1979, G.A. Settle personal communication), and males, prior to mating, deposit secretions from glands in the sternal and cloacal areas onto new objects (Braithwaite 1973, 1974, Lee 1972). Antechinus swainsonii exhibits similar marking behaviour, except that the deposition of scats near nests, usually by females, has been observed only in some captive individuals (unpublished findings). The precise functions of marking behaviour in Antechinus are poorly known (but see Braithwaite 1973), and except for the sternal gland secretions of male A. stuartii (Braithwaite 1973, 1974), the effects of such behaviour on individuals of the same species or other species are unknown.

To investigate intra- and interspecific responses to odours in the field, no attempt was made to separate the effects of odours derived from different sources (faecal, urinal or glandular secretions). Instead, traps soiled by all three kinds of secretions were used to test the subsequent trap responses of individuals of both species. Such responses were tested in two ways:

First, six separate trap lines were established within 19 km of the control study area in areas of similar habitat. These lines used 100-185 Elliott type B live traps, placed singly at intervals of about 5 m, and were operated for sessions of 3-5 consecutive days in selected months between June 1978 and January 1980. Traps were checked each morning during a trapping session. All traps were soaked for 36 h in "Deogen" deodorising detergent before use. Trapping and animal handling procedures were as described in sections 2.4.1 and 2.4.2 (except that no head-body measurements were taken), but after

the capture of an individual, some of the soiled cottonwool bedding material was replaced. A second individual encountering the already used trap may then be attracted, repulsed or respond neutrally to the lingering odours of the individual captured first. Unfortunately, since up to five captures could occur in one trap on consecutive nights of a trapping session, individuals captured on nights 3 to 5 may respond to the odours of two or more individuals captured previously. I have assumed (with no justification other than convenience) that the odour of only the last captured individual remains on a trap, so that only ordered or sequential pairs of captures are counted. If, for example, individuals A, B, C and D were captured on consecutive nights, the response to trap odour was assessed only by counting the ordered pairs AB, BC and CD. The frequencies of ordered pairs recorded over all line trapping sessions were cast into a 3 x 3 table, and tested for association by χ^2.

Second, a more critical assessment of the response to trap odour was attempted in the control study area between March and July 1979. Four traps were set at each of 48 trap stations; at each station the traps were placed in a cross formation, opening inwards with about 10 cm between opposite entrances, so there was an equal chance of capture of an individual in each trap. Traps were deodorised and baited as described above, but the cotton wool insulation differed in each of the four traps in the cross. Thus, one trap contained no odour (clean cotton wool), but each of the other three traps contained cotton wool soiled with urine and faecal material taken 6-12 hours earlier from captive individuals of either A. stuartii or A. swainsonii or the Bush Rat Rattus fuscipes. Following the capture of an animal in the field, the used trap was removed and replaced with a

deodorised trap containing cotton wool soiled with the appropriate odour, and the positions of the traps in the cross were shuffled. Traps were operated for three days a month mid-way between regular grid trapping sessions. The frequencies of captures of each species in traps containing different odours were arranged in a 3 x 4 table, and tested for association by χ^2.

6.2.3. The "perception" of changes in competitor numbers.

To assess how long it took A. stuartii to perceive changes in the numbers of A. swainsonii in field conditions, it was necessary to manipulate the numbers of the latter species and measure the response of A. stuartii over very short time intervals. This presented very considerable logistic difficulties, since trapping procedures were relatively slow and the numbers of individuals of both species in an area could not be accurately censured in less than 3-4 days. However, earlier experience had suggested that A. swainsonii became more active in wet conditions, when increasing numbers of individuals encountered traps. Assuming that the "effective density" of A. swainsonii changes in wet or dry conditions, it was felt that short-term fluctuations in the numbers were best effected during wet weather. The response of A. stuartii to changes in the numbers of A. swainsonii was then assessed by investigating shifts in the arboreal activity of the former species (see sections 2.5.4.1 and 3.4.3.1). Finally, to check that A. stuartii responded to changes in the numbers of A. swainsonii rather than to changes in the weather, the arboreal activity of A. stuartii was investigated during wet weather after A. swainsonii had been removed.

In a small section of experimental area E3 only where relatively large numbers of A. stuartii and A. swainsonii occurred, 27 traps were set on grid points at ground level, and 26 traps were placed > 2 m above ground on the lower limbs of Acacia melanoxylon and Bedfordia salicina, or in the more slender branches of Pomaderris aspera, or on the trunks of fallen eucalypts or acacias (Fig. 6.1). Traps were baited and insulated as before, checked hourly for 24 h, and the numbers of captures of A. stuartii and A. swainsonii were recorded. Such trapping was conducted on three occasions: June 23 1979 (dry weather), June 27 1979 (wet weather) and July 2 1979 (wet weather). Trapping was also begun on 29 and 30 June 1979, but abandoned because little or no rain fell.

6.3 RESULTS

6.3.1. Direct interactions.

Both species of Antechinus were observed during night watches (Table 6.1), but no direct interspecific encounters occurred. On some nights both species of Antechinus and Rattus fuscipes were observed eating the scattered food, but invariably only one species was present at a time. In contrast, groups of up to 8 individuals of A. stuartii, 3 of A. swainsonii, and 2 of R. fuscipes used the food source at a time (Table 6.1). There appeared to be no consistent pattern of visitation by each species, except that R. fuscipes was seldom seen until about an hour after dusk. An individual of any species rarely remained in view for more than 10 consecutive minutes.

Two observations are worthy of note: First, the reactions of individuals of each species differed slightly if disturbed (by wind, bush noises or the investigator). Antechinus stuartii froze, often adopting an "indecision-alert" posture as also observed in Planigale

maculata (Van Dyck 1979). If no further disturbance occurred for about 30 seconds, activity was resumed. If further disturbance did occur, in 86% of observations (N = 29) the individual spiralled, corkscrew-like, rapidly up the nearest tree. Antechinus swainsonii also froze and adopted an "indecision-alert" posture, but this species usually resumed activities within 10-20 seconds of the original disturbance. If further disturbance occurred within this time, some individuals (32%, N = 19) bolted for cover under the ferns, but the others froze again. No A. swainsonii sought refuge on a tree. Second, the body of a male A. swainsonii that died in a trap on the morning of 2 August 1979 was placed at the base of a nest tree that evening. Soon after dusk, an A. stuartii approached the body slowly and with apparent caution. After several approaches and withdrawals, this individual began to bite the carcase, and continued biting, but not eating, for 6 minutes. After this time the carcase was left alone, and no subsequent A. stuartii activity was recorded. Almost two hours later, a female A. swainsonii approached the carcase slowly but with less hesitation. This female (the only A. swainsonii on the grid) uttered "chit-chit" calls (Fleay 1932) on her approach to the carcase, but after inflicting two bites she disappeared under cover, and no subsequent activity was observed.

These observations, made during some 60h of nocturnal vigil, show that direct encounters between A. stuartii and A. swainsonii occur infrequently, or not at all. Except when an A. stuartii individual approached a dead A. swainsonii, no interspecific encounters were recorded, whereas single species groups were observed on several occasions.

6.3.2. Indirect interactions.

Table 6.2a shows that there is an effect of the capture of one species on subsequent captures of the other two species. Trends in the levels of association between these pairs are shown in Table 6.2b as the deviation of observed to expected values in each cell of the table, expressed as a percentage of the expected values (Simpson et al. (1960)). Values along the diagonals of the table deviate positively from expected values, whereas all other values deviate negatively. This suggests that captures of conspecifics are more likely to occur consecutively than are captures of different species.

Table 6.3a similarly shows that there is an effect of the odour of one species on subsequent captures of the other two species. Table 6.3b shows further that each species was captured more frequently than expected in traps containing conspecific odours, but less frequently than expected in traps containing the odours of other species. In contrast, the frequencies of captures in odourless traps deviated little from expected frequencies.

These findings show that each species discriminates and responds to differences in trap odours.

6.3.3. The "perception" of changes in competitor numbers.

The patterns of activity of both species of Antechinus (Fig. 6.2) were similar to those recorded previously (Sections 2.5.4.4 and 2.5.6.4). Antechinus swainsonii was continuously active throughout 24 h, whereas A. stuartii was active only at night. As anticipated, the level of activity of A. swainsonii changed with the weather. In dry conditions on 23 June 1979, eight different individuals were captured over 24 h, but in wet conditions on June 27 1979 (Fig. 6.2)

11 different individuals were captured. The mean numbers of captures of A. swainsonii per hour over 24 h also differed, increasing from 3.7 ± 1.6 in dry weather to 7.3 ± 2.1 in wet weather (paired sample test, $t_{(23)} = 7.77$, $P < 0.001$). Only three captures of A. swainsonii occurred above ground (1%), and these are ignored.

Concommitant with the shifts in the level of terrestrial activity of A. swainsonii were shifts in the level of arboreal activity of A. stuartii (Fig. 6.2 and Table 6.4). In dry conditions when the hourly activity of A. swainsonii was relatively low, A. stuartii was captured equally on the ground and in the trees, but in wet conditions as the level of activity of A. swainsonii increased, most A. stuartii were captured in the trees. To further investigate whether rain or the increased activity of A. swainsonii caused the shift in arboreal activity of A. stuartii, trapping was again conducted in wet conditions but with A. swainsonii temporarily removed (Fig. 6.2). Under these conditions, there was no difference in the hourly capture rates of A. stuartii on the ground and in trees (Fig. 6.2, Table 6.4). This clearly suggests that the arboreal activity of A. stuartii increases only in response to elevated levels of activity of A. swainsonii on the ground.

In wet conditions on the night of June 27 1979, the numbers of A. stuartii and A. swainsonii captured on the ground were negatively correlated ($r_{(12)} = -0.60$, $P. < 0.05$). This suggests not only that A. stuartii responded to generally elevated levels of terrestrial activity of A. swainsonii, but further that such responses were measurable on an hourly basis.

6.4 DISCUSSION

Short answers to the questions posed in the introduction to this chapter are that 1) direct, physical interactions do not occur between A. stuartii and A. swainsonii, 2) indirect, olfactory interactions do occur, and 3) A. stuartii perceives changes in the numbers of A. swainsonii at least on an hourly basis. These answers are elaborated below, with some speculations on how competitor avoidance may have evolved.

Individuals of the two species of Antechinus were never observed in close proximity to each other, yet groups comprising only one species were seen on several occasions. These groups were largest in summer (Table 6.1) and probably represented members of one family (Dickman 1982b). Hall and Lee (1982) similarly failed to observe direct interactions between A. stuartii and A. swainsonii in field conditions. When forced into close proximity in laboratory cages, the two species generally move away from each other (Kenner 1972), although avoidance of A. swainsonii by A. stuartii is stronger than the converse situation (Seymour 1980).

The failure to observe direct interspecific interactions in the field was disappointing but not particularly surprising. As Croft (1982) pointed out, most dasyurids (including Antechinus) are solitary, and even direct intraspecific interactions appear to be limited to certain periods of an individual's life. Moreover, direct interspecific aggression is likely to be advantageous only if the aggressor species can expect to maximise its control of a shared resource, and this expectation can depend, in turn, on the structure of the habitat (Oksanen et al. 1979). In open habitats, subordinate species are easy to see and evict (Dow 1977), but in relatively complex habitats they may escape aggression by hiding. Both species

of Antechinus inhabit structurally complex tall open-forests, where the costs to one species of aggressively evicting the other presumably outweigh the benefits gained by controlling resources.

The increases in the terrestrial activity of A. swainsonii during wet weather and the concommitant increases in the arboreal activity of A. stuartii (section 6.3.3) suggest that A. stuartii avoided its larger congenor on an hourly, or perhaps even on a moment to moment, basis. This finding corroborates the suggestion of Hall and Lee (1982) that A. stuartii uses trees to avoid confrontations with A. swainsonii on the forest floor, as well as to obtain food. Before considering how A. stuartii perceived and avoided its larger congenor, it is of interest to consider briefly how weather affected the activity of A. swainsonii.

Weather affects the activity of many species of small mammals (Gentry et al. 1966, Doucet and Bider 1974, Vickery and Bider 1978, Sidorowicz 1960), but apparently not that of A. stuartii (Barry 1977, Fletcher 1977, Statham 1982b). The reason why A. swainsonii becomes more active in rain is unclear, but may be associated with the difficulty of finding food. Borowski and Dehnel (1952) (cited in Mystkowska and Sidorowicz 1961) suggested that shrews (Sorex spp.) increase their activity to find insects sheltering from rain. Mystkowska and Sidorowicz (1961) refuted this argument, and suggested rather mysteriously, that rain acts as a "capture regulator". Cockroaches, bugs and beetles were often found inside Elliott traps after rainy nights in this study, and so it is plausible that the activity of A. swainsonii increases to search for this cryptic food.

The lack of direct, physical encounters between the two species of Antechinus may be due in part to the mutual avoidance of each others odours. But, two kinds of odour avoidance can be envisaged. First, an individual could reduce the chance of being in the same place as a congeneric individual by avoiding sites, such as runways, burrows and nests, where congeneric odours are concentrated. (This will be termed "probablistic avoidance"). Second, an individual could avoid moment to moment encounters with congeneric individuals by smelling them and moving away before physical contact could be made. (This will be termed "instantaneous", or "moment to moment avoidance").

In Antechinus, in contrast to other species such as the possums Trichosurus vulpecula and T. caninus (Thomson and Pears 1962, Biggins 1979) and the salamanders Plethodon cinereus and P. nettingi (Jaeger and Gergits 1979), there is evidence that only instantaneous avoidance occurs. Thus, if A. stuartii avoided burrows and other sites bearing the odour of A. swainsonii, it would presumably not respond to the removal of the latter species until all lingering odours of A. swainsonii had disappeared. However, in Chapter 2 it was shown that A. stuartii responded within only a few days to the removal of A. swainsonii, and it was shown above that responses could even occur within an hour. Moreover, if avoidance was probablistic, actual physical encounters would be expected to occur by chance in lightly scented areas, or in the open. But, no such encounters between A. stuartii and A. swainsonii were observed in the present study, and none have been reported elsewhere. In contrast, a single example of what appears to have been instantaneous avoidance has been described by Hall and Lee (1982). These authors

observed individuals of A. swainsonii and R. fuscipes using a bait station in a forest clearing. Although observations were continued for over an hour, only one species was seen at the bait station at one time; individuals of the other species would enter and feed only seconds after the first species had left. Individuals of both species were seen sniffing the air at opposite ends of the clearing before venturing into the open, thus reinforcing the impression that instantaneous avoidance can indeed be mediated by smelling individuals of another species.

Olfactory responses to trap odours have been reported in many other studies of small mammals, and have led to useful inferences concerning their population structure and dynamics (Daly et al. 1980, Boonstra and Krebs 1976, Boonstra et al. 1982, Mazdzer et al. 1976, Rowe 1970). Such inferences often depend on a priori knowledge of the population under study. Rowe (1970), for example, attributed an unexpectedly high capture rate of male house mice (Mus musculus) in male scented traps to "latent aggressive behaviour", but an unexpectedly high capture rate of female mice in male scented traps to sexual interest. Conversely, Summerlin and Wolfe (1973) suggested that socially subordinate cotton rats (Sigmodon hispidus) avoided traps bearing the odour of dominant conspecifics, whereas Fulk (1972) attributed the avoidance of shrew (Blarina brevicauda) odour by voles (Microtus pennsylvanicus) to avoidance of predation. In the present study, the trapping methods used to demonstrate avoidance of interspecific odours could be sharpened by standardising the sexes and ages of odour donors (e.g. Daly et al. 1978), and by isolating the effects of odours from faeces, urine and other body secretions.

Although smell is probably important in allowing congeneric individuals to avoid one another, other senses, such as hearing, may also be used. Antechinus swainsonii is "noisier" than its smaller congenor. It "whitters" and utters sporadic "chit-chit" calls and, while foraging among dry fern fronds and leaf litter, it makes rustling sounds that are easily audible to a human listener at distances up to several metres (personal observations). In contrast, A. stuartii is the more responsive of the two species to auditory stimuli and, following wind noises or other bush disturbances, this species froze for longer periods than A. swainsonii and showed a greater tendency to move to an apparently safe arboreal refuge (section 6.3.1). Antechinus stuartii probably responds in a similar manner to the noises produced by its larger congenor. Such responses would clearly reduce the chances of a direct interspecific encounter, and hence support the conclusion that avoidance, especially of A. swainsonii by A. stuartii, occurs on a moment to moment basis.

It is doubtful that field observations can yield much further insight into the nature of avoidance responses in Antechinus, but experiments on interspecific communication could be easily conducted in the laboratory. For example, to assess the stimuli that elicit avoidance responses in A. stuartii, individuals could be presented with puppet skins of A. swainsonii (visual stimulus only), objects bearing the odour of A. swainsonii (olfactory stimulus only), or tape recordings of A. swainsonii vocalisations (auditory stimulus only). Control experiments would use the puppet skins, odours and sounds of other, unfamiliar A. stuartii. The anecdotal observation that A. stuartii approached and bit a dead A. swainsonii, where auditory and

possibly olfactory stimuli were absent, suggests that this approach would be fruitful. In addition, both species of Antechinus produce ultrasounds (D.P. Woodside, personal communication). Although the functional importance of ultrasound in these species is not known, it is conceivably yet another channel for interspecific communication.

To recap on the discussion so far, it has been shown that interference is the mechanism of competition between A. stuartii and A. swainsonii. There is no evidence that the two species interfere with each other directly, as by fighting, but much evidence that interference is indirect. The weight of evidence is that A. stuartii avoids its larger congenor on a moment to moment basis, using trees to escape physical encounters; these responses are elicited by the smell or sound of approaching A. swainsonii. In contrast, A. swainsonii avoids traps bearing the odour of its smaller congenor, but further evidence that it avoids A. stuartii individuals has not been obtained. The avoidance by A. stuartii of physical contact with A. swainsonii is of particular interest from an evolutionary point of view, and prompts the question as to how such behaviour evolved, and also, what are the current selection pressures that maintain it.

Antechinus stuartii responds to disturbances, such as A. swainsonii or bush noises, by freezing, and subsequently by climbing rapidly up into the trees. These responses may be effective against a wide range of enemies, especially predators. Throughout much of its range, A. stuartii occurs in relatively open-forest and woodland (Wakefield and Warneke 1967) where ground-level vegetation, and hence cover from avian predators such as Powerful Owls and Barn Owls, is sparse. In contrast, A. swainsonii occurs largely in forest gullies where ground level vegetation cover is dense, or at higher

altitudes (> 1500 m) in dense subalpine and alpine heath (Wakefield and Warneke 1963, Dickman et al. in press). Avian predation pressure in these habitats is likely to be less intense than in open habitats, so selection for avian anti-predator behaviour in A. swainsonii may be correspondingly less intense. Under such circumstances, it seems reasonable to suggest that the greater responsiveness of A. stuartii to bush disturbances has evolved primarily as an anti-predator defence, and that avoidance of A. swainsonii occurs because the larger species is seen as a potential predator.

Despite the general responsiveness of A. stuartii to bush disturbances, this species undoubtedly perceives its larger congenor as a specific threat and avoids contact with it more strongly than with rats. For example, increases in the terrestrial activity of A. stuartii immediately followed decreases in the activity of A. swainsonii (section 6.3.3), although rats were present and active on the ground at all times. Moreover, avoidance by A. stuartii of the odour of A. swainsonii was stronger than its avoidance of the odour of rats (Table 6.3b). However, since earlier findings demonstrated that A. stuartii is seldom, if ever, eaten by its larger congenor (section 2.5.6.3), it is relevant to inquire why the avoidance response of A. stuartii to A. swainsonii is so marked.

A possible explanation is that, although A. swainsonii generally recognises the odour of A. stuartii, the former species sometimes mistakes its smaller congenor for a large insect. Cicadas (Homoptera), mole crickets and locusts (Orthoptera) attain the size of small A. stuartii, and all are eaten by the larger antechinus (section 2.5.6.3). Moreover, although it differs in body shape and colour,

the jerky movements of A. stuartii can be reminiscent of these insects. Since A. swainsonii opportunistically eats a wide range of invertebrates, it presumably lacks a specific search image and, by mistake, it could easily approach and even attack unwary A. stuartii. Although it is unlikely that A. swainsonii would expend the energy required to subdue and eat adult A. stuartii, it is presumably advantageous for the smaller species to recognise and move out of the way of its larger congenor, and so avoid risk of injury. In contrast to A. swainsonii, rats are largely omnivorous (Warneke 1971, Watts and Braithwaite 1978) or even herbivorous (Stewart 1979b), and hence would seldom approach A. stuartii in mistake for an item of food.

This explanation could account for the anomalous finding that juvenile female A. stuartii are more adversely affected by competition than males or parous females (section 2.6). Since juvenile females would be mistaken for insects by A. swainsonii more frequently than would the larger males and parous females, avoidance responses by these small individuals would also be more frequent, and their access to terrestrial sources of food would be curtailed. The removal of A. swainsonii would thus allow juvenile females to spend proportionately more time foraging in structurally complex, terrestrial habitats than males and parous females, and so produce the relatively large, expansive shifts, that were observed in their survival and resource use.

Direct harrassment of A. stuartii by A. swainsonii has probably selected for competitor recognition and avoidance responses in the smaller species, so that direct, physical encounters seldom occur. Such avoidance responses also confirm that interference is the mechanism of competition between these species.

6.5 SUMMARY

To investigate the kinds of interference interactions that occur between A. stuartii and A. swainsonii, three questions were asked: 1) do direct interactions (e.g. fighting) occur?, 2) do indirect interactions (e.g. mediated by odours) occur?, and 3) how long does it take the inferior competitor, A. stuartii, to perceive changes in the numbers of its larger congenor?

Direct interactions were investigated by watching for interspecific encounters at two bait stations in the field. During some 60 hours of observations over the course of a year, no direct, physical interspecific contacts were observed, although single species groups of each species of Antechinus, and of Bush Rats, were recorded frequently. This suggested that direct interference interactions seldom or never occur.

Indirect interactions were assessed by investigating the responses of each species of Antechinus, and of rats, to traps baited with their own and with other species odours. Each species was captured more frequently than expected in traps bearing conspecific odours, but less frequently than expected in traps bearing other odours. This suggested that each species discriminates and avoids the odours of other species, and hence that indirect, olfactory interactions do occur.

To assess the swiftness of response of A. stuartii to changes in the numbers of A. swainsonii, comparison was made of the hourly capture rates of the smaller species in trees and on the ground, at different levels of terrestrial activity of A. swainsonii. In dry conditions, when the terrestrial activity of A. swainsonii was low, A. stuartii was captured equally in the trees and on the ground, but in

wet conditions, when the terrestrial activity of A. swainsonii was high, the smaller antechinus was captured most frequently in trees. Furthermore, a negative correlation was recorded during wet conditions of the numbers of the two species captured on the ground, suggesting that A. stuartii responded at least hourly, and perhaps even on a moment to moment basis, to changes in the numbers of its larger congenor.

Antechinus stuartii probably detects A. swainsonii by smell and possibly by sound, and it avoids physical confrontations with congeneric individuals by climbing into the trees. It was suggested that A. swainsonii may sometimes mistake the smaller species for large insects, and that it could conceivably approach, attack and injure unwary individuals. Although there is no evidence that A. swainsonii eats its smaller congenor, such direct harrassment of A. stuartii could select for specific competitor recognition and avoidance in this species, so that direct, physical encounters seldom occur. In the final chapter, I will discuss some of the consequences of interference competition on the nature of coexistence between the two species of Antechinus, and consider why competition should occur at all.

Table 6.1. The minimum numbers of Antechinus stuartii, A. swainsonii and Rattus fuscipes observed at two sites in the control study area.

	Number of observation nights	Minimum numbers of animals observed					
		Site 1			Site 2		
		A.st.	A.sw.	R.f.	A.st.	A.sw	R.f.
Oct., 1978	1	1	0	1	-	-	-
Nov.	2	1	1	1	1	0	0
Dec.	3	3	3	1	4	1	0
Jan., 1979	3	8	3	1	6	0	1
Feb.	2	5	1	2	6	2	1
Mar.	3	4	0	2	6	2	0
Apr.	3	1	1	1	0	0	0
May	3	1	0	1	1	1	1
Jun.	2	0	2	0	0	1	2
Jul.	1	0	1	1	0	0	0
Aug.	1	1	1	0	0	0	0
Sep.	-	-	-	-	-	-	-
Oct.	1	0	0	0	0	1	1
Nov.	2	0	1	1	0	0	1

Table 6.2. The responses of Antechinus stuartii, A. swainsonii and Rattus fuscipes to trap odours, assessed by counting ordered pairs of captures. (a) raw frequency data; (b) the percentage deviations of observed from expected frequencies. Total trap nights = 3895.

(a)

		Second capture		
		A.stuartii	A.swainsonii	R.fuscipes
First capture	A. stuartii	108	29	73
	A. swainsonii	34	95	74
	R. fuscipes	60	56	308

$\chi^2_{(4)} = 219.5$, $P < 0.001$

(b)

		Second capture		
		A.stuartii	A.swainsonii	R.fuscipes
First capture	A. stuartii	+113.0	-35.8	-36.1
	A. swainsonii	-30.6	+117.4	-33.0
	R. fuscipes	-41.3	-38.6	+33.6

+ if O > E
- if O < E

Table 6.3. The responses of Antechinus stuartii, A. swainsonii and Rattus fuscipes to trap odours, assessed by counting captures of each species given the choice of four different trap odours. (a) raw frequency data; (b) the percentage deviations of observed from expected frequencies. Total trap nights = 2880.

(a)

		Trap odour			
		A. stuartii	A. swainsonii	R. fuscipes	None
Species captured	A. stuartii	45	21	42	40
	A. swainsonii	14	47	33	31
	R. fuscipes	42	32	91	55

$\chi^2_{(6)} = 44.5$, $P < 0.001$

(b)

		Trap odour			
		A. stuartii	A. swainsonii	R. fuscipes	None
Species captured	A. stuartii	+48.5	-30.0	-15.7	+5.8
	A. swainsonii	-45.3	+85.0	-21.6	-3.1
	R. fuscipes	-6.9	-28.3	+22.8	-2.1

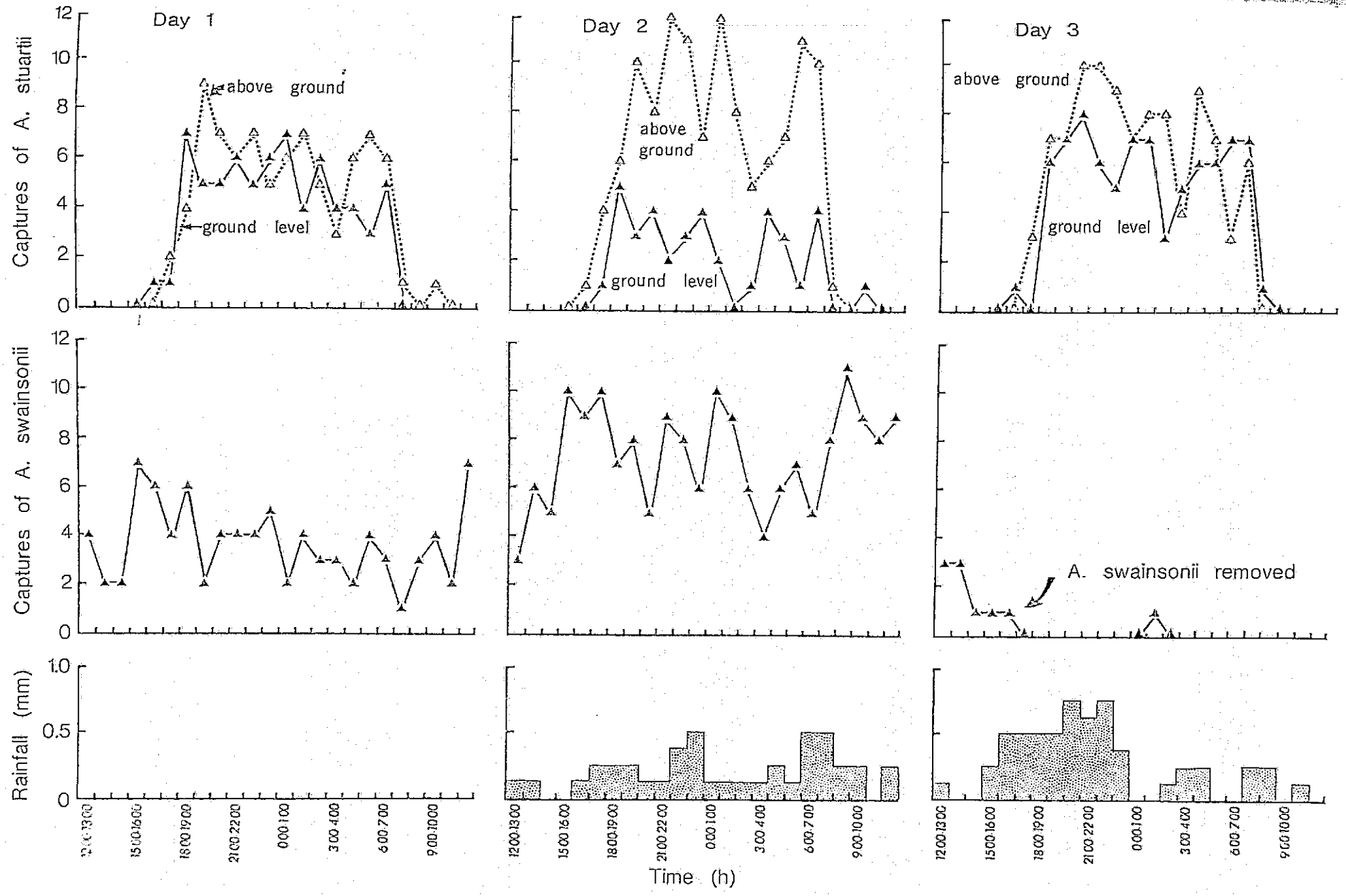
\+ if O > E
\- if O < E

Table 6.4. Comparison of the activity of Antechinus stuartii (mean no. of captures/h, ± standard deviation) on the ground and in trees, at different levels of terrestrial activity of A. swainsonii. (Sample sizes (total numbers of captures) are shown in brackets). Differences in activity of A. stuartii are detected by paired sample t tests.

Activity of A. stuartii	Level of activity of A. swainsonii		
	Low (dry conditions)	High (wet conditions)	Nil (wet conditions)
On ground	4.9±1.6(68)	2.6±1.5 (37)	5.7±2.1(80)
In trees	5.7±1.8(80)	8.4±2.7(117)	7.0±2.3(98)
$t_{(d.f.)}$	$1.52_{(13)}$	$6.84_{(13)}$	$1.98_{(13)}$
p	n.s	<0.001	n.s.

Fig. 6.1. Traps set on fallen trees.

Fig. 6.2. The response of A. stuartii (captures per hour in ground level and above ground traps) to changes in the terrestrial activity of A. swainsonii. Above ground captures are shown by open triangles, ground level captures by solid triangles. The bar at the top of the figure represents hours of darkness.


Day 1
Day 2
Day 3
above ground
ground level
Captures of A. stuartii
Captures of A. swainsonii
A. swainsonii removed
Rainfall (mm)
Time (h)
12-13:00
15:00-16:00
18:00-19:00
21:00-22:00
0:00-1:00
3:00-4:00
6:00-7:00
9:00-10:00

CHAPTER 7

GENERAL DISCUSSION

7.1 INTRODUCTION

In earlier chapters, I have described the results of field experiments designed to test the hypothesis that competition occurs between A. stuartii and A. swainsonii. In general, manipulation of the numbers of A. swainsonii had very marked effects on the population parameters and resource use of A. stuartii, whereas reciprocal manipulations of the numbers of the smaller species had much less effect on A. swainsonii. Investigation of the diets of the two species, and of the seasonal abundances of their invertebrate prey, suggested that A. stuartii faces a shortage of food in winter. The food shortage for this species is exacerbated by the presence of A. swainsonii, and it was suggested that, by interfering with A. stuartii on the forest floor, the larger antechinus denies its smaller congenor access to alternative sources of prey in the forest soil and litter. Further experiments, in which supplementary food was provided to A. stuartii, supported this suggestion. These combined findings show that A. stuartii and A. swainsonii compete for food, and further, that the effects of competition are more evident in the smaller of the two species.

Why do A. stuartii and A. swainsonii compete? The two species appear to have had ample opportunity to evolve divergent specialisations to reduce competition: They overlap broadly in their geographical distributions (Dickman 1982a), and they have been sympatric since Pleistocene times (Wakefield 1967) and probably earlier (Archer 1982). In this Chapter, I will first discuss a mechanism

involving gene flow that may prolong or suspend competition in Antechinus throughout evolutionary time, and then discuss other, apparently contradictory evidence, that divergence in their body sizes reduces competition.

7.2 GENE FLOW AND THE MAINTENANCE OF INTERSPECIFIC COMPETITION

Schoener et al. (1979) proposed that where the ranges of two competing species are narrowly sympatric, directional selection for phenotypic divergence in the overlap zone can be impeded by gene flow. A variation of this proposal can be applied to Antechinus. Antechinus stuartii occurs alongside A. swainsonii in relatively wet, densely forested localities, but it also occurs alone in a wide range of drier and more sparsely wooded areas. In sympatry, there may be directional selection for divergence, but in allopatry such selection would be absent. Thus if gene flow from larger allopatric to smaller sympatric populations of A. stuartii occurred, the sympatric selection pressures would be "swamped" and sympatric phenotypes would be adapted more to the area of allopatry than to the smaller overlap area. In this situation, competition would be suspended indefinitely. But, there is a problem: if gene flow prevents local adaptation in A. stuartii, what is to prevent A. swainsonii - which almost always occurs alongside its smaller congenor - diverging "unilaterally?" Because A. swainsonii is far less adversely affected by competition from A. stuartii than vice versa, competition-mediated selection pressure on A. swainsonii is likely to be weak. Moreover, A. swainsonii may experience selection from opposite directions (towards convergence, see discussion of body sizes, section 7.3.1), so that overall fitness is maximised when weak competition effects still occur.

How can gene flow in A. stuartii be assessed? Since gene flow depends on individuals successfully breeding in localities different from those where they were born, the most direct approach would be to track animals from birth until mating. This would involve live trapping on a massive scale, and is obviously impractical. However, an indirect approach, used below, is to compare marker gene frequencies in adjacent sympatric and allopatric populations. If the gene frequencies are similar in both, this implies that gene flow does indeed occur, but if the gene frequencies are different, gene flow is likely to be extremely limited.

An appropriate protein for studying genetical variation is transferrin because it is polymorphic in A. stuartii, present in blood plasma (and hence obtainable without killing animals) and easy to run and stain using gel electrophoresis (Moritz 1982). In 1980 and 1981 ten localities were sampled to investigate allele frequencies for transferrin in A. stuartii (Table 7.1). Eight localities were in or near the Brindabella Range; A. stuartii was sympatric with A. swainsonii in five of these but allopatric, and at varying distances from the nearest A. swainsonii population, in the other three. The remaining two localities were geographically isolated from the Brindabellas and served as controls (that is, no gene flow was expected between them and the Brindabella Range). Tallaganda is some 40 km east of the Brindabellas, whereas Kioloa is over 100 km to the east on the New South Wales coast.

Animals were captured using standard live trapping methods (section 2.4.1), lightly anaesthetised with ether, and a blood sample was collected from the sub-orbital sinus in a heparinised microhaematocrit tube. Measurements of body weight, head-body,

tail, hind foot and ear lengths were made, and the animals released at the point of capture. The blood was packed immediately on ice and subsequently stored, after separation of the red blood and plasma, at -20°C. Electrophoresis was performed by Drs P.R. Baverstock and M. Adams at the Institute of Medical and Veterinary Science, Adelaide, using procedures described in Baverstock et al. (1977, 1980).

Two alleles, designated "a" and "b" were variable in A. stuartii (Table 7.1). In all localities in the Brindabella Range, allele "a" predominated irrespective of whether the population was allopatric or sympatric with A. swainsonii, and no differences in gene frequency among any of the populations could be detected (test on allele frequencies of sympatric versus allopatric populations: $G_{(1d.f.)} = 0.02$, P n.s.). In contrast, outside of the Brindabellas allele "b" predominated (Table 7.1). Overall, the frequencies of alleles "a" and "b" differed strongly between the Brindabella and non-Brindabella populations (test of Brindabella vs non-Brindabella populations: $G_{(1d.f.)} = 28.27$, $P < 0.001$), suggesting, as expected, that no gene flow occurs between them.

These findings show that gene frequencies of sympatric and allopatric populations of Brindabella A. stuartii are the same, and hence support the idea that gene flow occurs between them. Moritz (1982) also found a lack of variation in transferrin allele frequencies in neighbouring Victorian populations of A. stuartii and, as in the present study, some of these populations were allopatric and sympatric with A. swainsonii (C. Moritz, personal communication). Unfortunately, the sample sizes collected by Moritz (1982) and the

present study were rather small (189 and 107 animals, respectively) and involved only transferrin. Due to unexpected financial difficulties and consequent delay in the electrophoresis, many samples collected from the Brindabellas "went off", and funding was not available for studying a large number of enzyme systems. Nevertheless, gene flow remains the best explanation for the constancy of allele frequency in neighbouring populations, and the best explanation for why A. stuartii and A. swainsonii still compete. Other possibilities, such as fixing of allele frequencies by stabilising selection, can be discounted because of the large differences that occurred between Brindabella and non-Brindabella populations.

7.3 DIVERGENCE AND THE REDUCTION OF INTERSPECIFIC COMPETITION

7.3.1 Divergence in body size

In Antechinus and other species of small dasyurids, congenors usually coexist only if they differ in their body sizes (Fox 1982a). Body size is not of itself a niche difference, however, but is related to the exploitation of different sources of food. Fox (1982a), for example, suggested that different sized dasyurids could exploit different sized prey (see also Hall 1980b), while Wilson (1975) demonstrated that, in general, larger predators can take large prey that are not available to smaller predators. Since the two species of Antechinus compete for food (Chapter 5), it seems reasonable to expect that divergence in their body sizes should be especially effective in reducing competition.

However, before proceeding with this line of thought, it is necessary to reassess some earlier, apparantly contradictory findings,

concerning body size and competition. The problem is why juvenile female A. stuartii - the smallest individuals in A. stuartii populations - appear to be more adversely affected by competition from A. swainsonii than either males or parous females (section 2.6). Apart from speculation that A. swainsonii mistakes juvenile females for insects more often than the larger males or parous females (section 6.4), two explanations can be proposed. First, sample sizes for juvenile females were usually arger than for males and parous females, and variances were often smaller, so that statistically significant effects were easier to detect. Second, juvenile females may be socially subordinate to larger conspecific males and parous females (Lee 1972), and so face interference competition from conspecific as well as congeneric individuals. The removal of A. swainsonii would eliminate interspecific competition and temporarily reduce intraspecific competition on juvenile females, and thus allow them to expand their use of resources proportionately more than either males or parous females. Both explanations suggest that the responses of male and female A. stuartii to interspecific competition may not be markedly different, and hence that the paradox of intense competition between individuals of very different body sizes is more apparent than than real.

Sympatric A. stuartii and A. swainsonii differ in their head-body lengths by a ratio of 1.3-1.35, and it has been suggested that this difference in maintained, in part, by differences in when they breed (Dickman 1982a). Both species breed only once a year and live, on average, for little more than a year, so the species that breeds first gains an advantage in growth over the other species. Since in this case the earlier breeding species (A. swainsonii) is already the larger

of the pair, its early growth advantage further enhances and maximises the interspecific difference in size. The amount of size enhancement due to "staggering" of breeding can be illustrated as follows. In the Brindabellas, A. swainsonii mates a month earlier than A. stuartii, so except for a few parous females, individuals of the two species differ in age by one month. In July 1979, when A. swainsonii was aged 11 months and A. stuartii 10 months, mean head-body measurements (mm) of the two species were:

	A. stuartii	A. swainsonii	Size ratio
♂	97.2 (n=11)	128.8 (n=8)	1.33
♀	89.3 (n=11)	116.2 (n=5)	1.30

If A. stuartii had mated at the same time as A. swainsonii, the size ratio between the species would inevitably diminish. By how much? In August 1979, when A. stuartii was aged 11 months, mean head-body measurements (mm) had increased from the previous month:

	A. stuartii
♂	100.7 (n=11)
♀	91.4 (n=11)

Thus, if the time of mating of the two species was synchronised, the size ratio between the two species would decline to only 1.28 (males) and 1.27 (females). Clearly, selection need not simply favour absolute differences in the size of the two species, since some divergence can also be effectively maintained by differences in when they breed. This argument is strengthened by the observation that A. stuartii mates later than A. swainsonii in 27 out of 28 localities where they occur together (Dickman 1982a).

Seasonal breeding in Antechinus has obviously not evolved simply as a mechanism to maintain interspecific size differences, and it is influenced by a range of other parameters. Lee et al. (1977) suggested that mating is so timed that lactation and the weaning of young coincide with a flush in insect abundance in spring and summer, while Wainer (1976) proposed further that reproductive phase differences between Victorian populations of A. stuartii and A. minimus were a result of dietary preferences for insect groups that peak at different times. Antechinus stuartii and A. swainsonii also mate later at higher altitudes, and the former species also mates later at lower latitudes (Dickman 1982a).

In view of these many influences on the timing of mating, it is difficult to disentangle the interspecific effects alone. Nevertheless, the times of matings of the two species of Antechinus were investigated in populations at 43 localities in a relatively small area (39,000 km^2) of their respective geographical ranges. Times of matings were obtained from five sources: published records, unpublished theses, museum specimens, personal observations, and field observations provided by other researchers (Dickman 1982a). For each population, a mean time of mating was estimated to the nearest quarter of a month and assigned a corresponding numerical value. (For example, a population mating in the last two weeks of August was assigned a value of 8.75 on the assumption that mating was centred about the third quarter of the eighth month). This procedure assumes that mating in any population is synchronous and varies little from year to year (Wood 1970, Lee et al. 1982, Dickman et al. in press), and it assigns a mean value for time of mating but ignores the variance.

Times of matings were then investigated in relation to seven parameters:

1) Altitude (m)

2) Latitude (degrees and minutes south).

3) Longitude (degrees and minutes east).

4) Congeneric effect. This was calculated from trapping results in each locality as the ratio of numbers of one species to the other. For A. stuartii, for example, the congeneric effect is 0 if no A. swainsonii are present, 1 if equal numbers of the two species are present, and >1 if A. swainsonii is the more abundant species.

5) Distance (km) to the nearest congeneric population. For A. stuartii sympatric with A. swainsonii this value is 0, but for allopatric A. stuartii it is >0.

6) Structural habitat complexity. Measurement of this parameter was described in section 2.4.3. The mean of 100 scores in each locality was used as a measure of mean habitat complexity ($\bar{x}$).

7) Habitat variability. The standard deviation, S, of $\bar{x}$ was used as a measure of the variation in habitat complexity. This was standardised by calculating:

$$V = \frac{100S}{\bar{x}},$$

where V represents the coefficient of habitat variability.

Multiple regression analysis showed that, in A. stuartii, altitude (R^2 = 42%, F = 25.49, P < 0.001) and congeneric effect (R^2 = 34.5%, F = 19.62, P < 0.001) influenced time of mating, but in A. swainsonii only altitude (R^2 = 77%, F = 39.86, P < 0.001) was important. In

both species mating began later at higher altitudes, and in A. stuartii it was delayed further when the numbers of sympatric A. swainsonii were high. At altitudes of less than 1000 m the two species are usually sympatric and mate at different times, but at higher altitudes (> 1500 m) they are allopatric and mate at the same time (Dickman et al. in press). When regression slopes (time of mating versus altitude) of sympatric and allopatric A. stuartii are plotted separately, mating in sympatric populations is significiantly later than in allopatric ones (Fig. 3b, in Dickman et al. in press).

These findings show that the time of mating of A. stuartii is delayed by altitude and by the presence of A. swainsonii, and hence support the suggestion above that temporal differences in breeding enhance the differences in size between the two species. This is prima facie evidence for an unusual kind of character displacement, in which divergence in a morphological parameter (body size) is produced indirectly by divergence in a reproductive one (time of mating). However, the divergence is one-sided and involves A. stuartii only, the species most adversely affected by interspecific competition.

What is the advantage to A. stuartii in being small relative to A. swainsonii? It was mentioned above that differences in body size between species could promote differences in the food resources they exploit. Such differential exploitation could be achieved in two ways. Two sympatric species could diverge in (a) the kinds of food they eat, or (b) where they forage. In (a) the two species could overlap in their foraging microhabitats and not compete (syntopic coexistence, after Rivas 1964), whereas in (b) they could eat the same types and sizes of prey and not compete (allotopic coexistence). Overlap in

foraging microhabitat is probably possible only if no interference effects occur between species, so that for Antechinus, where interspecific interference is important (Chapter 6), we should expect to find that coexistence of the two species is allotopic. I will suggest below that interspecific differences in body size also promote allotopic co-existence, and that syntopy does not occur.

The case for syntopic coexistence rests on the belief that different sized animals eat different sized prey. Wilson (1975) concluded, in part, that larger predators use food sizes that are unavailable to smaller predators, whereas the reverse is much less true; this gives larger predators a competitive advantage. Hall (1980b) found that the prey taken by A. swainsonii were, on average, 23% larger than those taken by A. stuartii; this, and the competitive superiority of A. swainsonii that was found in the present study, ostensibly fit the Wilson (1975) model. Fox (1982a) has suggested further that body size differences and prey size separation could play an important role in dasyurid community organisation.

It is not clear, however, why predator body size should correlate with prey size. Hutchinson (1959) proposed that coexisting species should differ instead in the sizes of their trophic apparatuses (e.g. beaks or jaws), and showed that the minimum size difference between the larger and smaller members of a pair was usually about 1.3. But, this ratio is not obtained when skull parameters of A. stuartii and A. swainsonii are compared. The following data (mean measurements in mm for males and females combined, from a sympatric population in Victoria (Wakefield and Warneke 1963, 1967)) illustrate this:

	A. stuartii	A. swainsonii	Size ratio
Basalar length	22.79	28.20	1.24
Zygomatic breadth	14.76	16.04	1.09
Palatar length	12.46	15.71	1.26
Length M^{1-3}	4.79	5.31	1.11
Breadth at M^3	8.21	8.78	1.07

Compared these ratios with the ratios for head-body lengths (1.3-1.35, see above), it is obvious that the two species are convergent in the sizes of their trophic apparatuses. Hence, it is doubtful that body size differences really do reflect differences in prey size.

Despite finding that A. swainsonii takes larger prey than A. stuartii, Hall (1980b) still concluded that the two species are generalist, opportunistic feeders. In the present, study A. stuartii also ate generally smaller prey than its larger congenor, but when A. swainsonii was removed, the proportion of large prey in the diet of A. stuartii increased (section 2.5.4.3). Clearly this species is capable of eating large prey, but in the presence of its terrestrial congenor it simply encounters them less frequently. In captivity, both species selectively take longer prey ($\geq$ 20 mm) in preference to smaller ones ($<$ 10 mm) irrespective of whether the prey are beetles, cockroaches, locusts or mealworms (unpublished findings). Except for rare invertebrates, such as Embioptera and Onychophora, both species took every type of prey that was collected in the pitfall, litter and casual sampling programmes, and moreover, they also ate occasional vertebrates and fruits.

These combined findings dispel any last doubt that the body size differences of the two species of Antechinus are related to the size or type of prey they eat. Before going further, it is worth considering why this is so. The largest invertebrates that are potentially available to A. stuartii are cicadas centipedes, locusts oligochaete worms and certain larvae. All except locusts have soft cuticles, and all may be killed or immobilised by the same deft bites to the head region with which the antechinus despatches smaller prey. Hence, there is little risk or energetic loss for A. stuartii to attack large prey when it encounters them, and the potential benefits in energy gain are relatively great. In addition, A. stuartii is an active rather than a sit-and-wait predator. Since many of its prey are also active and free-moving, this species probably cannot afford to develop a specific search image but realises its highest capture success by pursuing and attacking prey swiftly.

The case for allotopic coexistence in Antechinus rests largely on the assumption that body size differences allow differential access to prey. Very simply, the small size of A. stuartii allows it access to a wide range of arboreal prey (e.g. foliage insects, trunk and bark fauna), whereas the larger size of A. swainsonii allows it access to prey in the forest litter (e.g. larvae, Amphipoda). The bark of several species of Eucalyptus is rough and fissured, and it can provide a suitable environment for a wide range of invertebrates (e.g. Lawrie 1974). However, the fissures are narrow (1-2 cm), so that only the smaller antechinus could gain access to them. Other Eucalyptus trees periodically shed their bark, and for much of the year a narrow gap (½-2 cm) exists between the loosening bark and the main tree trunk. When the bark detaches fully from the trunk it

frequently curls lengthwise to form tubes, and hangs loosely over tree forks or shrubs. Although bark peeling displaces many invertebrates from the tree trunks onto the forest floor (Chapter 4), the tubes and the gaps between the bark and tree trunk harbour a rich invertebrate fauna, but they are accessible only to predators such as A. stuartii that are small enough to squeeze into them. Access for the larger A. swainsonii would be prohibited.

Although small size may favour arboreal foraging, it is not clear why a relatively large body size should, of itself, favour access to invertebrates of the forest litter. The two species of Antechinus can exploit terrestrial sources of food (although A. stuartii does so only in the absence of A. swainsonii), and McNab (1979) concluded that - other things being equal - small animals dig and burrow more efficiently than larger ones. If, however, larger body size is associated with greater "strength" (ability to displace soil and litter), it is likely that A. swainsonii more rapidly exposes buried invertebrates than its smaller congenor, and hence achieves a higher success rate.

Although interspecific competition may select for small bodied A. stuartii and large bodied A. swainsonii, there are presumably other ecological, physical and physiological constraints on size. For A. swainsonii, which is the superior competitor, the selective advantages of being much bigger are probably minimal and balanced by the rate at which it would need to harvest larger amounts of food. This species takes many sessile prey that are buried in the forest litter; they are presumably available day and night. Since A. swainsonii already forages throughout the 24h cycle, it may simply be unable to maintain a larger body size. In addition, over much of its

geographical range (but not in the Brindabellas), A. swainsonii occurs alongside the Long-nosed Bandicoot Perameles nasuta and the Southern Brown Bandicoot Isoodon obesulus. Competition with these larger, partly insectivorous marsupials could conceivably place a further constraint on the upper body size of this species. (Very large A. swainsonii, up to 178g and 188mm head-body, have been collected on the north and central coast of New South Wales (e.g. Australian Museum specimen No. AM9834). Unfortunately, further ecological information from these localities is completely lacking).

For A. stuartii, in contrast, most prey are free moving and many (e.g. huntsman spiders, Dermaptera, some Coleoptera) emerge only at night. The smaller antechinus forages for only this part of the 24h cycle and hence may be unable to gather enough energy to maintain a larger body size. Conversely, although a smaller body size may facilitate access to a larger population of bark invertebrates, this advantage may be weighed against physiological (e.g. thermoregulatory) costs, and the disadvantages of specialising on a seasonal food source. Further, in drier and more sparsely wooded habitats where A. swainsonii is absent, A. stuartii often occurs alongside one of two smaller species of dasyurids, the Common Dunnart Smithopsis murina or the White-footed Dunnart S. leucopus. Competition between the antechinus and dunnarts is suspected (Fox 1982b, Dickman in press, a), and although A. stuartii is probably the superior competitor, the dunnarts could place a lower limit on the size of this species. Conceivably selection for large size in A. stuartii where it is sympatric with a dunnart, and for small size where it is sympatric with A. swainsonii, could contribute to the differences in body sizes of A. stuartii populations that are allopatric and sympatric with A. swainsonii (Table 7.2).

Body size differences promote coexistence among other species of mammals, such as mustelids (Simms 1979, King and Moors 1979, Moors in press). King and Moors (1979) note that sympatric weasels and stoats differ in their head-body lengths by a ratio of 1.1-1.3 and also take prey of different sizes. However, the two species also differ in where they forage. The smaller and more elongate weasels forage in vole runways, whereas stoats frequently enter rabbit burrows. Stoats are too large to enter vole runs and so "lose" in exploitation competition with weasels, but they exclude their smaller congenors elsewhere and hence "win" in interference competition (King and Moors 1979). Body size differences exist in other mammal communities (McNab 1971, Coe 1975, Brown 1975) but their function and importance are less well understood.

7.3.2. Divergence in other parameters

Although body size differences allow the two species to exploit different arboreal and terrestrial sources of food, it is possible that divergence may also occur in tail size. Thus tail lengths of A. stuartii (measured as a percentage of head-body length) are relatively long in populations that occur with A. swainsonii, but short in populations that occur alone (Table 7.2). When it is climbing or changing direction, the tail of A. stuartii flicks from one side of the body to the other and presumably helps the animal maintain its balance. If tail length is associated with climbing ability (see Horner 1954, Martin 1968, Hickman 1979), the longer tails of sympatric A. stuartii may facilitate greater access to arboreal sources of food, and hence alleviate competition with the terrestrial A. swainsonii. In this context, it is of interest to note that the tail lengths of the three

New Guinea species of Antechinus are always 111-126% longer than their respective head-body lengths (Bishop Museum (Honolulu) Records, courtesy of Dr. A.C. Ziegler). All three species are partially arboreal inhabitants of rainforest (Ziegler 1977, 1982), and their relatively long tails presumably increase their climbing ability. Tail length may obviously be influenced by factors other than those suggested above (indeed there is evidence suggestive of a north-south cline in Table 7.2), but with a larger data set, multivariate methods could again be used to separate their relative importance.

In some genera of rodents, species that inhabit complex three-dimensional environments have relatively large brains, whereas those inhabiting simple terrestrial environments have small brains (Lemen 1980, Mace and Eisenberg 1982). In Antechinus, however, there is no further information available to investigate whether divergence occurs in this, or in other parameters.

7.3.3 Sexual dimorphism in body size

In Australia, usually no more than two or three species of dasyurids coexist (Fox 1982a), whereas in New Guinea up to six or seven species can occur together (Gressitt and Nadkarni 1978). Australian dasyurids, in contrast to their New Guinea relatives, show marked sexual dimorphism in size; Fox (1982a) has suggested that this increases the niche width of each species and so reduces the resources available for additional species.

In the present study, male and female A. stuartii and A. swainsonii differed strongly in size, and this complicates the argument (Section 7.3.1.) that simple interspecific differences in size alone

facilitate coexistence. Adult male A. swainsonii are 1.12 times longer (in head-body) than females, but 1.33 times and 1.47 times longer, respectively, than male and female A. stuartii. In contrast, female A. swainsonii are only 1.19 times larger than male A. stuartii, but 1.33 times longer than females. Considering body size alone, male A. swainsonii and female A. stuartii would be expected to compete slightly, whereas male A. stuartii and female A. swainsonii would be expected to compete more strongly. Further, since selection for divergence should also be strongest in the latter pair, this should lead to smaller dimorphic ratios in sympatric populations than in allopatric ones. There is some evidence that this occurs: In allopatric populations of A. stuartii males are 1.18 times longer (in head-body) than females, whereas in sympatric populations males are only 1.12 times longer (combined data for all populations in Table 7.2).

Sex ratios of A. stuartii pouch young are usually female biassed, whereas those of A. swainsonii are male biassed (sections 2.5.3.2 and 2.5.5.2). Although these differences may be due to interspecific differences in female longevity and differential probability of mother-daughter competition (Cockburn et al., manuscript), it is of interest that they could also reduce interspecific competition. If, for example, sex ratios of pouch and independent young of both species were 0.5 and individuals of both species "mixed" randomly, the probability of a male A. stuartii encountering a female A. swainsonii is 0.25. (This species-sex combination is chosen as an example since, on body size, they would be expected to compete most strongly). If, however, the sex ratio of A. stuartii were 0.4 (40% male) and that of A. swainsonii 0.6 (60% male), the probability of a

male A. stuartii encountering a female A. swainsonii would be only 0.16. Although the two species of Antechinus do not, of course, mix randomly, this simple example shows that sex ratio variations could alter the probability of encounters between individuals of particular species-sex classes. It would be of interest to investigate whether sex ratios of allopatric populations approach parity.

As with body size, dimorphic size ratios probably represent a trade-off of different selective pressures. In eastern Australia, all species of Antechinus mate once a year (Braithwaite and Lee 1979, Lee et al. 1982). Males die shortly after mating, and competition among males for mates is probably intense. In A. stuartii, large "dominant" males probably mate before small males, thus maximising their fitness, and most offspring may be fathered by relatively few individuals (Braithwaite 1979). Hence large males probably contribute disproportionately to the gene pool and contribute both to the maintenance of strong sexual dimorphism and to the unusual life history of this species (Braithwaite 1973, 1979). However, males that are too large may suffer in competition from other species, or kill females before or during copulation (personal observations). These individuals would contribute nothing to the gene pool. Lucid discussions of sexual and ecological aspects of size dimorphism are found in Selander 1969, 1971, 1972; Glucksmann 1978).

7.4 CONCLUSIONS

I have suggested that gene flow between populations of A. stuartii in the Brindabella Range results in continued interspecific competition, but also argued that divergence in body size, and perhaps tail size, promotes allotopic coexistence and reduces

competition. Although these notions appear to be contradictory, a balance between gene flow and divergence may depend on the local distributions of the two species. The Brindabella distribution pattern (A. swainsonii localised, A. stuartii widespread) is more or less typical throughout the ranges of the species. In general, assuming that gene flow occurs elsewhere, competition may always occur if the overlap area for A. stuartii is small relative to the adjacent area of allopatry. Conversely, if the overlap area is large relative to the area of allopatry, locally sympatric A. stuartii may diverge so that competition is reduced. A gradient in the intensity of competition may then result, being most intense near the allopatry/sympatry border and least in the centre of the area of overlap. It would be of great interest to measure gene flow and body size in other populations of Antechinus to examine whether these expectations are generally true.

Multivariate methods could be used, as above, to assess whether divergence was due to competition or to other factors.

Further research into competition among Antechinus should try to measure the diffuse effects of species in other, more distantly related taxa, as well as intraspecific effects. Fenton and Fleming (1975), Brown and Davidson (1977) and Landeen et al. (1979) have already demonstrated that competition occurs between taxonomically unrelated species, and Fox (1981) has pioneered a potentially very useful method for investigating diffuse effects in diverse natural communities of small mammals. In the Brindabellas, a large number of partly or wholly insectivorous vertebrate species could compete with Antechinus; these include the Eastern Pygmy-possum Cercartetus nanus, the Feathertail Glider Acrobates pygmaeus, the Sugar Glider

Petaurus breviceps and many species of birds, reptiles and amphibians. Although large scale manipulation studies of all these species would not be possible or even desirable, initial investigations could profitably attempt to measure basic patterns of resource use and overlap. Subsequent manipulations of selected species could then investigate individual niche shifts or shifts in control of trophic energy (Van Valen 1976). Judging from the preliminary results of Montgomerie (1977), analysis of energy budgets may prove to be most fruitful for studying intensity and mechanisms of competition in diverse communities.

In Chapter 1, a hypothesis was proposed that A. stuartii and A. swainsonii compete with each other under natural conditions. It was further proposed to document any changes in the population parameters or patterns of resource use of the two species that were attributable to competition, and to investigate in detail the nature of interspecific interactions. Much evidence has subsequently been presented that the two species do compete, and the null hypothesis of "no competition" has been rejected. Moreover, competition between A. stuartii and A. swainsonii was seen to be a complex but subtle and dynamic process, varying on a local and geographical scale, and differing in intensity at different times of the year. The abundance, trappability and simple life history of these shy but curious and beautiful animals renders them ideal for further research. They should serve as an ideal starting point for investigations of competition throughout the Marsupialia.

Table 7.1 Allele frequencies (%) for transferrin in plasma of Antechinus stuartii

Locality	Distance to nearest A.sw population (km)	Sample size (N)	Alleles "a"	Alleles "b"
Brindabella region				
Bushranger Creek	0	23	78	22
Warks Road	0	19	79	21
Blundell Creek	0	13	92	8
Lees Creek	0	23	83	17
Tidbinbilla	0	3	83	17
Kangaroo Creek	0.5	8	81	19
Bullen Range	6	3	83	17
Nr. Murrumbateman	33	1	100	0
Non Brindabella region				
Tallaganda	0	2	25	75
Kioloa	0	12	33	67

Table 7.2. Head-body and tail measurements of A. stuartii in populations allopatric and sympatric with A. swainsonii. All measurements are of animals aged 9-12 months.

Locality	Sex	Head-body length (mm) ± s.d. (N)	Tail length (mm) ± s.d. (N)	Tail as % of head body	Source
(a) Sympatric populations					
Lees/Blundell	♂	99.3 ± 3.2 (18)	91.5 ± 3.4 (18)	92	1
Creeks, A.C.T.	♀	88.7 ± 2.2 (16)	80.8 ± 3.4 (16)	91	
Tidbinbilla,	♂	98.0 ± 5.1 (4)	92.3 ± 4.6 (4)	94	2
A.C.T.	♀	88.5 ± 3.8 (5)	80.6 ± 3.2 (5)	91	
Thredbo,	♂	92.9 ± 3.1 (9)	90.0 ± 3.0 (9)	97	3,4
N.S.W.	♀	84.7 ± 3.0 (7)	81.3 ± 2.9 (5)	96	
Bega	♂	96.4 ± 3.5 (16)	94.7 ± 5.6 (17)	98	5
N.S.W.	♀	85.7 ± 2.3 (13)	85.8 ± 2.6 (13)	100	
Newnes	♂	104.7 ± 7.3 (22)	94.8 ± 11.3 (22)	91	5
Plateau, N.S.W.	♀	89.6 ± 5.1 (14)	79.9 ± 6.2 (14)	89	
Barrington,	♂	96.2 ± 4.4 (27)	86.2 ± 3.8 (27)	90	6
N.S.W.	♀	84.2 ± 4.9 (13)	78.6 ± 3.5 (13)	93	
Bungwahl,	♂	97.8 ± 16.5 (21)	86.3 ± 7.1 (21)	88	7
N.S.W.	♀	88.3 ± 11.8 (11)	80.1 ± 14.2 (11)	91	
Kioloa,	♂	100.9 ± 4.3 (10)	98.5 ± 4.0 (10)	98	1,8
N.S.W.	♀	90.8 ± 3.9 (9)	86.7 ± 4.3 (9)	95	
Guy Fawkes	♂	112.1 ± 4.6 (17)	98.9 ± 5.3 (17)	88	4,9
N.S.W.	♀	97.4 ± 4.0 (8)	88.2 ± 4.1 (8)	91	
Loch Valley,	♂	95.3 ± 6.5 (58)	98.0 ± 5.6 (58)	103	10
Vic.	♀	84.9 ± 5.2 (13)	87.5 ± 6.2 (13)	103	

Table 7.2 (continued)

Powelltown, Vic.	♂	104.0 ± 5.0 (6)	102.0 ± 4.0 (6)	98	11
	♀	95.0 ± 3.0 (10)	86.0 ± 9.0 (10)	91	
Mean				94	
(b) Allopatric populations					
Bullen Range, A.C.T.	♂	101.8 ± 2.1 (6)	90.8 ± 4.9 (6)	89	1
	♀	88.5 ± 2.7 (5)	80.1 ± 3.6 (5)	91	
Murrumbateman, N.S.W.	♂	99.3 ± 5.9 (15)	84.0 ± 3.7 (15)	85	12
	♀	91.5 ± 4.2 (12)	78.1 ± 6.2 (12)	85	
Wandandian, N.S.W.	♂	115.4 ± 3.6 (5)	104.8 ± 4.1 (5)	91	9
	♀	99.9 ± 5.2 (9)	92.1 ± 4.4 (9)	92	
Sunny Corner, N.S.W.	♂	109.9 ± 6.7 (18)	82.6 ± 3.2 (18)	75	3,13
	♀	91.0 ± 4.5 (7)	70.4 ± 3.1 (7)	77	
Kuringai, N.S.W.	♂	119.9 ± 12.3 (17)	95.2 ± 2.5 (16)	79	3
	♀	93.1 ± 7.2 (9)	80.8 ± 4.1 (9)	87	
Levers Plateau, N.S.W.	♂	119.5 ± 5.3 (15)	99.8 ± 5.5 (15)	84	3
	♀	98.0 ± 5.4 (4)	83.0 ± 12.2 (4)	85	
Mt. Glorious Qld	♂	116.6 ± 6.8 (115)	96.5 ± 5.8 (114)	83	14
	♀	102.2 ± 5.8 (32)	88.5 ± 5.1 (32)	87	
Mean				85	

Sources: 1, this study; 2, P. Filmer (pers. comm.); 3, A.B. Rose (pers. comm.); 4, CSIRO Museum, Division of Wildlife Research; 5, Australian Museum, 6, A. Press (pers. comm.); 7, Lim (1979); 8, C.R. Tidemann and D.P. Woodside (pers. comms); 9, British Museum (Natural History) and American Museum of Natural History; 10, Wakefield and Warneke (1967); 11, Leonard (1972); 12, Dickman (1980); 13, D. Goldney (pers. comm); 14, Van Dyck (1982).

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Appendix 1. Studies concerning the small marsupials of Australia and New Guinea. (On microfiche). This is a bibliography of studies that have been reviewed for evidence suggestive of competition.

APPENDIX I.

Appendix 2. Summary of some aspects of the biology of Antechinus. References on general physiology, the physiological aspects of male die-off, palaeontology and responses to fire and habitat destruction are not listed, but may be found in Archer (1982).

(a) Antechinus stuartii

Subject	Biological notes and reference sources
Taxonomy	Two subspecies are recognised, A. s. stuartii and A. s. adustus (Wakefield and Warneke 1967, Van Dyck 1982). All following notes refer to A. s. stuartii.
Range	Geographical: Western Victoria to south-eastern Queensland (Wakefield and Warneke 1967, Dickman 1982a, Van Dyck 1982). Altitudinal: 0-2000 m (Newsome and Catling 1979, Green and Osborne 1979).
Habitat*	Tall closed-forest (rainforest) (Wood 1970, Braithwaite 1979); tall open-forest (Tyndale-Biscoe and Calaby 1975, Stewart 1979a, Gullan and Robinson 1980); open-forest and woodland (Dickman 1980, Statham and Harden 1982); lowland heath (Braithwaite et al. 1978, Fox 1982b); rock tors (Green and Osborne 1979, Dickman et al. in press), coastal dunes and cliffs (Wakefield and Warneke 1967); exotic pines (Barnett et al 1976, Suckling and Heislers 1978). Statham and Harden (1982) record maximum densities (numbers per hectare) as 2.8 in tall woodland and logged tall closed-forest, 4.4 in tall open-forest and 1.9 in open forest.

Appendix 2. (cont'd.)
(a) A. stuartii

Subject	Biological notes and reference sources
Breeding	Mating occurs only for a short period (about 2 weeks) in winter, after which all males die (Wood 1970). Gestation lasts for about 27 days (Selwood 1980), pouch life for 5 weeks and nest life for about 8 weeks, after which the young are independent (Woolley 1966, Wood 1970). Nipple numbers vary from 6-10 (Lee et al. 1982).
Population dynamics	Numbers are highest in spring and summer following the influx of juveniles into the population. Numbers decline thereafter and are lowest after male die-off in winter (Wood 1970, Statham and Harden 1982).
Movements	Males range further than females, especially near mating (Wood 1970, Barnett et al. 1977). Both sexes are partly arboreal (Wood 1970, Hall and Lee 1982).
Behaviour	Copulation is violent and protracted (Marlow 1961, Woolley 1966). Maternal behaviour and nest building are described by Settle and Croft (1982a); the development of young by Settle and Croft (1982b). Agonistic interactions among males lead to the formation of a male dominance hierarchy 4-5 months before mating (Braithwaite 1974); a female-dominated hierarchy was described by Rigby (1972), but this study used senile males.
Activity	Nocturnal/crepuscular (Wood 1970, Hall 1980a, Warden and Wallis 1979).

Appendix 2 (cont'd.)
(a) A. stuartii

Subject	Biological notes and reference sources
Diet	Invertebrates, especially arthropods (Leonard 1972, Hall 1980b) and occasionally plant material (Statham 1982a).
Predators	Foxes (Townsend 1977, Green and Osborne 1981), feral cats (Jones and Coman 1981) and owls (Seebeck 1976; ?Tilley 1982).

* Habitat classification follows Specht (1970).

Appendix 2 (cont'd.)

(b) Antechinus swainsonii

Subject	Biological notes and reference sources
Taxonomy	Two subspecies are recognised, A. s. swainsonii (Tasmania) and A. s. mimetes (mainland Australia) (Wakefield and Warneke 1963). Notes on the biology of A. s. swainsonii are given by Wakefield and Warneke (1963), Green (1972) and Hocking (1975); all following notes refer to A. s. mimetes.
Range	Geographical: Western Victoria to south-eastern Queensland (Wakefield and Warneke 1963, Dickman 1982a, Van Dyck and Ogilvie 1977). Altitudinal: 0-2227 m (Newsome and Catling 1979, Dimpel 1976).
Habitat*	Tall closed-forest (Van Dyck and Ogilvie 1977); tall open-forest (Tyndale-Biscoe and Calaby 1975, Stewart 1979a, Gullan and Robinson 1980); open-forest and woodland (Wakefield and Warneke 1963); lowland heath (Braithwaite et al. 1978, Newsome and Catling 1979); upland (alpine) heath (Newsome and Catling 1979, Dickman et al. in press); rock tors (Green and Osborne 1979, Dickman et al. in press); coastal dunes (Wakefield and Warneke 1963); exotic pines (Suckling and Heislers 1978). These studies suggest that the order of abundance is : alpine heath J tall open-forest J open-forest J woodland and tall closed-forest.

Appendix 2 (cont'd.)

(b) A. swainsonii

Subject	Biological notes and reference sources
Breeding	Mating occurs only for a short period (about 2 weeks) in winter, after which all males die (Lee et al. 1977, 1982). Gestation lasts for 29-35 days (Williams and Williams 1982), pouch life for 5½-8 weeks and nest life for up to 7 weeks, after which the young are independent (unpublished findings, Fleay 1932, Williams and Williams 1982). Nipple numbers vary from 6-10 (Lee et al. 1982).
Population dynamics and movements	Similar to A. stuartii (Leonard 1972), but appears to be less arboreal (Hall and Lee 1982).
Behaviour	Copulation, some aspects of the development of young, and maternal behaviour, are similar to A. stuartii (Williams and Williams 1982). Quantitative descriptions of behaviour have not been published, but qualitative notes are given by Fleay (1932) and Dickman (in press,b).
Activity	Equally active by and by night (Hall 1980a, Warden and Wallis 1979).
Diet	Invertebrates, especially arthropods (Leonard 1972, Hall 1980b).
Predators	Foxes (Green and Osborne 1981), feral cats (Jones and Coman 1981) and owls (?Tilley 1982).

* Habitat classification follows Specht (1970).

Appendix 3a. Body weights of male Antechinus stuartii. Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	C1	E1	E2	F_a	F_p	Conclusion
1978		Antechinus swainsonii not manipulated				
May	23.2±2.1 (9)	23.7±2.3 (7)	24.0±1.9 (9)	0.33	-	C1 E1 E2
June	23.7±2.0 (10)	24.6±1.7 (7)	24.8±2.5 (8)	0.68	-	C1 E1 E2
July I	24.3±2.1 (8)	24.8±1.8 (8)	25.2±2.0 (12)	0.52	-	C1 E1 E2
		Antechinus swainsonii removed from E1 and E2				
July II	24.9±2.1 (9)	24.8±1.4 (9)	25.9±2.2 (9)	0.88	0.37	C1 E1 E2
August	28.1±2.2 (10)	25.8±2.8 (8)	26.9±2.5 (12)	2.11	3.14	C1 E1 E2
1979						
January	18.0 (1)	15.0±2.0 (3)	15.0 (1)	-	-	-
February	21.1±3.3 (7)	18.7±1.3 (10)	18.0±1.5 (7)	4.23^{*}	8.08^{**}	C1 E1 E2
March	25.6±2.9 (7)	22.8±1.5 (9)	24.2±1.8 (8)	3.59^{**}	5.07^{**}	C1 E1 E2
April I	23.3±2.3 (9)	20.7±2.0 (16)	20.4±1.7 (10)	6.01	11.95	C1 E1 E2
		Antechinus swainsonii reintroduced only to E1				
April II	24.8±2.6 (9)	20.3±2.3 (13)	21.1±2.7 (9)	8.83^{**}	1.65	C1 E1 E2
May	23.9±2.0 (9)	21.5±1.8 (12)	21.5±1.9 (13)	5.61	2.49	C1 E1 E2
June	23.3±2.9 (9)	21.9±2.2 (11)	21.4±1.6 (10)	1.78	1.49	C1 E1 E2
July	24.6±2.0 (7)	23.1±2.5 (7)	23.5±2.9 (12)	0.61	0.15	C1 E1 E2
August I	27.6±2.4 (11)	25.5±2.7 (13)	25.0±2.5 (13)	3.26	2.77	C1 E1 E2
August II	-	26.5±2.3 (7)	26.1±3.2 (9)	0.07	-	-

Appendix 3b. Body weights of female Antechinus stuartii (<1yr old). Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	C1	E1	E2	F_o	F_p	Conclusion
1978		Antechinus swainsonii not manipulated				
May	16.3±1.1 (8)	15.7±1.1 (7)	16.7±1.4 (9)	1.17	-	C1 E1 E2
June	17.6±2.1 (7)	17.1±1.1 (6)	16.3±1.2 (8)	1.48	-	C1 E1 E2
July I	16.4±1.1 (7)	16.4±0.8 (7)	15.8±1.2 (8)	0.86	-	C1 E1 E2
		Antechinus swainsonii removed from E1 and E2				
July II	16.2±0.6 (7)	16.0±1.0 (8)	16.2±0.9 (7)	0.15	0.08$_*$	C1 E1 E2
August	18.1±1.1 (8)	17.2±1.2 (8)	16.8±0.9 (6)	2.76	4.95*	C1 E1 E2
1979						
January	14.3±0.4 (2)	11.9±1.2 (5)	11.0±1.2 (4)	5.49$^*_*$	9.59$^*_*$	C1 E1 E2
February	16.4±1.5 (10)	14.9±1.3 (14)	14.9±1.5 (13)	3.71$_{***}$	7.41$_{***}$	C1 E1 E2
March	18.6±1.3 (8)	16.0±0.9 (14)	16.2±1.3 (16)	15.22$_{***}$	30.52$_{***}$	C1 E1 E2
April I	18.2±1.6 (9)	16.0±1.2 (14)	15.6±1.2 (15)	12.50	24.47	C1 E1 E2
		Antechinus swainsonii reintroduced only to E1				
April II	17.2±1.1 (8)	16.1±1.2 (13)	16.4±1.2 (13)	2.16	0.06	C1 E1 E2
May	16.6±1.7 (7)	16.0±1.2 (12)	15.4±1.4 (14)	1.78$_*$	2.69	C1 E1 E2
June	17.7±2.4 (6)	15.7±1.3 (11)	16.2±1.1 (11)	3.44	0.07	C1 E1 E2
July	17.1±0.7 (6)	16.5±1.3 (10)	15.9±1.2 (9)	1.94	2.76	C1 E1 E2
August I	17.0±1.0 (6)	16.1±0.6 (9)	16.2±0.7 (10)	3.16	0.58	C1 E1 E2
August II	-	18.6±1.8 (7)	18.0±0.8 (9)	0.76	-	-

Appendix 3c. Body weights of female Antechinus stuartii (>1yr old). Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	C1	E1	E2	F_o	F_p	Conclusion
1978		Antechinus swainsonii not manipulated				
May	24.0 (1)	22.0 (1)	-	-	-	-
June	22.0 (1)	24.5 (1)	-	-	-	-
July I	21.0 (1)	-	-	-	-	-
		Antechinus swainsonii removed from E1 and E2				
September	22.3±1.8 (6)	22.2±1.9 (7)	21.9±1.7 (4)	0.06	0.03	C1 E1 E2
October	27.1±1.7 (4)	27.9±2.3 (5)	27.7±2.5 (3)	0.15	0.28	C1 E1 E2
November	25.3±1.2 (5)	24.8±1.3 (5)	25.0±1.8 (4)	0.15	0.27	C1 E1 E2
December	23.8±1.1 (5)	25.8±1.7 (4)	25.5±3.0 (4)	1.28	2.52	C1 E1 E2
1979						
January	27.0±2.3 (4)	25.5±3.3 (4)	25.1±2.8 (4)	0.50	0.96	C1 E1 E2
February	24.3±2.2 (4)	23.9±1.3 (4)	22.0±1.1 (4)	2.23	1.77	C1 E1 E2
March	24.9±1.4 (5)	22.6±2.1 (4)	22.5±2.4 (4)	2.14	4.27	C1 E1 E2
April I	22.8±1.8 (2)	22.0±3.5 (2)	21.4±1.9 (4)	0.24	0.39	C1 E1 E2
		Antechinus swainsonii reintroduced only to E1				
April II	21.5±2.1 (2)	22.5±2.1 (2)	21.7±2.1 (3)	0.13	0.04	C1 E1 E2
May	23.5±0.7 (2)	27.0 (1)	22.0±2.8 (2)	-	-	-
June	21.0 (1)	21.5±2.8 (2)	20.5 (1)	-	-	-
July	-	20.5±0.7 (2)	21.5 (1)	-	-	-
August I	-	21.0 (1)	22.0 (1)	-	-	-
August II	-	-	25.0 (1)	-	-	-
September	23.0±1.7 (5)	22.2±1.8 (6)	22.3±1.8 (8)	0.35*	0.12	C1 E1 E2
October	27.0±1.4 (5)	29.8±1.2 (6)	27.3±2.3 (7)	4.46*	2.09	C1 E1 E2
November	25.0±1.2 (5)	25.0±2.1 (4)	25.6±1.5 (4)	0.21	0.41	C1 E1 E2
December	26.1±0.9 (4)	25.8±1.7 (4)	24.8±1.9 (4)	0.84	1.56	C1 E1 E2

Appendix 3d. Head-body lengths of male Antechinus stuartii. Values are means (mm) ± standard deviation. Sample sizes are in brackets.

	C1	E1	E2	F_o	F_p	Conclusion
1978		Antechinus swainsonii not manipulated				
June	97.5±2.1 (9)	98.3±2.6 (7)	97.0±2.5 (10)	0.65	-	C1 E1 E2
July I	98.7±4.7 (8)	98.0±3.4 (8)	96.3±2.0 (11)	1.28	-	C1 E1 E2
		Antechinus swainsonii removed from E1 and E2				
July II	97.1±3.6 (9)	97.3±3.0 (9)	97.1±4.2 (8)	0.01	0.00	C1 E1 E2
August	99.8±2.1 (10)	99.7±3.4 (8)	97.3±3.6 (10)	2.08	1.35	C1 E1 E2
1979						
January	-	86.5±2.1 (2)	-	-	-	-
February	85.8±2.6 (6)	86.4±4.1 (8)	85.3±2.2 (6)	0.18	0.01	C1 E1 E2
March	88.7±3.1 (6)	89.4±4.1 (7)	90.7±3.2 (6)	0.49	0.59	C1 E1 E2
April I	91.3±2.5 (8)	91.0±2.9 (12)	90.9±3.1 (9)	0.03	0.06	C1 E1 E2
		Antechinus swainsonii reintroduced only to E1				
April II	91.2±2.7 (6)	92.0±3.2 (12)	89.2±2.5 (9)	2.38	4.46*	C1 E1 E2
May	90.9±4.0 (8)	93.1±4.1 (10)	92.7±3.8 (10)	0.70	0.14*	C1 E1 E2
June	95.8±2.4 (8)	95.5±2.7 (10)	93.1±3.3 (8)	2.25	4.44*	C1 E1 E2
July	97.8±3.5 (7)	96.4±2.4 (7)	98.4±4.5 (10)	0.58	0.69	C1 E1 E2
August I	99.9±2.5 (11)	98.9±2.6 (12)	100.9±2.6 (13)	1.82	2.85	C1 E1 E2
August II	-	99.2±4.4 (6)	98.8±3.0 (8)	0.03	-	-

Appendix 3e. Head-body lengths of female Antechinus stuartii (<1yr old). Values are means (mm) ± standard deviation. Sample sizes are in brackets.

	C1	E1	E2	F_o	F_p	Conclusion
1978		Antechinus swainsonii not manipulated				
June	89.4±3.3 (7)	87.9±2.6 (6)	87.1±4.2 (7)	0.78*	-	C1 E1 E2
July I	87.1±2.3 (5)	87.5±2.3 (6)	90.4±1.7 (6)	4.41	-	C1 E1 E2
		Antechinus swainsonii removed from E1 and E2				
July II	87.6±2.4 (7)	89.0±3.6 (6)	88.0±3.6 (6)	0.33	0.37	C1 E1 E2
August	88.9±2.4 (8)	88.8±4.6 (7)	91.2±5.2 (5)	0.65	0.25	C1 E1 E2
1979						
January	77.5±3.5 (2)	77.5±3.1 (4)	79.5±3.4 (4)	0.44	0.15	C1 E1 E2
February	81.9±3.7 (9)	81.9±4.1 (12)	79.7±3.1 (10)	1.21	0.45	C1 E1 E2
March	83.8±3.7 (6)	81.3±4.5 (12)	83.9±3.4 (13)	1.54	0.44	C1 E1 E2
April I	85.0±3.4 (7)	84.4±3.1 (11)	85.8±4.9 (12)	0.35	0.01	C1 E1 E2
		Antechinus swainsonii reintroduced only to E1				
April II	84.8±3.9 (8)	87.6±4.2 (11)	85.2±3.6 (10)	1.61	0.65	C1 E1 E2
May	86.1±2.8 (7)	83.6±4.5 (10)	84.0±4.3 (12)	0.85	0.16	C1 E1 E2
June	87.4±2.7 (5)	88.6±2.8 (8)	87.8±3.0 (9)	0.29	0.07	C1 E1 E2
July	86.9±2.1 (6)	89.1±3.6 (9)	88.9±3.9 (7)	0.81	0.18*	C1 E1 E2
August I	88.3±2.8 (6)	87.6±2.4 (7)	90.9±2.6 (8)	3.27	6.36	C1 E1 E2
August II	-	87.4±4.4 (5)	89.3±2.3 (7)	0.95	-	-

Appendix 3f. Head-body lengths of female Antechinus stuartii (>1yr old). Values are means (mm) ± standard deviation. Sample sizes are in brackets.

	C1	E1	E2	F_o	F_p	Conclusion		
1978		Antechinus swainsonii removed from E1 and E2						
September	92.5±3.5 (4)	91.0±3.3 (5)	92.8±4.4 (4)	0.25	0.14	C1	E1	E2
1979								
January	95.8±3.1 (4)	94.2±2.8 (4)	92.3±2.2 (4)	1.68	2.26	C1	E1	E2
February	97.0±3.2 (4)	98.0±4.7 (4)	92.8±3.4 (4)	2.14	0.48	C1	E1	E2
March	93.5±4.0 (4)	97.5±3.9 (4)	95.5±2.1 (4)	1.35	2.02	C1	E1	E2
April I	97.0±4.2 (2)	94.5±3.5 (2)	95.0±2.1 (4)	0.41	0.79	C1	E1	E2
		Antechinus swainsonii reintroduced only to E1						
April II	96.5±2.1 (2)	91.0±1.4 (2)	95.5±3.5 (2)	2.71	0.65	C1	E1	E2
May	98.5±0.7 (2)	95.0 (1)	94.5±2.1 (2)	-	-		-	
September	96.9±2.6 (5)	94.8±2.8 (5)	92.6±3.7 (7)	2.72	4.37	C1	E1	E2
November	97.5±4.0 (4)	99.8±2.1 (4)	95.0±3.6 (4)	2.04	3.16	C1	E1	E2

Appendix 4a. Body weights of male Antechinus swainsonii.
Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	C1	E3	E4	F_o	F_p	Conclusion
1978		Antechinus stuartii not manipulated				
May	62.6±9.8 (11)	73.2±14.0 (9)	70.1±17.3 (11)	1.57	-	C1 E3 E4
June	63.7±9.6 (10)	67.4±12.0 (8)	70.9±15.7 (10)	0.80	-	C1 E3 E4
July I	72.4±10.2 (10)	68.0±14.1 (10)	81.3±12.8 (10)	2.95	-	C1 E3 E4
		Antechinus stuartii removed from E3 and E4				
July II	73.3±13.5 (4)	65.0±6.0 (3)	-	0.94	-	-
November	17.5±1.9 (6)	18.4±2.3 (5)	17.6±3.1 (5)	0.21	0.16	C1 E3 E4
December	36.9±3.1 (8)	34.7±4.2 (10)	34.2±4.8 (12)	1.04	2.00	C1 E3 E4
1979						
January	49.5±6.7 (13)	48.6±6.0 (14)	51.7±8.1 (13)	0.71	0.07	C1 E3 E4
February	54.9±6.3 (9)	54.7±9.7 (11)	57.5±9.5 (12)	0.35	0.14	C1 E3 E4
March	61.1±7.9 (10)	56.1±10.2 (9)	63.7±8.0 (10)	1.84	0.09	C1 E3 E4
April I	59.5±7.6 (11)	59.9±12.1 (9)	65.0±10.7 (10)	0.93	0.66	C1 E3 E4
		Antechinus stuartii reintroduced only to E3				
April II	60.0±8.3 (11)	62.9±11.9 (8)	66.5±11.7 (10)	0.99	1.64	C1 E3 E4
May	60.3±8.7 (12)	63.3±16.5 (7)	69.7±10.6 (10)	1.85	3.39	C1 E3 E4
June	60.3±14.1 (3)	63.8±11.0 (9)	66.4±13.2 (10)	0.30	0.43	C1 E3 E4
July	64.8±10.9 (4)	68.7±10.5 (9)	73.8±17.1 (11)	0.71	1.21	C1 E3 E4
November	-	16.5±1.0 (4)	15.0±1.0 (3)	3.86	-	-
December	36.0±5.7 (2)	37.0±4.1 (8)	38.1±3.4 (9)	0.32	0.53	C1 E3 E4

Appendix 4b. Body weights of female Antechinus swainsonii (<1yr old). Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	C1	E3	E4	F_o	F_p	Conclusion
1978		Antechinus stuartii not manipulated				
May	38.6±2.7 (5)	36.0±3.7 (5)	34.2±4.8 (5)	1.69	-	C1 E3 E4
June	40.0±1.0 (3)	40.4±7.7 (5)	34.8±3.8 (4)	1.29	-	C1 E3 E4
July I	46.8±4.8 (4)	38.6±5.1 (5)	38.3±4.7 (4)	4.01	-	C1 E3 E4
		Antechinus stuartii removed from E3 and E4				
July II	49.0±4.6 (3)	42.6±5.5 (5)	42.7±5.9 (3)	1.54	3.09	C1 E3 E4
November	15.0±0.8 (4)	15.0 (1)	18.0 (1)	-	-	-
December	28.0±1.0 (3)	29.3±2.9 (3)	26.8±3.0 (4)	0.88	0.01	C1 E3 E4
1979						
January	32.8±3.4 (5)	30.8±4.0 (5)	30.3±3.6 (4)	0.63	1.20	C1 E3 E4
February	36.8±4.6 (4)	39.0±4.4 (5)	36.4±6.1 (5)	0.37	0.10	C1 E3 E4
March	39.6±3.9 (5)	45.8±5.1 (5)	46.5±7.1 (4)	2.41	4.79*	C1 E3 E4
April I	37.4±3.4 (5)	42.8±4.1 (4)	45.3±7.5 (4)	2.77	5.06	C1 E3 E4
		Antechinus stuartii reintroduced only to E3				
April II	38.2±7.2 (5)	42.8±4.1 (4)	42.8±3.6 (4)	1.07*	0.59*	C1 E3 E4
May	39.5±2.6 (6)	42.0±2.6 (4)	45.0±2.7 (3)	4.57	6.92	C1 E3 E4
June	40.0 (1)	44.0±3.5 (3)	46.0±4.0 (3)	0.43	-	-
July	41.0 (1)	40.5±5.5 (4)	43.3±6.4 (3)	0.40	-	-
November	-	16.3±0.4 (2)	16.8±1.8 (2)	-	-	-
December	25.0 (1)	24.0±1.4 (4)	22.3±3.2 (3)	0.89	-	-

Appendix 4c. Body weights of female Antechinus swainsonii (>1yr old). Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	C1	E3	E4	F_o	F_p	Conclusion		
1978		Antechinus stuartii not manipulated						
May	56.5±3.5 (2)	53.5±6.4 (2)	50.5±5.0 (2)	0.70	-	C1	E3	E4
June	50.5±2.1 (2)	47.0±4.2 (2)	45.0 (1)	-	-		-	
July I	54.5±2.1 (2)	48.5±7.8 (2)	47.0 (1)	-	-		-	
		Antechinus stuartii removed from E3 and E4						
July II	52.5±3.5 (2)	53.5±7.8 (2)	47.0 (1)	-	-		-	
August	51.8±1.7 (4)	48.6±3.5 (7)	53.3±3.6 (4)	3.13	0.64	C1	E3	E4
September	56.0±2.7 (3)	58.3±8.1 (4)	61.3±6.9 (4)	0.55	0.69	C1	E3	E4
October	55.5±2.5 (4)	51.8±4.2 (4)	57.3±6.7 (3)	1.45	0.23	C1	E3	E4
November	54.3±2.5 (3)	49.3±1.2 (3)	48.7±3.1 (3)	5.08	10.03*	C1	E3	E4
December	57.3±7.8 (4)	55.5±4.8 (4)	49.5±5.0 (3)	1.82	0.53	C1	E3	E4
1979								
January	48.7±6.8 (3)	52.3±7.4 (4)	49.3±5.5 (3)	0.29	0.25	C1	E3	E4
February	48.7±7.8 (3)	48.7±5.1 (3)	46.0±7.1 (2)	0.12	0.05	C1	E3	E4
March	52.0±2.8 (2)	51.2±5.1 (3)	55.5±2.1 (2)	0.60	0.13	C1	E3	E4
April I	54.0±1.4 (2)	50.3±3.5 (3)	50.5±3.5 (2)	0.95	1.89	C1	E3	E4
		Antechinus stuartii reintroduced only to E3						
April II	45.0±5.7 (2)	48.3±4.7 (3)	52.0±5.7 (2)	0.90	1.31	C1	E3	E4
May	50.0±0.0 (2)	46.5±3.5 (2)	52.0±4.2 (2)	1.52	1.84	C1	E3	E4
June	50.0 (1)	48.3±7.6 (3)	54.0±5.7 (2)	0.78	-		-	
July	52.0 (1)	49.0±1.4 (2)	53.5±5.0 (2)	1.53	-		-	
August	54.0 (1)	53.3±7.3 (4)	58.4±6.2 (5)	0.95	-		-	
September	56.0 (1)	60.8±9.2 (4)	63.0±11.8 (4)	0.09	-		-	
October	53.0 (1)	52.3±6.7 (4)	58.3±3.8 (3)	1.97	-		-	
November	58.0 (1)	52.7±3.8 (3)	60.3±1.5 (3)	10.58*	-		-	
December	54.0 (1)	52.0±5.3 (3)	58.0±4.2 (2)	1.75	-		-	

Appendix 4d. Head-body lengths of male Antechinus swainsonii.
Values are means (grammes) ± standard deviation. Sample sizes are in brackets.

	C1	E3	E4	F_o	F_p	Conclusion		
1978		Antechinus stuartii not manipulated						
June	120.8±4.9 (8)	121.8±6.3 (8)	119.0±3.5 (9)	0.68	-	C1	E3	E4
July I	126.0±7.0 (9)	125.1±8.1 (8)	122.0±7.0 (9)	0.73	-	C1	E3	E4
		Antechinus stuartii removed from E3 and E4						
July II	129.5±5.0 (4)	125.2±6.3 (4)	-	1.1	-		-	
November	85.4±3.8 (5)	82.2±2.5 (5)	80.8±4.3 (5)	2.16	3.93	C1	E3	E4
December	96.9±3.2 (7)	93.6±3.0 (7)	95.3±3.7 (10)	1.64	2.21	C1	E3	E4
1979								
January	106.1±5.9 (10)	104.2±4.2 (8)	104.0±3.8 (9)	0.54	1.06*	C1	E3	E4
February	107.8±4.4 (9)	112.0±5.2 (9)	112.9±5.3 (11)	2.84	5.52*	C1	E3	E4
March	114.9±4.6 (10)	113.3±4.7 (9)	115.1±4.9 (9)	0.38	0.13	C1	E3	E4
April I	116.3±4.2 (10)	116.8±4.7 (9)	118.4±4.1 (8)	0.54	0.50	C1	E3	E4
		Antechinus stuartii reintroduced only to E3						
April II	121.3±4.5 (8)	122.4±3.3 (8)	123.4±3.5 (8)	0.71	0.99	C1	E3	E4
May	123.3±3.9 (10)	120.7±3.8 (7)	125.6±4.1 (7)	2.67	3.56	C1	E3	E4
June	-	123.9±4.3 (8)	125.3±4.4 (8)	0.40	-		-	
July	129.8±7.1 (4)	125.6±6.4 (9)	125.8±3.8 (10)	0.95	0.29	C1	E3	E4
November	-	84.8±2.1 (4)	80.0±1.7 (3)	10.31*	-		-	
December	92.5±3.5 (2)	93.6±3.3 (8)	96.1±3.9 (8)	1.35	2.53	C1	E3	E4

Appendix 4e. Head-body lengths of female Antechinus swainsonii (<1yr old). Values are means (mm) ± standard deviation. Sample sizes are in brackets.

	C1	E3	E4	F_o	F_p	Conclusion		
1978		Antechinus stuartii not manipulated						
June	107.0±5.3 (3)	112.2±5.4 (5)	104.3±4.7 (4)	2.80	-		-	
July I	114.3±5.0 (4)	117.2±4.8 (5)	111.5±6.4 (4)	1.27	-		-	
		Antechinus stuartii removed from E3 and E4						
July II	115.5±4.4 (4)	118.2±3.5 (5)	116.3±4.0 (3)	0.56	0.69	C1	E3	E4
November	78.8±3.3 (4)	78.0 (1)	82.5 (1)	-	-		-	
December	92.3±2.5 (3)	89.7±1.5 (3)	85.3±3.6 (4)	5.62*	7.06*	C1	E3	E4
1979								
January	100.5±2.2 (5)	99.0±2.9 (5)	98.8±4.3 (4)	0.43	0.84	C1	E3	E4
February	101.5±2.4 (4)	97.8±2.2 (5)	98.8±2.6 (5)	2.79	5.14	C1	E3	E4
March	103.6±3.5 (5)	101.0±3.2 (5)	105.5±2.7 (4)	2.30	0.12	C1	E3	E4
April I	105.0±3.4 (5)	104.0±4.1 (4)	107.3±2.2 (4)	1.01	0.11	C1	E3	E4
		Antechinus stuartii reintroduced only to E3						
April II	105.4±4.3 (5)	106.8±5.1 (4)	104.8±4.2 (4)	0.20	0.21*	C1	E3	E4
May	110.7±2.7 (6)	108.5±4.0 (4)	114.3±1.5 (3)	3.22	5.21	C1	E3	E4
June	-	109.3±3.5 (3)	110.0±7.2 (3)	0.02	-		-	
July	119.0 (1)	115.3±5.5 (4)	114.0±5.0 (3)	0.10	-		-	
November	-	79.0 (1)	83.0±1.4 (2)	-	-		-	
December	93.0 (1)	90.3±3.1 (3)	89.7±4.0 (3)	0.05	-		-	

Appendix 5. The diversity of prey types obtained by pitfall sampling. Five habitats were sampled:

(a) Ribbon Gum

(b) Fern

(c) Under log

(d) Open

(e) Slopes

The Appendix tables 5(a)-5(e) show the components of diversity (Brillouin's H) for each pitfall sample. The components are the numbers of individuals in the sample, the numbers of types of invertebrate prey in the sample, and the evenness, J, with which they are represented. The W statistic - Kendall's coefficient of concordance - was used to test for differences in the prey type distributions between the enclosures, and was computed after the actual frequencies of the prey types were converted to ranks. A significant χ^2 value associated with the W statistic denotes that the abundance distributions of prey types were concordant between the enclosures, whereas a non-significant χ^2 implies that they differed.

In the tables, unbracketed numbers show the components of prey type diversity for all prey. The bracketed numbers show the equivalent information, but with all Collembola omitted.

\+ after a pitfall site denotes that the pitfall was flooded in that month;

++ after a pitfall site denotes that the pitfall dried up in that month.

The measurements of diversity were based on the recognition of 46 types of prey:

Appendix 5 (Cont'd).

Phylum Arthropoda

Class Insecta:

(a) Collembola
Diplura
Thysanura
Ephemeroptera
Odonata
Plecoptera
Orthoptera
Phasmida
Dermaptera
Embioptera
(b) Dictyoptera
Isoptera
(c) Hemiptera
Thysanoptera
Neuroptera
Lepidoptera
Trichoptera
Diptera
Siphonaptera
(d) Hymenoptera
(e) Coleoptera

Phylum Arthropoda

Class Arachnida:

Scorpionones
Pseudoscorpiones
Araneida
Opiliones
(f) Acari

Class Crustacea

Isopoda
Amphipoda

Class Chilopoda

Class Diplopoda

Phylum Onychophora

Phylum Annelida

Sub-class Oligochaeta

Sub-class Hirudinea

Phylum Nematoda

Phylum Platyhelminthes

Notes: (a) Subdivided into four groups, loosely Entomobryidae (3 groups) and Poduroidea + Symphypleona (1 group); (b) subdivided into cockroaches and mantids; (c) subdivided into Homoptera and Heteroptera; (d) subdivided into ants (Formicoidea) and "others"; (e) subdivided into scarab, rove, weevil, tenebrionid and "others"; (f) subdivided into mites and ticks. Classification follows Clark and Panchen (1971). Snails, crayfish and certain beetles (Carabidae, Lycidae) were found in pitfall traps, but are not included in analyses of diversity.

Appendix 5. Components of prey type diversity: pitfall trap samples
(a) Ribbon Gum

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	x^2(d.f)
Aug. 1978	E1	12	(3)	63	(28)	1.79	(1.44)	0.82	(0.77)	0.65	39.29*** (12)
	E2	14	(4)	60	(28)	1.90	(1.62)	0.83	(0.85)		
	E3	14	(4)	70	(31)	1.92	(1.72)	0.82	(0.88)		
	E4	12	(4)	62	(26)	1.93	(1.60)	0.88	(0.90)		
	C1	10	(1)	42	(9)	1.82	(1.72)	0.93	(0.93)		
Sept. 1978	E1	5	(2)	36	(23)	0.89	(0.39)	0.63	(0.44)	0.13	4.45 (7)
	E2+	5	(2)	16	(5)	0.96	(0.43)	0.76	(0.50)		
	E3	7	(2)	20	(7)	1.27	(0.94)	0.82	(0.77)		
	E4+	3	(1)	7	(2)	0.76	(0.46)	1.00	(1.00)		
	C1+	5	(2)	12	(2)	1.00	(0.71)	0.84	(0.86)		
Oct. 1978	E1	17	(3)	120	(31)	2.31	(2.07)	0.89	(0.87)	0.82	65.39*** (16)
	E2	13	(2)	123	(49)	1.74	(1.51)	0.73	(0.70)		
	E3	18	(3)	139	(49)	2.25	(1.96)	0.85	(0.80)		
	E4	14	(3)	115	(23)	2.01	(1.73)	0.83	(0.79)		
	C1	15	(2)	99	(31)	2.11	(1.93)	0.86	(0.85)		
Nov. 1978	E1	18	(2)	157	(30)	2.31	(2.13)	0.86	(0.84)	0.72	71.79*** (20)
	E2	21	(4)	155	(31)	2.45	(2.24)	0.87	(0.86)		
	E3	20	(4)	162	(45)	2.38	(2.14)	0.86	(0.84)		
	E4+	17	(2)	123	(13)	1.78	(1.56)	0.69	(0.63)		
	C1	17	(3)	159	(47)	2.23	(2.01)	0.85	(0.83)		
Dec. 1978	E1	22	(3)	280	(45)	2.48	(2.29)	0.85	(0.82)	0.85	110.31*** (26)
	E2	28	(4)	294	(76)	2.63	(2.46)	0.84	(0.83)		
	E3	28	(3)	294	(81)	2.74	(2.67)	0.87	(0.89)		
	E4+	24	(4)	271	(46)	2.70	(2.51)	0.90	(0.89)		
	C1	22	(3)	309	(77)	2.47	(2.28)	0.84	(0.82)		
Jan. 1979	E1	25	(3)	349	(42)	2.51	(2.31)	0.82	(0.78)	0.80	108.04*** (27)
	E2	24	(3)	338	(35)	2.37	(2.17)	0.78	(0.75)		
	E3	27	(4)	310	(44)	2.57	(2.38)	0.83	(0.81)		
	E4	24	(4)	293	(42)	2.60	(2.38)	0.88	(0.85)		
	C1	23	(3)	302	(61)	2.44	(2.21)	0.83	(0.79)		
Feb. 1979	E1	19	(2)	157	(34)	2.23	(2.06)	0.82	(0.80)	0.76	91.34*** (24)
	E2	20	(2)	222	(23)	2.36	(2.21)	0.84	(0.81)		
	E3	19	(3)	161	(23)	2.32	(2.11)	0.85	(0.82)		
	E4	25	(4)	217	(31)	2.54	(2.35)	0.85	(0.83)		
	C1	22	(3)	183	(34)	2.48	(2.32)	0.86	(0.85)		
Mar. 1979	E1	17	(3)	127	(24)	2.23	(1.99)	0.86	(0.83)	0.89	79.79*** (18)
	E2	19	(3)	209	(28)	2.18	(1.97)	0.79	(0.76)		
	E3	16	(3)	193	(53)	2.31	(2.06)	0.88	(0.86)		
	E4	19	(3)	170	(33)	2.43	(2.25)	0.89	(0.88)		
	C1	19	(4)	163	(57)	2.29	(2.22)	0.84	(0.90)		
Apr. 1979	E1	17	(3)	131	(40)	2.11	(1.93)	0.81	(0.81)	0.76	68.65*** (18)
	E2	12	(2)	190	(10)	1.12	(0.95)	0.47	(0.43)		
	E3	15	(3)	115	(25)	2.08	(1.77)	0.48	(0.79)		
	E4	19	(3)	112	(18)	2.35	(2.13)	0.88	(0.85)		
	C1	15	(3)	93	(28)	2.19	(1.93)	0.89	(0.88)		
May 1979	E1	10	(2)	27	(3)	1.59	(1.41)	0.86	(0.83)	0.49	34.62** (14)
	E2	11	(1)	54	(1)	1.64	(1.60)	0.78	(0.79)		
	E3	11	(2)	33	(5)	1.68	(1.45)	0.85	(0.81)		
	E4	14	(3)	57	(6)	1.94	(1.76)	0.85	(0.85)		
	C1	12	(1)	31	(5)	1.82	(1.70)	0.85	(0.82)		

Appendix 5(a) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1979	E1	11	(3)	71	(45)	1.56	(1.44)	0.73	(0.85)	0.54	35.05*** (13)
	E2	13	(1)	61	(21)	1.77	(1.78)	0.79	(0.85)		
	E3	11	(3)	64	(26)	1.82	(1.53)	0.85	(0.85)		
	E4	14	(3)	87	(45)	1.95	(1.77)	0.82	(0.87)		
	C1	12	(2)	99	(59)	1.42	(1.64)	0.62	(0.84)		
July 1979	E1	9	(4)	45	(36)	1.05	(0.89)	0.55	(0.80)	0.66	45.96*** (14)
	E2	13	(4)	90	(55)	1.60	(1.56)	0.69	(0.84)		
	E3	10	(3)	50	(27)	1.71	(1.47)	0.85	(0.93)		
	E4	13	(3)	111	(81)	1.51	(1.65)	0.64	(0.87)		
	C1	15	(3)	79	(39)	1.84	(1.65)	0.76	(0.79)		
Aug. 1979	E1	11	(2)	59	(32)	1.67	(1.56)	0.79	(0.87)	0.78	54.51*** (14)
	E2	14	(2)	72	(33)	2.00	(1.94)	0.85	(0.94)		
	E3	14	(4)	94	(49)	1.75	(1.62)	0.73	(0.82)		
	E4	13	(3)	51	(25)	1.85	(1.74)	0.84	(0.95)		
	C1	13	(2)	69	(33)	1.86	(1.82)	0.82	(0.91)		
Sept. 1979	NO DATA COLLECTED										
Oct. 1979	E1	16	(4)	95	(48)	2.05	(1.92)	0.82	(0.90)	0.55	49.75*** (18)
	E2	15	(2)	259	(13)	1.80	(1.67)	0.69	(0.68)		
	E3	17	(3)	97	(18)	2.30	(2.10)	0.90	(0.89)		
	E4	16	(3)	86	(12)	2.13	(1.92)	0.86	(0.84)		
	C1	18	(3)	213	(34)	2.05	(1.77)	0.75	(0.70)		
Nov. 1979	E1	20	(3)	150	(36)	2.36	(2.15)	0.86	(0.83)	0.83	82.59*** (20)
	E2	21	(4)	245	(42)	2.39	(2.13)	0.83	(0.80)		
	E3	18	(4)	190	(72)	2.40	(2.18)	0.89	(0.90)		
	E4	18	(3)	203	(44)	2.44	(2.19)	0.90	(0.87)		
	C1	17	(3)	246	(44)	2.32	(2.07)	0.86	(0.83)		
Dec. 1979	E1	22	(2)	342	(27)	2.24	(2.10)	0.76	(0.73)	0.75	78.51*** (26)
	E2	22	(3)	348	(47)	2.33	(2.12)	0.79	(0.75)		
	E3	28	(4)	358	(57)	2.60	(2.35)	0.82	(0.78)		
	E4	24	(4)	280	(69)	2.63	(2.38)	0.87	(0.85)		
Jan. 1980	E1	19	(3)	152	(18)	2.23	(2.01)	0.82	(0.79)	0.71	62.14*** (22)
	E2	19	(2)	84	(14)	2.10	(1.92)	0.81	(0.78)		
	E3	22	(3)	179	(44)	2.55	(2.35)	0.89	(0.87)		
	E4	21	(3)	183	(32)	2.38	(2.17)	0.84	(0.81)		
Feb. 1980	E1	22	(2)	163	(20)	2.50	(2.37)	0.88	(0.86)	0.69	58.09*** (21)
	E2	20	(2)	194	(41)	2.17	(2.05)	0.77	(0.77)		
	E3	19	(2)	191	(44)	2.40	(2.24)	0.87	(0.85)		
	E4	20	(2)	266	(59)	2.22	(2.00)	0.78	(0.74)		
Mar. 1980	E1	22	(3)	92	(9)	2.34	(2.18)	0.86	(0.84)	0.52	45.99** (22)
	E2	17	(2)	142	(15)	2.14	(2.01)	0.82	(0.80)		
	E3	18	(3)	60	(16)	2.22	(2.04)	0.90	(0.90)		
	E4	19	(3)	51	(10)	2.18	(2.00)	0.89	(0.88)		
Apr. 1980	E1	15	(3)	116	(61)	1.82	(1.84)	0.73	(0.85)	0.48	26.99* (14)
	E2	19	(3)	98	(58)	1.85	(1.99)	0.70	(0.88)		
	E3++	14	(2)	55	(17)	1.98	(1.89)	0.87	(0.91)		
	E4++	13	(2)	62	(22)	1.99	(1.83)	0.88	(0.90)		
May 1980	E1	16	(4)	106	(71)	1.84	-	0.79	-	0.57	34.36** (15)
	E2	13	(1)	49	(14)	1.88	(1.85)	0.86	(0.90)		
	E3	13	(2)	68	(21)	1.92	(1.78)	0.84	(0.86)		
	E4	14	(2)	60	(14)	1.84	(1.58)	0.80	(0.75)		

Appendix 5(a) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1980	E1	3	(1)	5	(3)	0.60	(0.35)	0.88	(1.00)	0.31	8.60 (7)
	E2	12	(2)	36	(8)	1.80	(1.62)	0.87	(0.87)		
	E3	8	(3)	26	(11)	1.59	(1.21)	0.93	(0.95)		
	E4	8	(3)	26	(14)	1.50	(1.10)	0.89	(0.92)		
July 1980	E1	2	(1)	4	(3)	0.35	(0)	0.77	(0)	0.18	5.17 (7)
	E2	10	(2)	24	(6)	1.69	(1.49)	0.93	(0.94)		
	E3+	8	(3)	21	(9)	1.51	(1.00)	0.92	(0.84)		
	E4+	9	(3)	21	(8)	1.55	(1.18)	0.91	(0.88)		
Aug. 1980	E1	6	(1)	33	(15)	1.25	(1.14)	0.81	(0.88)	0.36	16.02 (11)
	E2	10	(1)	35	(6)	1.67	(1.53)	0.87	(0.85)		
	E3	11	(4)	33	(12)	1.68	(1.24)	0.85	(0.79)		
	E4++	9	(3)	20	(7)	1.46	(1.09)	0.86	(0.82)		
Sept. 1980	E1	14	(4)	49	(22)	1.97	(1.71)	0.88	(0.92)	0.55	30.94** (14)
	E2	13	(3)	67	(40)	1.76	(1.71)	0.77	(0.92)		
	E3	14	(3)	70	(42)	1.83	(1.75)	0.78	(0.91)		
	E4	11	(3)	65	(36)	1.77	(1.51)	0.83	(0.88)		
Oct. 1980	E1	8	(1)	58	(5)	1.60	(1.46)	0.86	(0.84)	0.58	23.36** (10)
	E2	14	(2)	40	(11)	1.94	(1.79)	0.89	(0.91)		
	E3	8	(2)	39	(14)	1.24	(0.81)	0.69	(0.54)		
	E4++	7	(2)	40	(12)	1.44	(1.04)	0.85	(0.75)		
Nov. 1980	E1	16	(2)	78	(12)	2.12	(1.96)	0.86	(0.85)	0.69	44.03*** (16)
	E2	19	(2)	93	(16)	2.23	(2.06)	0.86	(0.84)		
	E3	12	(2)	77	(13)	1.87	(1.67)	0.84	(0.81)		
	E4	14	(2)	65	(9)	1.64	(1.41)	0.71	(0.65)		
Dec. 1980	E1	12	(2)	52	(13)	1.73	(1.46)	0.80	(0.75)	0.49	27.37* (14)
	E2	17	(3)	157	(86)	1.92	(2.08)	0.73	(0.89)		
	E3	13	(3)	62	(31)	1.81	(1.64)	0.80	(0.86)		
	E4	15	(2)	67	(33)	1.68	(1.75)	0.71	(0.84)		
Jan. 1981	E1	19	(3)	159	(16)	2.22	(2.06)	0.81	(0.80)	0.65	44.40*** (17)
	E2	19	(3)	139	(64)	2.15	(2.23)	0.80	(0.91)		
	E3	16	(3)	131	(41)	2.02	(1.77)	0.79	(0.76)		
	E4	17	(3)	145	(54)	2.01	(1.78)	0.77	(0.75)		
Feb. 1981	E1	17	(2)	126	(22)	2.31	(2.14)	0.89	(0.87)	0.55	41.44** (19)
	E2	16	(3)	176	(99)	1.86	(1.71)	0.71	(0.75)		
	E3	16	(2)	82	(18)	2.06	(1.95)	0.83	(0.84)		
	E4	18	(2)	71	(12)	2.11	(1.95)	0.84	(0.82)		
Mar. 1981	E1	12	(2)	69	(19)	1.72	(1.40)	0.78	(0.70)	0.21	12.69 (15)
	E2	18	(2)	98	(10)	2.28	(2.13)	0.88	(0.86)		
	E3	16	(2)	51	(86)	1.53	(1.77)	0.59	(0.86)		
	E4	16	(2)	109	(42)	1.91	(2.01)	0.76	(0.86)		
Apr. 1981	E1	13	(3)	69	(47)	1.39	(1.59)	0.61	(0.89)	0.26	14.55 (14)
	E2	14	(3)	45	(19)	1.92	(1.86)	0.87	(0.98)		
	E3	9	(2)	26	(12)	1.44	(1.35)	0.81	(0.93)		
	E4	11	(3)	40	(18)	1.59	(1.39)	0.79	(0.84)		
May 1981	E1	10	(3)	101	(89)	0.63	(1.34)	0.30	(0.98)	0.54	21.47* (10)
	E2	10	(2)	41	(27)	1.16	(1.42)	0.59	(0.95)		
	E3	8	(1)	32	(21)	1.01	(1.24)	0.58	(0.93)		
	E4	7	(1)	20	(11)	1.14	(1.19)	0.74	(1.00)		

Appendix 5(a) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1981	E1	12	(3)	336	(307)	0.54	(1.70)	0.22	(0.94)	0.66	34.56*** (13)
	E2	13	(3)	90	(52)	1.80	(1.69)	0.77	(0.87)		
	E3	13	(4)	67	(45)	1.58	(1.49)	0.70	(0.92)		
	E4	11	(4)	57	(34)	1.87	(1.50)	0.89	(0.95)		
July 1981	E1+	7	(3)	15	(11)	1.01	(0.79)	0.69	(1.00)	0.26	10.57 (10)
	E2+	5	(2)	10	(4)	1.01	(0.57)	0.87	(0.76)		
	E3	11	(3)	25	(12)	1.73	(1.35)	0.92	(0.92)		
	E4	12	(4)	26	(13)	1.74	(1.41)	0.89	(0.96)		
Aug. 1981	E1+	5	(2)	14	(11)	0.72	(0.60)	0.58	(1.00)	0.26	8.28 (8)
	E2+	6	(1)	14	(2)	1.09	(0.90)	0.81	(0.75)		
	E3	7	(3)	20	(8)	1.35	(0.81)	0.88	(0.75)		
	E4	9	(3)	19	(9)	1.54	(1.12)	0.92	(0.91)		
Sept. 1981	E1	17	(4)	120	(66)	2.06	(1.93)	0.80	(0.87)	0.60	38.27** (16)
	E2	13	(4)	148	(113)	1.49	(1.65)	0.62	(0.89)		
	E3	14	(4)	140	(93)	1.82	(1.74)	0.74	(0.87)		
	E4	15	(4)	110	(77)	1.76	(1.81)	0.71	(0.91)		
Oct. 1981	E1	16	(3)	194	(72)	1.68	(1.27)	0.64	(0.54)	0.61	38.84** (16)
	E2+	13	(2)	94	(60)	1.53	(1.76)	0.66	(0.89)		
	E3	13	(3)	80	(38)	1.84	(1.73)	0.80	(0.88)		
	E4	13	(3)	120	(56)	1.83	(1.79)	0.73	(0.82)		

Appendix 5. Components of prey type diversity: pitfall trap samples
(b) Fern

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
Aug. 1978	E1	10	(4)	86	(55)	1.33	(1.28)	0.63	(0.83)	0.79	51.37*** (1
	E2	12	(4)	67	(40)	1.75	(1.58)	0.79	(0.92)		
	E3	14	(3)	75	(45)	1.63	(1.72)	0.70	(0.89)		
	E4	13	(4)	54	(26)	1.88	(1.55)	0.85	(0.86)		
	C1	12	(3)	43	(21)	1.72	(1.58)	0.82	(0.92)		
Sept. 1978	E1	8	(3)	34	(10)	1.45	(0.93)	0.82	(0.69)	0.31	14.06 (9)
	E2+	6	(1)	31	(14)	1.19	(1.03)	0.78	(0.80)		
	E3+	6	(3)	23	(18)	1.14	(0.68)	0.77	(1.00)		
	E4+	4	(1)	29	(18)	0.89	(0.77)	0.74	(0.90)		
	C1	9	(2)	42	(2)	1.25	(1.13)	0.66	(0.67)		
Oct. 1978	E1	11	(3)	73	(43)	1.74	(1.35)	0.81	(0.78)	0.71	49.81*** (14)
	E2	15	(3)	91	(41)	2.05	(1.82)	0.84	(0.85)		
	E3	17	(4)	132	(77)	1.84	(1.88)	0.71	(0.85)		
	E4	14	(3)	108	(50)	2.00	(1.83)	0.83	(0.87)		
	C1	13	(3)	77	(37)	1.95	(1.73)	0.85	(0.88)		
Nov. 1978	E1	13	(3)	165	(23)	1.62	(1.30)	0.67	(0.60)	0.79	67.47*** (17)
	E2+	14	(3)	189	(62)	1.88	(1.51)	0.76	(0.67)		
	E3+	18	(3)	117	(24)	2.30	(2.10)	0.88	(0.86)		
	E4+	17	(4)	94	(20)	2.32	(2.08)	0.91	(0.91)		
	C1	14	(2)	157	(35)	2.11	(1.88)	0.85	(0.82)		
Dec. 1978	E1	20	(2)	208	(32)	2.46	(2.30)	0.88	(0.85)	0.77	88.31*** (23)
	E2+	19	(3)	201	(30)	2.23	(2.01)	0.81	(0.77)		
	E3+	20	(3)	189	(51)	2.31	(2.07)	0.83	(0.79)		
	E4	24	(3)	255	(68)	2.41	(2.21)	0.80	(0.78)		
	C1	24	(3)	226	(54)	2.55	(2.42)	0.86	(0.86)		
Jan. 1979	E1	20	(3)	172	(36)	2.40	(2.18)	0.86	(0.84)	0.75	93.70*** (25)
	E2	22	(3)	216	(35)	2.47	(2.26)	0.85	(0.82)		
	E3	24	(3)	227	(66)	2.52	(2.42)	0.85	(0.86)		
	E4	19	(2)	140	(34)	2.30	(2.14)	0.85	(0.83)		
	C1	23	(4)	158	(38)	2.60	(2.33)	0.90	(0.87)		
Feb. 1979	E1	19	(2)	171	(33)	2.34	(2.17)	0.86	(0.83)	0.70	70.22*** (20)
	E2	16	(2)	155	(22)	2.23	(2.05)	0.87	(0.84)		
	E3	15	(2)	131	(19)	2.16	(1.99)	0.86	(0.84)		
	E4	20	(2)	158	(42)	2.34	(2.26)	0.85	(0.86)		
	C1	18	(2)	145	(30)	2.34	(2.17)	0.88	(0.86)		
Mar. 1979	E1	17	(3)	94	(41)	2.07	(1.94)	0.82	(0.85)	0.84	67.38*** (16)
	E2	15	(3)	92	(22)	2.13	(1.87)	0.87	(0.84)		
	E3	18	(3)	90	(24)	2.22	(1.97)	0.86	(0.83)		
	E4	16	(3)	117	(38)	2.07	(1.80)	0.82	(0.78)		
	C1	15	(3)	79	(28)	2.18	(1.90)	0.91	(0.89)		
Apr. 1979	E1	13	(2)	73	(14)	2.03	(1.81)	0.89	(0.86)	0.61	48.75*** (16)
	E2	16	(3)	110	(31)	1.87	(1.69)	0.74	(0.73)		
	E3	16	(3)	126	(42)	2.16	(1.95)	0.85	(0.84)		
	E4	18	(4)	96	(30)	2.24	(2.01)	0.86	(0.87)		
	C1	16	(3)	133	(61)	1.97	(1.77)	0.77	(0.78)		
May 1979	E1	10	(2)	21	(4)	1.63	(1.40)	0.92	(0.88)	0.57	42.65*** (15)
	E2	11	(2)	66	(11)	1.39	(1.07)	0.65	(0.55)		
	E3	11	(3)	52	(12)	1.87	(1.57)	0.90	(0.87)		
	E4	16	(2)	59	(4)	1.99	(1.87)	0.84	(0.82)		
	C1	10	(2)	47	(19)	1.52	(1.39)	0.76	(0.81)		

Appendix 5(b) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	x^2(d.f)
June 1979	E1	6	(1)	15	(1)	1.21	(1.10)	0.89	(0.89)		
	E2	8	(2)	13	(6)	1.38	(1.12)	0.94	(1.00)		
	E3	9	(2)	27	(8)	1.68	(1.41)	0.94	(0.92)		
	E4	12	(3)	65	(23)	1.74	(1.36)	0.79	(0.72)	0.36	23.34*
	C1	9	(2)	49	(31)	1.48	(1.38)	0.77	(0.92)		(13)
July 1979	E1	9	(3)	59	(44)	1.34	(1.16)	0.69	(0.85)	-	
	E2	9	(3)	71	(40)	1.55	(1.28)	0.78	(0.83)		
	E3	7	(2)	58	(29)	1.57	(1.20)	0.89	(0.87)		
	E4	15	(4)	92	(52)	1.87	(1.68)	0.77	(0.83)	0.71	42.84***
	C1	9	(2)	56	(36)	1.51	(1.37)	0.77	(0.89)		(12)
Aug. 1979	E1	8	(2)	50	(35)	1.26	(1.27)	0.69	(0.93)		
	E2	14	(3)	97	(57)	1.72	(1.69)	0.72	(0.83)		
	E3	13	(3)	82	(40)	1.79	(1.75)	0.77	(0.89)		
	E4	10	(3)	91	(69)	1.20	(1.33)	0.57	(0.85)	0.88	48.13***
	C1	12	(3)	63	(40)	1.65	(1.48)	0.75	(0.85)		(11)
Sept. 1979	NO DATA COLLECTED										
Oct. 1979	E1	21	(3)	104	(23)	2.29	(2.08)	0.84	(0.82)		
	E2	19	(3)	127	(21)	2.23	(2.02)	0.83	(0.80)		
	E3	15	(3)	113	(24)	2.20	(1.98)	0.89	(0.87)		
	E4	22	(4)	146	(48)	2.51	(2.29)	0.89	(0.88)	0.38	43.93**
	C1	17	(2)	128	(29)	2.20	(2.01)	0.85	(0.82)		(23)
Nov. 1979	E1	18	(2)	166	(35)	2.27	(2.14)	0.85	(0.84)		
	E2	21	(4)	234	(71)	2.31	(2.12)	0.80	(0.81)		
	E3	20	(4)	171	(59)	2.31	(2.07)	0.83	(0.82)		
	E4	19	(3)	138	(25)	2.38	(2.21)	0.88	(0.87)	0.64	66.84***
	C1	16	(2)	175	(66)	2.15	(2.04)	0.83	(0.84)		(21)
Dec. 1979	E1	23	(3)	210	(28)	2.43	(2.26)	0.83	(0.81)		
	E2	20	(4)	185	(17)	2.18	(1.98)	0.78	(0.76)		
	E3	24	(4)	207	(26)	2.56	(2.37)	0.86	(0.85)	0.82	75.73***
	E4	20	(4)	221	(44)	2.45	(2.25)	0.87	(0.86)		(23)
Jan. 1980	E1	19	(2)	79	(12)	2.15	(2.03)	0.83	(0.82)		
	E2	17	(3)	111	(44)	2.15	(1.94)	0.83	(0.84)		
	E3	18	(3)	111	(24)	2.16	(1.92)	0.82	(0.79)	0.70	53.50***
	E4	18	(4)	118	(58)	2.18	(2.04)	0.83	(0.89)		(19)
Feb. 1980	E1	14	(2)	200	(7)	1.96	(1.87)	0.79	(0.79)		
	E2	15	(2)	67	(9)	2.12	(1.95)	0.90	(0.87)		
	E3	16	(2)	78	(15)	2.11	(2.00)	0.86	(0.87)	0.63	40.22***
	E4	14	(1)	59	(6)	2.12	(2.02)	0.92	(0.91)		(16)
Mar. 1980	E1	16	(2)	170	(4)	1.43	(1.35)	0.55	(0.54)		
	E2	15	(3)	55	(13)	2.22	(1.97)	0.95	(0.94)		
	E3	17	(3)	64	(7)	2.08	(1.90)	0.85	(0.83)	0.51	34.51**
	E4	19	(3)	67	(10)	2.32	(2.12)	0.91	(0.89)		(17)
Apr. 1980	E1	14	(2)	42	(4)	2.04	(1.91)	0.92	(0.92)		
	E2	13	(1)	58	(6)	1.92	(1.81)	0.86	(0.84)		
	E3	12	(2)	59	(13)	2.00	(1.79)	0.92	(0.90)	0.52	35.46**
	E4	16	(3)	55	(11)	2.15	(1.90)	0.91	(0.88)		(17)
May 1980	E1	12	(2)	113	(4)	1.32	(1.21)	0.57	(0.56)		
	E2	13	(2)	29	(2)	1.84	(1.73)	0.91	(0.91)		
	E3	8	(1)	31	(2)	1.49	(1.38)	0.86	(0.85)	0.44	21.30*
	E4	12	(2)	34	(8)	1.80	(1.64)	0.89	(0.89)		(12)

Appendix 5(b) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1980	E1	5	(1)	19	(6)	1.07	(0.78)	0.82	(0.73)	0.45	10.88 (6)
	E2	9	(1)	15	(3)	1.53	(1.40)	0.97	(0.98)		
	E3	7	(2)	14	(8)	1.23	(0.98)	0.85	(1.00)		
	E4	6	(3)	13	(8)	1.25	(0.68)	0.94	(1.00)		
July 1980	E1	6	(2)	17	(5)	1.24	(0.84)	0.88	(0.79)	0.34	13.74 (10)
	E2	7	(2)	10	(3)	1.26	(0.96)	0.97	(0.94)		
	E3	8	(3)	20	(13)	1.39	(1.02)	0.86	(1.00)		
	E4	11	(3)	20	(10)	1.65	(1.37)	0.91	(1.00)		
Aug. 1980	E1	8	(3)	22	(13)	1.31	(0.99)	0.79	(0.89)	0.16	2.60 (4)
	E2	4	(1)	8	(3)	0.93	(0.68)	0.95	(1.00)		
	E2	3	(1)	7	(4)	0.66	(0.37)	0.87	(1.00)		
	E4	4	(1)	7	(4)	0.76	(0.60)	0.83	(1.00)		
Sept. 1980	E1	10	(3)	26	(15)	1.44	(1.30)	0.78	(0.97)	0.35	11.23 (8)
	E2++	6	(1)	7	(2)	1.12	(0.96)	1.00	(1.00)		
	E3	10	(3)	20	(7)	1.67	(1.30)	0.95	(0.92)		
	E4	7	(3)	17	(9)	1.26	(0.73)	0.85	(0.74)		
Oct. 1980	E1	18	(2)	72	(20)	2.09	(1.96)	0.83	(0.83)	0.63	40.31*** (16)
	E2	16	(3)	26	(7)	2.05	(1.85)	0.98	(1.00)		
	E3	11	(2)	30	(7)	1.76	(1.53)	0.90	(0.88)		
	E4++	11	(2)	21	(7)	1.66	(1.44)	0.91	(0.93)		
Nov. 1980	E1	5	(1)	26	(10)	1.72	(1.60)	0.94	(0.94)	0.55	26.25** (12)
	E2	14	(2)	54	(14)	2.01	(1.88)	0.88	(0.90)		
	E3	10	(2)	32	(11)	1.77	(1.58)	0.90	(0.92)		
	E4	5	(2)	24	(9)	1.64	(1.39)	0.94	(0.91)		
Dec. 1980	E1	19	(3)	86	(45)	2.14	(2.09)	0.82	(0.92)	0.69	41.39*** (15)
	E2	14	(2)	58	(14)	2.02	(1.88)	0.88	(0.89)		
	E3	10	(1)	35	(4)	1.72	(1.59)	0.90	(0.87)		
	E4	10	(1)	26	(4)	1.77	(1.66)	0.96	(0.96)		
Jan. 1981	E1	16	(3)	177	(56)	2.21	(1.90)	0.85	(0.80)	0.75	51.31*** (17)
	E2	20	(3)	205	(57)	2.07	(1.83)	0.74	(0.70)		
	E3	15	(3)	88	(23)	2.16	(1.85)	0.89	(0.84)		
	E4	14	(3)	73	(20)	2.06	(1.74)	0.88	(0.83)		
Feb. 1981	E1	20	(2)	121	(30)	2.20	(2.01)	0.81	(0.78)	0.63	37.51** (15)
	E2	12	(2)	72	(36)	1.75	(1.56)	0.79	(0.81)		
	E3	15	(3)	95	(29)	1.80	(1.65)	0.74	(0.75)		
	E4	14	(2)	70	(18)	1.94	(1.76)	0.83	(0.82)		
Mar. 1981	E1	10	(2)	46	(13)	1.71	(1.41)	0.86	(0.80)	0.62	36.94** (15)
	E2	17	(3)	95	(37)	2.05	(1.81)	0.81	(0.79)		
	E3	15	(3)	53	(24)	1.74	(1.70)	0.75	(0.86)		
	E4	12	(2)	39	(16)	1.73	(1.66)	0.83	(0.92)		
Apr. 1981	E1	15	(2)	35	(7)	2.06	(1.94)	0.94	(0.96)	0.36	17.33 (12)
	E2	13	(2)	41	(8)	1.91	(1.71)	0.89	(0.87)		
	E3	7	(2)	9	(3)	1.27	(0.98)	1.00	(1.00)		
	E4	6	(2)	11	(7)	0.79	(0.79)	1.00	(1.00)		
May 1981	E1	10	(1)	26	(4)	1.71	(1.58)	0.93	(0.92)	0.41	14.60 (9)
	E2	10	(2)	27	(10)	1.59	(1.36)	0.86	(0.86)		
	E3	6	(2)	8	(4)	1.10	(0.79)	0.96	(1.00)		
	E4++	4	(2)	6	(4)	0.80	(0.35)	0.92	(1.00)		

Appendix 5(b) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	x^2(d.f)
June 1981	E1	12	(4)	38	(21)	1.83	(1.47)	0.89	(0.93)	0.37	16.12 (11)
	E2	12	(2)	88	(48)	1.79	(1.72)	0.79	(0.88)		
	E3+	7	(1)	22	(2)	1.20	(1.04)	0.78	(0.73)		
	E4+	8	(2)	25	(2)	1.17	(0.99)	0.69	(0.67)		
July 1981	E1+	5	(3)	6	(4)	0.98	(0.35)	1.00	(1.00)	0.15	3.58 (8)
	E2+	13	(4)	42	(18)	1.82	(1.49)	0.85	(0.85)		
	E3+	3	(1)	27	(1)	0.72	(0.62)	0.74	(1.00)		
	E4+	2	(0)	23	(0)	0.40	(0.40)	0.64	(0.64)		
Aug. 1981	E1+	6	(2)	7	(3)	1.12	(0.79)	1.00	(1.00)	0.24	7.82 (8)
	E2+	12	(3)	55	(25)	1.69	(1.36)	0.81	(0.79)		
	E3+	5	(0)	22	(0)	0.93	(0.93)	0.69	(0.69)		
	E4+	3	(0)	21	(0)	0.60	(0.60)	0.64	(0.64)		
Sept. 1981	E1	14	(4)	94	(52)	1.82	(1.38)	0.76	(0.70)	0.60	33.32** (14)
	E2	13	(4)	95	(66)	1.77	(1.63)	0.76	(0.90)		
	E3	12	(4)	46	(24)	1.67	(1.52)	0.79	(0.92)		
	E4	12	(4)	50	(30)	1.59	(1.54)	0.74	(0.95)		
Oct. 1981	E1	13	(2)	77	(46)	1.67	(1.77)	0.73	(0.91)	0.36	19.94 (14)
	E2+	14	(3)	75	(56)	1.53	(1.70)	0.65	(0.96)		
	E3	10	(2)	47	(29)	1.24	(1.44)	0.62	(0.91)		
	E4	7	(3)	43	(36)	0.76	(0.76)	0.44	(0.83)		

Appendix 5. Components of prey type diversity: pitfall trap samples
(c) Under log.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	x^2(d.f)
	E1	9	(4)	38	(28)	1.25	(1.12)	0.67	(0.97)		
Aug.	E2	10	(2)	46	(27)	1.61	(1.48)	0.81	(0.92)		
1978	E3	12	(4)	80	(60)	1.34	(1.50)	0.60	(0.93)	0.59	32.45***
	E4	8	(2)	28	(18)	1.36	(1.19)	0.79	(0.97)		(11)
	C1	10	(2)	46	(31)	1.28	(1.33)	0.64	(0.86)		
	E1	4	(1)	15	(2)	1.04	(0.85)	0.94	(0.96)		
Sept.	E2+	7	(2)	36	(9)	1.23	(0.79)	0.73	(0.58)		
1978	E3+	5	(1)	11	(2)	0.93	(0.69)	0.79	(0.70)	0.14	5.52
	E4+	7	(4)	21	(12)	1.46	(0.79)	0.93	(0.96)		(8)
	C1+	6	(2)	10	(2)	1.19	(0.93)	0.97	(0.95)		
	E1	12	(3)	89	(37)	1.92	(1.57)	0.85	(0.81)		
Oct.	E2	14	(3)	163	(85)	1.84	(1.69)	0.74	(0.78)		
1978	E3	14	(3)	87	(31)	2.04	(1.68)	0.86	(0.80)	0.65	45.62***
	E4	17	(3)	88	(23)	2.21	(1.98)	0.87	(0.86)		(14)
	C1	12	(3)	70	(35)	1.64	(1.61)	0.74	(0.87)		
	E1	19	(3)	199	(23)	2.47	(2.29)	0.89	(0.88)		
Nov.	E2+	10	(1)	76	(3)	1.27	(1.17)	0.61	(0.59)		
1978	E3+	9	(2)	36	(5)	1.49	(1.24)	0.80	(0.76)	0.44	36.98**
	E4+	12	(1)	65	(6)	1.35	(1.17)	0.61	(0.56)		(17)
	C1	20	(3)	188	(29)	2.52	(2.33)	0.90	(0.89)		
Dec.	E1	22	(4)	219	(33)	2.57	(2.36)	0.89	(0.87)		
1978	E2+	15	(3)	69	(17)	2.00	(1.74)	0.84	(0.81)		
	E3+	15	(2)	61	(3)	1.86	(1.76)	0.79	(0.79)	0.62	64.63***
	E4	24	(3)	270	(54)	2.74	(2.55)	0.91	(0.89)		(21)
	C1	24	(3)	259	(46)	2.63	(2.44)	0.88	(0.85)		
Jan.	E1	16	(2)	237	(27)	1.91	(1.69)	0.73	(0.68)		
1979	E2	21	(3)	244	(21)	2.49	(2.33)	0.87	(0.85)		
	E3	20	(3)	221	(43)	2.47	(2.28)	0.87	(0.86)	0.71	85.23***
	E4	22	(2)	160	(17)	2.51	(2.40)	0.88	(0.87)		(24)
	C1	18	(2)	177	(16)	2.15	(1.99)	0.80	(0.77)		
Feb.	E1	16	(2)	144	(25)	2.19	(2.00)	0.85	(0.82)		
1979	E2	18	(2)	277	(52)	2.43	(2.26)	0.88	(0.86)		
	E3	17	(2)	192	(37)	2.36	(2.19)	0.89	(0.88)	0.66	69.78***
	E4	24	(3)	171	(14)	2.44	(2.30)	0.83	(0.82)		(21)
	C1	18	(2)	171	(17)	1.90	(1.71)	0.71	(0.66)		
Mar.	E1	13	(3)	85	(18)	2.08	(1.78)	0.90	(0.86)		
1979	E2	15	(3)	117	(19)	1.77	(1.50)	0.71	(0.66)		
	E3	16	(2)	104	(21)	2.03	(1.90)	0.81	(0.80)	0.77	61.45***
	E4	15	(3)	91	(17)	2.13	(1.91)	0.87	(0.86)		(16)
	C1	12	(2)	99	(12)	1.86	(1.65)	0.82	(0.78)		
Apr.	E1	14	(2)	58	(13)	2.12	(1.92)	0.92	(0.91)		
1979	E2	15	(2)	65	(5)	2.14	(2.03)	0.91	(0.91)		
	E3	14	(2)	75	(7)	2.01	(1.86)	0.86	(0.84)	0.58	49.34***
	E4	18	(3)	101	(25)	2.32	(2.09)	0.89	(0.87)		(17)
	C1	13	(3)	52	(11)	2.01	(1.77)	0.91	(0.90)		
May	E1	10	(3)	46	(14)	1.71	(1.26)	0.86	(0.76)		
1979	E2++	3	(1)	7	(3)	0.76	(0.45)	1.00	(1.00)		
	E3	10	(3)	49	(14)	1.61	(1.20)	0.80	(0.72)	0.51	27.83**
	E4	12	(4)	42	(21)	1.87	(1.54)	0.89	(0.94)		(11)
	C1	10	(3)	38	(24)	1.36	(1.25)	0.73	(0.94)		

Appendix 5(c) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1979	E1	12	(4)	98	(68)	1.64	(1.37)	0.72	(0.79)		
	E2++	3	(2)	5	(4)	0.60	(0.60)	0.88	(0.88)		
	E3	9	(2)	39	(18)	1.63	(1.37)	0.87	(0.87)	0.53	31.85**
	E4	12	(4)	52	(25)	1.81	(1.43)	0.84	(0.84)		(12)
	C1	10	(3)	60	(27)	1.62	(1.25)	0.79	(0.75)		
July 1979	E1	11	(3)	66	(41)	1.54	(1.32)	0.72	(0.78)		
	E2	10	(3)	74	(46)	1.41	(1.35)	0.68	(0.83)		
	E3	8	(2)	63	(40)	1.47	(1.28)	0.78	(0.87)	0.82	41.05***
	E4	12	(3)	53	(29)	1.75	(1.54)	0.81	(0.88)		(10)
	C1	11	(2)	62	(36)	1.50	(1.56)	0.71	(0.88)		
Aug. 1979	E1	8	(2)	64	(44)	1.35	(1.17)	0.72	(0.81)		
	E2	10	(4)	56	(35)	1.61	(1.35)	0.79	(0.93)		
	E3	12	(2)	58	(35)	1.60	(1.65)	0.73	(0.92)	0.86	38.54***
	E4	11	(3)	51	(25)	1.69	(1.47)	0.81	(0.86)		(9)
	C1	9	(2)	37	(20)	1.58	(1.36)	0.84	(0.91)		
Sept. 1979					NO DATA COLLECTED						
Oct. 1979	E1	18	(3)	51	(9)	2.15	(1.96)	0.89	(0.88)		
	E2	15	(2)	34	(7)	2.00	(1.81)	0.92	(0.90)		
	E3	14	(2)	63	(9)	2.03	(1.86)	0.88	(0.86)	0.44	37.64**
	E4	14	(1)	91	(18)	2.03	(1.94)	0.85	(0.85)		(17)
	C1	15	(2)	91	(24)	1.94	(1.77)	0.79	(0.78)		
Nov. 1979	E1	13	(2)	114	(15)	2.13	(1.96)	0.90	(0.89)		
	E2	19	(2)	132	(10)	2.16	(2.03)	0.80	(0.78)		
	E3	17	(2)	124	(20)	2.20	(2.02)	0.85	(0.82)	0.63	53.88***
	E4	18	(2)	113	(7)	2.20	(2.10)	0.84	(0.83)		(17)
	C1	15	(2)	170	(73)	1.77	(1.80)	0.70	(0.77)		
Dec. 1979	E1	19	(2)	135	(7)	2.14	(2.03)	0.79	(0.78)		
	E2	25	(3)	377	(46)	2.22	(2.01)	0.72	(0.68)		
	E3	23	(3)	238	(38)	2.43	(2.21)	0.82	(0.79)	0.73	72.92***
	E4	24	(3)	244	(10)	2.36	(2.26)	0.79	(0.79)		(25)
Jan. 1980	E1	13	(3)	47	(5)	1.87	(1.68)	0.86	(0.85)		
	E2	17	(2)	91	(19)	1.97	(1.73)	0.78	(0.72)		
	E3	17	(2)	90	(33)	2.08	(1.93)	0.82	(0.83)	0.70	47.38***
	E4	15	(2)	88	(25)	2.03	(1.92)	0.84	(0.85)		(17)
Feb. 1980	E1	13	(2)	61	(7)	1.96	(1.78)	0.87	(0.85)		
	E2	16	(2)	82	(21)	2.14	(1.95)	0.87	(0.85)		39.82***
	E3	19	(2)	136	(33)	2.19	(2.04)	0.81	(0.80)	0.62	(16)
	E4	13	(1)	88	(10)	1.90	(1.77)	0.82	(0.79)		
Mar. 1980	E1	12	(2)	41	(8)	1.95	(1.77)	0.94	(0.93)		
	E2	12	(1)	37	(3)	1.61	(1.48)	0.78	(0.75)		
	E3	17	(4)	105	(24)	2.07	(1.87)	0.81	(0.81)	0.25	14.03
	E4	18	(3)	90	(23)	2.18	(2.02)	0.85	(0.85)		(14)
Apr. 1980	E1	16	(2)	91	(2)	1.83	(1.77)	0.73	(0.74)		
	E2++	3	(0)	4	(0)	0.62	(0.62)	1.00	(1.00)	0.39	20.07
	E3	15	(2)	93	(19)	1.79	(1.60)	0.73	(0.70)		(13)
	E4	11	(1)	117	(10)	1.73	(1.59)	0.78	(0.75)		
May 1980	E1	10	(1)	50	(6)	1.64	(1.48)	0.81	(0.78)		
	E2	8	(1)	16	(2)	1.44	(1.31)	0.92	(0.90)		16.79
	E3	11	(1)	27	(8)	1.59	(1.49)	0.83	(0.86)	0.38	(11)
	E4	10	(1)	24	(5)	1.54	(1.38)	0.85	(0.82)		

Appendix 5(c) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	x^2(d.f)
June 1980	E1	8	(2)	20	(3)	1.36	(1.12)	0.84	(0.80)		
	E2	9	(2)	17	(4)	1.50	(1.26)	0.91	(0.89)		
	E3	7	(2)	11	(4)	1.30	(1.02)	0.97	(1.00)	0.19	7.65
	E4	8	(2)	12	(4)	1.40	(1.15)	0.98	(1.00)		(10)
July 1980	E1	7	(2)	16	(3)	1.31	(1.04)	0.89	(0.85)		
	E2	6	(2)	17	(6)	1.07	(0.63)	0.76	(0.60)		
	E3	11	(4)	19	(10)	1.70	(1.27)	0.96	(1.00)	0.28	13.23
	E4	11	(4)	20	(9)	1.73	(1.34)	0.96	(1.00)		(12)
	E1	8	(2)	11	(2)	1.30	(1.07)	0.93	(0.90)		
Aug. 1980	E2	5	(1)	14	(8)	0.94	(0.87)	0.76	(1.00)	0.16	5.00
	E3	9	(3)	13	(5)	1.52	(1.15)	1.00	(1.00)		(8)
	E4	7	(3)	14	(6)	1.39	(0.93)	0.96	(0.95)		
Sept. 1980	E1	11	(4)	25	(12)	1.71	(1.23)	0.91	(0.87)		
	E2	8	(3)	26	(12)	1.56	(1.13)	0.92	(0.91)	0.56	26.64**
	E3	9	(2)	19	(3)	1.50	(1.28)	0.89	(0.87)		(12)
	E4	8	(2)	22	(8)	1.40	(1.06)	0.85	(0.79)		
	E1	10	(2)	26	(7)	1.65	(1.46)	0.90	(0.91)		
Oct. 1980	E2	8	(3)	39	(23)	1.42	(0.86)	0.79	(0.68)		
	E3	9	(2)	22	(4)	1.52	(1.29)	0.89	(0.86)	0.40	15.94
	E4	9	(2)	24	(3)	1.37	(1.15)	0.78	(0.74)		(10)
	E1	7	(1)	31	(3)	1.47	(1.33)	0.89	(0.88)		
Nov. 1980	E2	11	(2)	95	(16)	1.41	(1.15)	0.64	(0.57)		
	E3	8	(2)	40	(16)	1.44	(0.99)	0.80	(0.66)	0.41	19.48
	E4	10	(2)	32	(12)	1.57	(1.24)	0.82	(0.76)		(12)
	E1	17	(3)	85	(40)	2.06	(2.08)	0.82	(0.94)		
Dec. 1980	E2	10	(1)	52	(15)	1.63	(1.50)	0.81	(0.80)	0.41	24.33
	E3	12	(2)	55	(13)	1.86	(1.71)	0.86	(0.87)		(15)
	E4	10	(2)	22	(2)	1.62	(1.47)	0.90	(0.91)		
Jan. 1981	E1	18	(3)	121	(34)	2.41	(2.22)	0.91	(0.91)		
	E2	10	(1)	68	(26)	1.57	(1.52)	0.76	(0.80)		
	E3	16	(2)	159	(13)	1.71	(1.52)	0.66	(0.62)	0.60	48.28***
	E4	18	(3)	105	(18)	2.12	(1.91)	0.81	(0.78)		(20)
Feb. 1981	E1	16	(2)	134	(35)	2.12	(1.98)	0.83	(0.82)		
	E2	14	(2)	82	(19)	2.00	(1.78)	0.84	(0.81)		42.94***
	E3	17	(2)	97	(43)	1.97	(2.00)	0.77	(0.86)	0.77	(14)
	E4	14	(2)	79	(28)	2.00	(1.94)	0.85	(0.90)		
Mar. 1981	E1	11	(2)	31	(9)	1.72	(1.56)	0.88	(0.91)		
	E2	12	(2)	68	(23)	1.65	(1.51)	0.75	(0.76)		
	E3	13	(2)	72	(23)	1.97	(1.91)	0.87	(0.92)	0.59	32.87**
	E4	13	(1)	34	(3)	1.85	(1.75)	0.89	(0.87)		(14)
Apr. 1981	E1	3	(0)	3	(0)	0.60	(0.60)	1.00	(1.00)		
	E2++	6	(1)	9	(1)	1.15	(1.01)	0.96	(0.95)		
	E3	10	(2)	22	(7)	1.62	(1.44)	0.90	(0.93)	0.67	14.14*
	E4	8	(2)	18	(6)	1.35	(1.06)	0.85	(0.80)		(7)
May 1981	E1++	2	(0)	2	(0)	0.35	(0.35)	1.00	(1.00)		
	E2++	3	(1)	4	(2)	0.62	(0.35)	1.00	(1.00)		
	E3	6	(1)	13	(2)	1.18	(0.99)	0.88	(0.84)	0.38	5.67
	E4	6	(1)	11	(3)	1.20	(1.01)	0.94	(0.95)		(5)

Appendix 5(c) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1981	E1	9	(3)	57	(30)	1.67	(1.25)	0.85	(0.83)		
	E2	7	(1)	23	(8)	1.36	(1.21)	0.86	(0.89)		
	E3+	3	(1)	3	(1)	0.60	(0.35)	1.00	(1.00)	0.37	5.13
	E4+	3	(1)	5	(2)	0.68	(0.37)	1.00	(1.00)		(7)
July 1981	E1	7	(2)	10	(5)	1.26	(0.96)	0.97	(1.00)		
	E2	4	(1)	23	(17)	0.65	(0.57)	0.55	(0.76)	0.54	5.43
	E3+	3	(0)	5	(0)	0.60	(0.60)	0.88	(0.88)		(5)
	E4+	2	(0)	7	(0)	0.43	(0.43)	0.86	(0.86)		
Aug. 1981	E1	7	(3)	14	(5)	0.37	(0.95)	0.94	(0.95)		
	E2	3	(1)	14	(11)	0.50	(0.37)	0.56	(1.00)		
	E3+	4	(0)	7	(0)	0.86	(0.86)	0.94	(0.94)	0.08	1.57
	E4+	4	(0)	9	(0)	0.81	(0.81)	0.82	(0.82)		(5)
Sept. 1981	E1	12	(4)	75	(48)	1.76	(1.55)	0.79	(0.91)		
	E2	15	(4)	78	(49)	1.83	(1.74)	0.76	(0.90)		
	E3	9	(2)	18	(5)	1.48	(1.18)	0.88	(0.83)	0.44	21.23*
	E4	8	(2)	19	(5)	1.59	(1.37)	0.94	(0.95)		(12)
Oct. 1981	E1	16	(3)	46	(18)	2.02	(1.85)	0.87	(0.92)		
	E2	9	(2)	84	(61)	1.37	(1.44)	0.68	(0.91)		
	E3	13	(2)	30	(6)	1.80	(1.58)	0.88	(0.84)	0.39	20.47
	E4	10	(2)	44	(7)	1.66	(1.42)	0.84	(0.80)		(13)

Appendix 5. Components of prey type diversity: pitfall trap samples (d) Open

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
	E1	9	(2)	30	(12)	1.63	(1.40)	0.90	(0.93)		
Aug.	E2	10	(3)	30	(14)	1.69	(1.36)	0.89	(0.92)		
1978	E3	11	(3)	44	(26)	1.52	(1.48)	0.74	(0.93)	0.63	37.93***
	E4	10	(3)	37	(26)	1.36	(1.30)	0.70	(0.97)		(12)
	C1	6	(2)	54	(41)	1.09	(0.70)	0.67	(0.65)		
	E1	5	(3)	13	(6)	1.04	(0.28)	0.85	(0.55)		
Sept.	E2	5	(2)	14	(2)	0.84	(0.54)	0.67	(0.62)		
1978	E3	4	(1)	11	(3)	1.01	(0.76)	0.97	(0.95)	0.30	7.51
	E4+	4	(2)	8	(3)	0.84	(0.32)	0.86	(0.70)		(5)
	C1	4	(2)	12	(8)	0.91	(0.35)	0.85	(0.77)		
	E1+	13	(3)	99	(32)	2.04	(1.72)	0.87	(0.83)		
Oct.	E2+	16	(3)	101	(44)	1.98	(1.79)	0.79	(0.80)		
1978	E3	18	(3)	128	(57)	2.09	(2.05)	0.79	(0.86)	0.73	68.93***
	E4+	17	(3)	81	(26)	2.24	(1.97)	0.89	(0.87)		(19)
	C1	14	(3)	152	(30)	1.56	(1.16)	0.63	(0.52)		
	E1+	12	(3)	70	(19)	1.79	(1.54)	0.81	(0.80)		
Nov.	E2+	8	(1)	90	(1)	0.82	(0.78)	0.43	(0.43)		
1978	E3	20	(3)	209	(77)	2.45	(2.28)	0.87	(0.87)	0.35	33.21*
	E4	18	(3)	134	(33)	2.30	(2.02)	0.87	(0.82)		(19)
	C1+	10	(2)	60	(7)	1.55	(1.35)	0.76	(0.73)		
Dec.	E1	21	(3)	306	(70)	2.41	(2.15)	0.83	(0.79)		
1978	E2	25	(4)	291	(62)	2.50	(2.23)	0.82	(0.78)		
	E3	24	(4)	269	(96)	2.58	(2.43)	0.86	(0.87)	0.68	78.17***
	E4	21	(3)	366	(160)	2.27	(2.05)	0.78	(0.76)		(23)
	C1+	18	(3)	133	(37)	2.27	(2.00)	0.86	(0.82)		
Jan.	E1	16	(3)	156	(39)	2.42	(2.16)	0.94	(0.91)		
1979	E2+	25	(4)	242	(23)	2.32	(2.12)	0.77	(0.74)		
	E3	23	(4)	135	(28)	2.58	(2.37)	0.91	(0.89)	0.72	86.20***
	E4	23	(2)	190	(33)	2.43	(2.28)	0.83	(0.81)		(24)
	C1	20	(3)	150	(11)	2.45	(2.31)	0.89	(0.88)		
Feb.	E1	15	(2)	110	(25)	2.11	(1.90)	0.85	(0.82)		
1979	E2	21	(2)	334	(22)	1.88	(1.72)	0.65	(0.61)		
	E3	17	(3)	193	(52)	2.40	(2.15)	0.90	(0.88)	0.64	70.94***
	E4	24	(3)	165	(45)	2.51	(2.31)	0.86	(0.84)		(22)
	C1	19	(2)	242	(31)	1.95	(1.72)	0.70	(0.65)		
Mar.	E1	13	(3)	95	(34)	1.93	(1.56)	0.83	(0.76)		
1979	E2	14	(2)	137	(79)	1.66	(1.88)	0.68	(0.87)		
	E3	14	(3)	116	(65)	1.73	(1.65)	0.71	(0.79)	0.76	57.23***
	E4	14	(3)	82	(28)	2.00	(1.77)	0.85	(0.85)		(15)
	C1	18	(3)	110	(54)	2.11	(1.94)	0.81	(0.84)		
Apr.	E1	18	(2)	141	(43)	2.38	(2.25)	0.89	(0.89)		
1979	E2	13	(2)	46	(9)	1.99	(1.78)	0.91	(0.89)		
	E3	14	(2)	63	(19)	1.98	(1.80)	0.86	(0.85)	0.63	60.19***
	E4	18	(3)	102	(24)	2.39	(2.23)	0.92	(0.93)		(19)
	C1	17	(2)	111	(42)	1.92	(1.93)	0.75	(0.81)		
May	E1	13	(2)	101	(21)	1.85	(1.57)	0.79	(0.72)		
1979	E2	8	(1)	13	(4)	1.38	(1.27)	0.94	(1.00)		
	E3	8	(2)	52	(23)	1.62	(1.40)	0.88	(0.92)	0.51	35.65**
	E4	16	(3)	66	(15)	2.06	(1.79)	0.85	(0.81)		(14)
	C1	11	(3)	88	(12)	1.57	(1.26)	0.72	(0.66)		

Appendix 5(d). Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1979	E1	12	(2)	48	(18)	1.80	(1.72)	0.84	(0.91)		
	E2	10	(3)	31	(7)	1.64	(1.28)	0.86	(0.80)		
	E3	9	(1)	55	(14)	1.72	(1.59)	0.88	(0.88)	0.54	35.19***
	E4	15	(4)	88	(37)	1.81	(1.73)	0.75	(0.83)		(13)
	C1	13	(3)	70	(23)	1.94	(1.77)	0.85	(0.88)		
July 1979	E1	11	(2)	14	(4)	1.62	(1.44)	0.98	(1.0)		
	E2	7	(1)	15	(2)	1.39	(1.25)	0.95	(0.94)		
	E3	10	(2)	37	(19)	1.52	(1.44)	0.79	(0.91)	0.26	16.73
	E4	11	(2)	23	(6)	1.80	(1.60)	0.96	(0.97)		(13)
	C1	10	(2)	39	(19)	1.47	(1.47)	0.75	(0.91)		
Aug. 1979	E1	10	(2)	53	(39)	1.31	(1.39)	0.65	(0.93)		
	E2	11	(3)	63	(50)	1.24	(1.44)	0.58	(0.98)		
	E3	12	(3)	46	(27)	1.77	(1.52)	0.83	(0.90)	0.68	40.75***
	E4	12	(3)	36	(19)	1.74	(1.60)	0.85	(0.97)		(12)
	C1	10	(4)	44	(31)	1.43	(1.25)	0.72	(0.95)		
Sept. 1979	NO DATA COLLECTED										
Oct. 1979	E1	17	(3)	108	(35)	2.27	(2.08)	0.88	(0.89)		
	E2	14	(4)	96	(36)	1.67	(1.35)	0.70	(0.66)		
	E3	17	(3)	92	(40)	2.23	(2.02)	0.88	(0.89)		
	E4	22	(4)	194	(119)	1.90	(2.17)	0.66	(0.86)	0.80	87.90***
	C1	18	(4)	122	(60)	1.97	(2.01)	0.75	(0.87)		(22)
Nov. 1979	E1	18	(3)	151	(25)	2.22	(1.98)	0.83	(0.79)		
	E2	22	(4)	177	(29)	2.31	(2.05)	0.81	(0.77)		
	E3	21	(4)	180	(27)	2.16	(1.90)	0.76	(0.72)	0.66	65.92***
	E4	18	(4)	158	(40)	2.41	(2.18)	0.90	(0.90)		(20)
	C1	18	(3)	174	(68)	2.12	(2.18)	0.79	(0.88)		
Dec. 1979	E1	26	(2)	274	(48)	2.37	(2.27)	0.77	(0.76)		
	E2	27	(3)	300	(20)	2.43	(2.30)	0.78	(0.76)		
	E3	21	(3)	248	(31)	2.46	(2.30)	0.86	(0.84)	0.75	81.54***
	E4	26	(3)	286	(54)	2.56	(2.39)	0.83	(0.81)		(27)
Jan. 1980	E1	21	(3)	120	(45)	2.12	(1.88)	0.77	(0.74)		
	E2	21	(2)	166	(21)	2.24	(2.08)	0.80	(0.77)		
	E3	20	(3)	79	(10)	2.17	(1.97)	0.83	(0.80)	0.71	59.82***
	E4	14	(2)	91	(18)	2.04	(1.91)	0.85	(0.86)		(21)
Feb. 1980	E1	20	(3)	96	(38)	2.22	(2.10)	0.83	(0.87)		
	E2	18	(2)	85	(11)	2.12	(1.96)	0.83	(0.80)		
	E3	20	(1)	72	(8)	2.21	(2.12)	0.85	(0.84)	0.57	47.52***
	E4	17	(2)	92	(30)	2.13	(2.03)	0.84	(0.86)		(21)
Mar. 1980	E1	13	(3)	34	(7)	1.85	(1.56)	0.89	(0.84)		
	E2	11	(2)	40	(10)	1.82	(1.56)	0.90	(0.86)		
	E3	10	(2)	49	(18)	1.73	(1.50)	0.86	(0.86)	0.55	26.64**
	E4	10	(1)	37	(8)	1.77	(1.66)	0.92	(0.92)		(12)
Apr. 1980	E1	16	(3)	56	(26)	1.99	(1.88)	0.84	(0.92)		
	E2	13	(3)	100	(57)	1.59	(1.65)	0.68	(0.84)		
	E3	12	(2)	59	(10)	1.76	(1.52)	0.81	(0.76)	0.49	31.59*
	E4	13	(3)	84	(17)	1.83	(1.47)	0.79	(0.71)		(16)
May 1980	E1	11	(2)	20	(6)	1.66	(1.49)	0.92	(0.96)		
	E2	11	(3)	89	(66)	1.64	(1.60)	0.75	(0.96)		
	E3	8	(2)	17	(6)	1.52	(1.24)	0.96	(0.97)	0.39	18.65
	E4	11	(2)	32	(8)	1.81	(1.58)	0.92	(0.90)		(12)

Appendix 5(d). Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
	E1	9	(2)	36	(20)	1.49	(1.33)	0.80	(0.90)		
Jun.	E2	6	(2)	14	(5)	1.10	(0.69)	0.82	(0.70)		
1980	E3	7	(1)	12	(3)	1.34	(1.19)	0.98	(1.00)	0.15	5.51
	E4	7	(3)	11	(7)	1.30	(0.79)	0.97	(1.00)		(9)
	E1	6	(2)	34	(24)	1.23	(0.87)	0.80	(0.86)		
Jul.	E2	5	(2)	10	(4)	1.01	(0.57)	0.87	(0.76)		
1980	E3	9	(3)	14	(6)	1.52	(1.15)	0.98	(1.00)	0.26	7.17
	E4	9	(3)	13	(6)	1.49	(1.12)	0.98	(1.00)		(7)
	E1	7	(2)	21	(9)	1.31	(1.06)	0.84	(0.89)		
Aug.	E2	9	(2)	13	(4)	1.49	(1.27)	0.98	(1.00)		
1980	E3++	3	(2)	3	(2)	0.6	-	1.00	-	0.11	3.10
	E4++	2	(1)	2	(1)	0.35	-	1.00	-		(7)
	E1	13	(3)	63	(46)	1.46	(1.64)	0.65	(0.97)		
Sept.	E2	8	(2)	45	(37)	0.78	(1.15)	0.43	(1.00)		
1980	E3	8	(3)	40	(31)	1.27	(0.99)	0.70	(0.89)	0.45	16.93*
	E4	8	(3)	50	(40)	1.14	(0.85	0.62	(0.73)		(9)
	E1	9	(1)	45	(16)	1.42	(1.26)	0.74	(0.73)		
Oct.	E2	13	(3)	87	(63)	1.40	(1.61)	0.60	(0.89)		
1980	E3	6	(2)	22	(8)	1.35	(0.91)	0.92	(0.84)	0.32	15.25
	E4	6	(1)	24	(8)	1.31	(1.12)	0.88	(0.88)		(12)
Nov.	E1 ++	5	-	13	-	1.04	(1.04)	0.85	(0.85)		
1980	E2	15	(2)	89	(5)	2.00	(1.85)	0.82	(0.81)		
	E3	11	(1)	58	(15)	1.75	(1.64)	0.83	(0.83)	0.41	19.71
	E4	9	(1)	22	(1)	1.60	(1.53)	0.93	(0.94)		(12)
Dec.	E1	14	(3)	85	(45)	1.83	(1.66)	0.77	(0.82)		
1980	E2 +	12	(2)	60	(22)	1.67	(1.52)	0.76	(0.78)		
	E3	12	(2)	50	(9)	1.92	(1.76)	0.90	(0.89)	0.48	27.05*
	E4	15	(2)	48	(6)	1.97	(1.79)	0.86	(0.83)		(14)
Jan.	E1	16	(2)	110	(25)	2.21	(2.01)	0.87	(0.85)		
1981	E2	16	(3)	189	(81)	2.08	(1.73)	0.80	(0.74)	0.63	38.01***
	E3	14	(2)	57	(11)	2.08	(1.92)	0.91	(0.91)		(15)
	E4	13	(1)	67	(11)	1.91	(1.79)	0.84	(0.82)		
Feb.	E1	18	(2)	98	(41)	2.09	(2.02)	0.81	(0.85)		
1981	E2	18	(2)	70	(26)	2.07	(2.02)	0.82	(0.88)	0.72	46.27***
	E3	13	(2)	60	(12)	1.48	(1.19)	0.66	(0.57)		(16)
	E4	13	(2)	52	(8)	1.77	(1.56)	0.80	(0.76)		
Mar.	E1	15	(3)	42	(11)	2.03	(1.80)	0.90	(0.90)		
1981	E2	16	(2)	105	(38)	2.07	(2.00)	0.82	(0.86)		
	E3	10	(2)	41	(15)	1.67	(1.50)	0.85	(0.89)	0.72	40.21***
	E4	9	(2)	22	(6)	1.58	(1.36)	0.92	(0.92)		(14)
Apr.	E1	11	(1)	22	(3)	1.78	(1.68)	0.96	(0.96)		
1981	E2	12	(3)	54	(31)	1.82	(1.55)	0.84	(0.89)		
	E3	7	(2)	20	(7)	1.39	(1.12)	0.90	(0.92)	0.27	11.74 (11)
	E4	6	(1)	7	(1)	1.12	(0.98)	1.00	(1.00)		
May	E1	15	(2)	41	(9)	2.13	(2.00)	0.95	(0.97)		
1981	E2	8	(2)	35	(23)	1.39	(1.19)	0.79	(0.90)		
	E3	3	0	8	0	0.70	0	0.89	0	0.06	2.09
	E4	5	(2)	8	(3)	1.01	(0.60)	0.95	(0.88)		(11)

Appendix 5(d). Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
Jun. 1981	E1+	9	(2)	39	(23)	1.21	(1.07)	0.64	(0.73)		
	E2	8	(1)	14	(1)	1.36	(1.26)	0.90	(0.89)		
	E3	5	(1)	21	(6)	1.04	(0.73)	0.79	(0.66)	0.49	13.63
	E4	7	(2)	19	(6)	1.34	(1.04)	0.88	(0.85)		(7)
Jul. 1981	E1+	5	(2)	8	(2)	0.93	(0.57)	0.87	(0.76)		
	E2+	4	(2)	15	(2)	0.53	(0.20)	0.48	(0.34	0.48	5.78
	E3	4	(2)	4	(2)	0.79	(0.35)	1.00	(1.00)		(3)
	E4	3	(2)	6	(4)	0.68	0	0.91	0		
Aug. 1981	E1+	5	(1)	16	(1)	0.92	(0.79)	0.72	(0.72)		
	E2+	4	(2)	26	(2)	0.37	(0.13)	0.31	(0.21)		
	E3	6	(3)	11	(8)	1.20	(0.60)	0.94	(1.00)	0.34	6.75
	E4	4	(1)	7	(3)	0.86	(0.62)	0.94	(1.00)		(5)
Sept. 1981	E1	17	(3)	94	(49)	2.02	(2.01)	0.79	(0.91)		
	E2	14	(3)	48	(26)	1.62	(1.72)	0.72	(0.92)		
	E3	10	(4)	55	(45)	1.23	(1.19)	0.61	(0.97)	0.43	24.22*
	E4	8	(3)	58	(47)	1.00	(1.18)	0.54	(1.00)		(14)
Oct. 1981	E1	17	(2)	95	(33)	2.13	(1.99)	0.84	(0.85)		
	E2+	14	(2)	46	(23)	1.72	(1.76)	0.77	(0.92)	0.54	36.61**
	E3	13	(3)	104	(59)	1.71	(1.43)	0.73	(0.72)		(17)
	E4	15	(2)	46	(11)	1.96	(1.76)	0.86	(0.84)		

Appendix 5. Components of prey type diversity: pitfall trap samples
(e) Slopes

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
	E1	7	(3)	31	(21)	1.35	(0.94)	0.82	(0.93)		
Aug.	E2	11	(3)	47	(14)	1.57	(1.06)	0.76	(0.61)		
1978	E3	11	(4)	76	(36)	1.55	(0.92)	0.71	(0.54)	0.71	35.71***
	E4	8	(3)	47	(26)	1.54	(0.84)	0.84	(0.63)		(10)
	C1	9	(2)	69	(41)	1.40	(0.93)	0.70	(0.57)		
	E1+	6	(1)	26	(2)	1.14	(1.00)	0.76	(0.74)		
Sept.	E2	6	(2)	61	(7)	1.06	(0.79)	0.65	(0.62)		
1978	E3+	6	(2)	15	(3)	1.16	(0.85)	0.85	(0.80)	0.18	7.35
	E4+	7	(2)	15	(4)	1.33	(0.99)	0.91	(0.84)		(8)
	C1	5	(1)	29	(3)	0.97	(0.77)	0.70	(0.64)		
	E1	12	(4)	125	(57)	1.83	(1.52)	0.79	(0.81)		
Oct.	E2	16	(2)	132	(49)	1.99	(1.77)	0.78	(0.75)		
1978	E3	16	(3)	161	(84)	1.99	(1.95)	0.77	(0.85)	0.73	62.47***
	E4	14	(3)	127	(48)	2.11	(1.75)	0.86	(0.81)		(17)
	C1	13	(4)	124	(63)	1.98	(1.68)	0.83	(0.86)		
	E1	20	(4)	193	(81)	2.37	(2.22)	0.85	(0.88)		
Nov.	E2	16	(4)	178	(61)	2.28	(2.00)	0.88	(0.87)		
1978	E3+	10	(3)	44	(22)	1.47	(1.00)	0.74	(0.63)	0.44	39.77**
	E4+	6	(2)	20	(16)	0.96	(0.79)	0.67	(1.00)		(18)
	C1	18	(3)	178	(82)	2.14	(2.08)	0.79	(0.85)		
	E1	25	(4)	275	(104)	2.21	(2.00)	0.80	(0.82)		
Dec.	E2	24	(3)	301	(62)	2.43	(2.18)	0.81	(0.76)		
1978	E3+	14	(3)	92	(19)	2.14	(1.87)	0.90	(0.87)	0.82	103.10***
	E4	24	(4)	302	(49)	2.20	(1.91)	0.73	(0.67)		(25)
	C1	22	(3)	255	(94)	2.35	(2.27)	0.80	(0.83)		
	E1	19	(4)	190	(41)	2.06	(1.73)	0.75	(0.69)		
Jan.	E2	21	(3)	171	(32)	2.09	(1.79)	0.74	(0.67)		
1979	E3	21	(4)	166	(51)	2.43	(2.17)	0.86	(0.84)		
	E4	18	(4)	141	(56)	2.25	(1.93)	0.84	(0.81)	0.77	84.42***
	C1	17	(3)	220	(25)	1.76	(1.49)	0.66	(0.60)		(22)
	E1	15	(3)	144	(37)	2.19	(1.87)	0.87	(0.82)		
	E2	20	(3)	159	(45)	2.48	(2.26)	0.89	(0.88)		
Feb.	E3	19	(2)	131	(32)	2.38	(2.27)	0.88	(0.89)		
1979	E4	24	(4)	161	(87)	2.17	(2.16)	0.74	(0.83)	0.66	76.03***
	C1	17	(3)	173	(34)	2.08	(1.80)	0.79	(0.73)		(23)
	E1	13	(3)	105	(47)	1.98	(1.60)	0.84	(0.78)		
Mar.	E2	14	(3)	106	(40)	2.03	(1.75)	0.84	(0.82)		
1979	E3	20	(3)	143	(49)	2.16	(1.83)	0.78	(0.72)		
	E4	13	(3)	63	(17)	2.04	(1.75)	0.91	(0.88)	0.83	62.05***
	C1	13	(3)	74	(34)	1.93	(1.61)	0.85	(0.82)		(15)
	E1	14	(3)	137	(27)	1.95	(1.60)	0.80	(0.72)		
Apr.	E2	15	(3)	84	(23)	2.00	(1.73)	0.83	(0.79)		
1979	E3	16	(3)	88	(32)	2.19	(2.00)	0.88	(0.90)	0.54	45.74***
	E4	11	(2)	60	(12)	1.80	(1.55)	0.85	(0.81)		(17)
	C1	11	(2)	107	(41)	1.82	(1.64)	0.82	(0.83)		
	E1	12	(4)	69	(29)	1.93	(1.43)	0.87	(0.79)		
May	E2	12	(3)	61	(32)	1.74	(1.52)	0.80	(0.84)		
1979	E3	16	(4)	51	(16)	2.01	(1.65)	0.86	(0.80)		
	E4	12	(3)	69	(17)	1.86	(1.51)	0.84	(0.78)	0.64	48.00***
	C1	10	(3)	34	(15)	1.68	(1.40)	0.88	(0.92)		(15)

Appendix 5(e) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1979	E1	8	(2)	81	(32)	1.71	(1.36)	0.89	(0.84)	0.76	41.90*** (11)
	E2	14	(3)	63	(21)	1.92	(1.69)	0.83	(0.83)		
	E3	10	(4)	60	(19)	1.55	(0.98)	0.76	(0.62)		
	E4	11	(2)	73	(17)	1.84	(1.55)	0.85	(0.79)		
	C1	10	(2)	66	(39)	1.61	(1.52)	0.78	(0.89)		
July 1979	E1	8	(1)	37	(9)	1.53	(1.36)	0.86	(0.84)	0.62	33.96*** (11)
	E2	11	(3)	43	(20)	1.74	(1.44)	0.85	(0.86)		
	E3	9	(3)	30	(17)	1.52	(1.18)	0.84	(0.88)		
	E4	11	(2)	52	(25)	1.63	(1.68)	0.78	(0.94)		
	C1	8	(2)	29	(7)	1.54	(1.22)	0.89	(0.83)		
Aug. 1979	E1	9	(2)	35	(13)	1.69	(1.43)	0.91	(0.91)	0.62	30.78*** (10)
	E2	10	(1)	27	(4)	1.74	(1.62)	0.94	(0.94)		
	E3	11	(2)	44	(25)	1.63	(1.61)	0.79	(0.95)		
	E4	12	(3)	39	(22)	1.71	(1.53)	0.82	(0.93)		
	C1	12	(2)	41	(17)	1.79	(1.59)	0.86	(0.88)		
Sept. 1979	NO DATA COLLECTED										
Oct. 1979	E1	16	(2)	127	(27)	1.87	(1.58)	0.73	(0.66)	0.47	49.28*** (21)
	E2	16	(4)	127	(54)	2.13	(1.90)	0.84	(0.85)		
	E3	15	(3)	77	(30)	2.07	(1.86)	0.86	(0.87)		
	E4	20	(4)	145	(42)	1.92	(1.57)	0.70	(0.62)		
	C1	11	(3)	86	(22)	1.97	(1.62)	0.90	(0.86)		
Nov. 1979	E1	16	(3)	202	(59)	2.14	(1.79)	0.82	(0.75)	0.81	76.49*** (19)
	E2	20	(3)	134	(32)	2.47	(2.24)	0.90	(0.87)		
	E3	18	(3)	155	(59)	2.17	(2.05)	0.81	(0.84)		
	E4	20	(4)	143	(34)	2.35	(2.08)	0.86	(0.82)		
	C1	15	(3)	124	(29)	2.13	(1.83)	0.85	(0.81)		
Dec. 1979	E1	20	(4)	260	(81)	2.40	(2.19)	0.85	(0.84)	0.65	67.70*** (26)
	E2	23	(4)	388	(68)	2.46	(2.16)	0.82	(0.77)		
	E3	24	(3)	299	(38)	2.60	(2.45)	0.86	(0.85)		
	E4	17	(3)	169	(18)	2.29	(2.12)	0.87	(0.86)		
Jan. 1980	E1	16	(3)	118	(30)	2.13	(1.82)	0.86	(0.81)	0.60	35.72** (15)
	E2	13	(2)	60	(13)	2.03	(1.82)	0.87	(0.84)		
	E3	14	(2)	73	(16)	2.12	(1.94)	0.90	(0.89)		
	E4	14	(2)	72	(19)	1.95	(1.73)	0.85	(0.83)		
Feb. 1980	E1	21	(2)	310	(132)	2.22	(2.22)	0.76	(0.81)	0.83	73.47*** (22)
	E2	19	(2)	255	(52)	1.80	(1.55)	0.65	(0.58)		
	E3	20	(2)	125	(22)	2.44	(2.29)	0.89	(0.88)		
	E4	22	(2)	159	(44)	2.28	(2.16)	0.80	(0.80)		
Mar. 1980	E1	13	(2)	85	(44)	1.76	(1.60)	0.76	(0.79)	0.46	24.03* (13)
	E2	14	(2)	61	(25)	1.98	(1.86)	0.86	(0.90)		
	E3	13	(1)	85	(3)	1.85	(1.77)	0.80	(0.79)		
	E4	16	(2)	90	(11)	1.93	(1.77)	0.78	(0.75)		
Apr. 1980	E1++	13	(2)	47	(13)	1.86	(1.59)	0.85	(0.80)	0.47	31.75* (17)
	E2	18	(3)	166	(111)	1.94	(2.07)	0.72	(0.89)		
	E3++	15	(2)	60	(11)	2.06	(1.89)	0.88	(0.86)		
	E4++	13	(2)	43	(6)	2.00	(1.83)	0.93	(0.91)		
May 1980	E1	6	(3)	23	(17)	0.94	(0.75)	0.64	(1.00)	0.28	9.11 (8)
	E2	11	(1)	32	(2)	1.67	(1.58)	0.85	(0.84)		
	E3	8	(1)	13	(2)	1.44	(1.30)	0.98	(0.97)		
	E4	6	(0)	17	(0)	1.20	(1.20)	0.85	(0.85)		

Appendix 5(e) Cont'd.

Date	Pitfall site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
June 1980	E1	10	(4)	36	(20)	1.73	(1.28)	0.90	(0.92)	0.66	21.08** (8)
	E2	9	(3)	30	(10)	1.68	(1.24)	0.93	(0.86)		
	E3	9	(3)	37	(23)	1.61	(1.25)	0.86	(0.93)		
	E4	8	(2)	29	(18)	1.40	(1.14)	0.81	(0.89)		
July 1980	E1	8	(3)	14	(4)	1.42	(1.05)	0.95	(0.91)	0.47	14.98 (8)
	E2	7	(3)	17	(5)	1.45	(1.04)	0.97	(0.98)		
	E3	8	(3)	18	(10)	1.44	(1.01)	0.91	(0.95)		
	E4	9	(2)	16	(8)	1.49	(1.24)	0.91	(1.00)		
Aug. 1980	E1	11	(4)	45	(34)	1.47	(1.24)	0.71	(0.93)	0.63	25.20** (10)
	E2	9	(4)	43	(34)	1.15	(0.99)	0.61	(0.89)		
	E3	12	(4)	26	(13)	1.79	(1.41)	0.92	(0.96)		
	E4	12	(3)	24	(10)	1.84	(1.55)	0.95	(1.00)		
Sept. 1980	E1	12	(4)	59	(41)	1.58	(1.46)	0.73	(0.92)	0.65	31.10** (12)
	E2	11	(4)	42	(24)	1.77	(1.27)	0.87	(0.84)		
	E3	14	(4)	27	(13)	1.93	(1.54)	0.94	(0.96)		
	E4	13	(4)	31	(19)	1.82	(1.37)	0.91	(0.95)		
Oct. 1980	E1	10	(3)	44	(23)	1.41	(1.21)	0.71	(0.77)	0.40	17.45 (11)
	E2	8	(2)	45	(27)	1.29	(1.21)	0.71	(0.85)		
	E3	11	(1)	27	(5)	1.73	(1.62)	0.91	(0.90)		
	E4	9	(0)	15	(0)	1.53	(1.53)	0.97	(0.97)		
Nov. 1980	E1	15	(2)	87	(30)	2.02	(1.94)	0.83	(0.87)	0.64	35.69** (14)
	E2	11	(2)	47	(11)	1.83	(1.69)	0.90	(0.93)		
	E3	12	(1)	74	(19)	1.85	(1.77)	0.83	(0.84)		
	E4	11	(1)	48	(9)	1.91	(1.81)	0.92	(0.92)		
Dec. 1980	E1	13	(2)	84	(31)	1.83	(1.54)	0.79	(0.73)	0.58	34.53** (15)
	E2	14	(2)	75	(29)	1.97	(1.84)	0.84	(0.87)		
	E3	15	(2)	64	(21)	1.90	(1.86)	0.80	(0.86)		
	E4	13	(1)	51	(5)	1.93	(1.82)	0.88	(0.86)		
Jan. 1981	E1	17	(2)	144	(53)	2.11	(1.94)	0.80	(0.80)	0.83	59.40*** (18)
	E2	17	(2)	169	(59)	2.08	(1.90)	0.78	(0.77)		
	E3	16	(2)	98	(17)	2.27	(2.09)	0.91	(0.88)		
	E4	18	(2)	102	(12)	2.31	(2.16)	0.89	(0.87)		
Feb. 1981	E1	11	(2)	50	(15)	1.66	(1.31)	0.80	(0.71)	0.44	24.61* (14)
	E2+	10	(2)	33	(10)	1.75	(1.48)	0.92	(0.88)		
	E3+	14	(2)	62	(13)	2.03	(1.81)	0.88	(0.84)		
	E4+	13	(2)	44	(4)	2.03	(1.91)	0.94	(0.94)		
Mar. 1981	E1	13	(2)	59	(30)	1.50	(1.60)	0.67	(0.83)	0.62	39.52*** (16)
	E2	15	(3)	60	(33)	1.80	(1.79)	0.77	(0.91)		
	E3	16	(2)	82	(19)	2.12	(1.96)	0.86	(0.85)		
	E4	14	(1)	64	(19)	1.99	(2.01)	0.86	(0.93)		
Apr. 1981	E1	10	(2)	46	(21)	1.59	(1.53)	0.80	(0.91)	0.68	19.12** (7)
	E2	11	(2)	40	(6)	1.64	(1.43)	0.81	(0.77)		
	E3	8	(1)	17	(3)	1.49	(1.35)	0.94	(0.93)		
	E4	7	(1)	17	(5)	1.42	(1.29)	0.95	(0.97)		
May 1981	E1	5	(1)	19	(10)	1.04	(0.92)	0.79	(0.92)	0.58	9.25 (4)
	E2	6	(2)	15	(8)	1.08	(0.76)	0.79	(0.83)		
	E3	6	(1)	8	(2)	1.15	(0.98)	1.00	(1.00)		
	E4	5	(1)	8	(1)	1.01	(0.86)	0.95	(0.94)		

Appendix 5(e) Cont'd.

Date	Pitfall site	Numbers of prey types represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f)
June 1981	E1	10 (3)	44 (30)	1.67 (1.39)	0.84 (0.96)	0.67	26.64** (10)
	E2	11 (3)	29 (16)	1.67 (1.35)	0.87 (0.92)		
	E3	9 (4)	72 (54)	1.47 (1.12)	0.74 (0.86)		
	E4	11 (4)	42 (27)	1.39 (1.39)	0.95 (0.95)		
July 1981	E1	8 (3)	23 (16)	1.39 (0.96)	0.84 (0.94)	0.38	12.00 (8)
	E2	10 (4)	19 (11)	1.54 (1.10)	0.88 (0.96)		
	E3	4 (2)	5 (3)	0.82 (0.35)	1.00 (1.00)		
	E4	5 (3)	8 (5)	1.10 (0.60)	0.96 (1.00)		
Aug. 1981	E1	7 (3)	17 (11)	1.22 (0.87)	0.82 (1.00)	0.35	11.15 (8)
	E2	7 (3)	22 (16)	1.31 (0.80)	0.83 (0.92)		
	E3	7 (3)	20 (11)	1.39 (0.81)	0.90 (0.82)		
	E4	7 (3)	14 (8)	1.35 (0.87)	0.93 (1.00)		
Sept. 1981	E1	17 (4)	142 (102)	1.89 (1.95)	0.72 (0.91)	0.45	32.27* (18)
	E2	18 (4)	106 (73)	1.87 (1.99)	0.72 (0.94)		
	E3	14 (2)	78 (33)	1.87 (-.97)	0.79 (0.93)		
	E4	14 (1)	67 (17)	1.98 (1.94)	0.85 (0.88)		
Oct. 1981	E1	13 (3)	75 (50)	1.63 (1.54)	0.71 (0.84)	0.54	40.71** (19)
	E2	13 (3)	87 (43)	1.46 (0.88)	0.63 (0.45)		
	E3	19 (3)	113 (63)	2.02 (2.07)	0.76 (0.88)		
	E4	16 (2)	112 (73)	1.66 (1.97)	0.66 (0.91)		

Appendix 6. The diversity of prey sizes obtained by pitfall trap sampling.

Notes for this Appendix are the same as for Appendix 5, except that prey are classified by size, not type. The measurements of diversity were based on the recognition of 10 size classes (mm):

< 1.0

1.0-2.4

2.5-4.9

5.0-7.4

7.5-9.9

10.0-12.4

12.5-14.9

15.0-17.4

17.5-19.9

≥20.0

Appendix 6. Components of prey size diversity: pitfall trap samples.
(a) Ribbon Gum.

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
December 1979	E1	10	342	1.29	0.58	0.94	33.87*** (9)
	E2	8	348	1.38	0.68		
	E3	10	358	1.42	0.63		
	E4	10	280	1.69	0.76		
January 1980	E1	9	157	1.66	0.80	0.83	29.89*** (9)
	E2	10	84	1.51	0.72		
	E3	10	179	1.58	0.72		
	E4	10	183	1.61	0.73		
February 1980	E1	10	163	1.79	0.82	0.84	30.29*** (9)
	E2	9	191	1.45	0.69		
	E3	9	191	1.29	0.61		
	E4	10	266	0.99	0.45		
March 1980	E1	10	92	1.60	0.76	0.80	28.80*** (9)
	E2	9	142	1.43	0.69		
	E3	7	60	1.15	0.65		
	E4	8	51	1.30	0.71		
April 1980	E1	8	116	1.17	0.60	0.82	29.52*** (9)
	E2	9	98	1.23	0.60		
	E3	5	55	1.09	0.74		
	E4	5	62	1.09	0.74		
May 1980	E1	6	106	0.95	0.56	0.86	27.38*** (8)
	E2	6	49	1.23	0.77		
	E3	7	68	1.14	0.64		
	E4	6	60	1.04	0.64		
June 1980	E1	3	5	0.66	0.88	0.79	15.82** (5)
	E2	6	36	1.22	0.78		
	E3	4	27	0.95	0.79		
	E4	4	26	0.91	0.76		
July 1980	E1	2	4	0.35	0.77	0.63	15.11* (6)
	E2	5	24	1.01	0.75		
	E3	5	21	1.11	0.83		
	E4	6	21	1.29	0.89		
August 1980	E1	5	33	1.10	0.79	0.72	22.95** (8)
	E2	8	35	1.41	0.80		
	E3	6	33	1.08	0.70		
	E4	5	20	1.02	0.77		
September 1980	E1	9	49	1.45	0.75	0.71	25.46** (9)
	E2	7	67	1.21	0.68		
	E3	7	70	0.62	0.35		
	E4	6	65	0.89	0.54		
October 1980	E1	6	58	1.22	0.75	0.75	24.08** (8)
	E2	8	40	1.16	0.65		
	E3	5	39	0.90	0.63		
	E4	5	40	0.84	0.59		
November 1980	E1	8	78	1.32	0.69	0.85	30.76*** (9)
	E2	8	93	1.19	0.62		
	E3	8	77	1.19	0.63		
	E4	8	65	1.16	0.62		
December 1980	E1	6	52	1.03	0.64	0.73	26.30** (9)
	E2	8	157	1.21	0.61		
	E3	6	62	1.12	0.68		
	E4	7	67	1.22	0.69		

Appendix 6. Components of prey size diversity: pitfall trap samples.
(b) Fern

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
December 1979	E1	9	210	1.61	0.76	0.92	33.10*** (9)
	E2	8	185	1.47	0.74		
	E3	10	207	1.78	0.81		
	E4	10	221	1.71	0.78		
January 1980	E1	10	79	1.56	0.74	0.87	31.24*** (9)
	E2	7	111	1.15	0.63		
	E3	10	111	1.60	0.75		
	E4	8	118	1.45	0.74		
February 1980	E1	10	200	1.29	0.58	0.83	29.75*** (9)
	E2	7	67	1.33	0.75		
	E3	6	78	1.32	0.80		
	E4	7	59	1.48	0.84		
March 1980	E1	9	170	0.97	0.46	0.76	27.53** (9)
	E2	7	55	1.20	0.68		
	E3	7	64	1.30	0.73		
	E4	6	67	1.32	0.80		
April 1980	E1	6	42	1.14	0.72	0.79	25.25** (8)
	E2	6	58	1.25	0.77		
	E3	6	59	1.17	0.72		
	E4	7	55	1.16	0.66		
May 1980	E1	6	113	0.90	0.53	0.80	22.48** (7)
	E2	8	29	1.41	0.82		
	E3	6	31	1.28	0.83		
	E4	4	34	1.00	0.81		
June 1980	E1	4	19	0.89	0.78	0.70	11.15* (4)
	E2	5	15	1.10	0.87		
	E3	4	14	0.91	0.84		
	E4	3	13	0.71	0.81		
July 1980	E1	4	17	0.98	0.87	0.63	15.16* (6)
	E2	4	10	0.87	0.86		
	E3	4	20	1.03	0.89		
	E4	4	20	0.99	0.85		
August 1980	E1	6	22	1.22	0.83	0.40	8.00 (5)
	E2	3	8	0.79	1.00		
	E3	3	7	0.66	0.87		
	E4	3	7	0.53	0.70		
September 1980	E1	6	26	1.18	0.79	0.65	18.29* (7)
	E2	2	7	0.28	0.55		
	E3	5	20	1.15	0.87		
	E4	5	17	1.05	0.82		
October 1980	E1	6	72	1.24	0.75	0.73	26.45** (9)
	E2	5	26	1.19	0.87		
	E3	7	30	1.14	0.70		
	E4	6	21	1.07	0.74		
November 1980	E1	7	26	1.32	0.82	0.78	21.83** (7)
	E2	7	54	1.05	0.60		
	E3	6	32	1.14	0.74		
	E4	7	24	1.25	0.79		
December 1980	E1	6	86	1.09	0.66	0.81	22.69** (7)
	E2	6	58	1.23	0.76		
	E3	5	35	1.11	0.79		
	E4	5	26	0.99	0.72		

Appendix 6. Components of prey size diversity: pitfall trap samples.
(c) Under log.

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
December 1979	E1	8	135	1.38	0.70	0.96	34.69*** (9)
	E2	9	377	1.34	0.62		
	E3	10	238	1.30	0.59		
	E4	10	244	1.55	0.72		
January 1980	E1	7	47	1.26	0.73	0.84	30.12*** (9)
	E2	6	91	1.00	0.60		
	E3	8	90	1.36	0.71		
	E4	8	88	1.21	0.63		
February 1980	E1	5	61	1.29	0.87	0.77	27.64** (9)
	E2	8	82	1.34	0.70		
	E3	9	136	1.30	0.63		
	E4	7	88	1.31	0.73		
March 1980	E1	8	41	1.36	0.75	0.86	30.82*** (9)
	E2	6	37	1.09	0.70		
	E3	7	105	1.06	0.58		
	E4	7	90	1.18	0.65		
April 1980	E1	7	91	1.16	0.64	0.70	19.54** (7)
	E2	3	4	0.62	1.00		
	E3	6	93	1.02	0.61		
	E4	6	117	1.25	0.74		
May 1980	E1	6	50	1.11	0.69	0.74	20.63** (7)
	E2	4	16	1.05	0.94		
	E3	8	27	1.52	0.89		
	E4	6	24	1.33	0.89		
June 1980	E1	5	20	1.15	0.87	0.78	15.68** (5)
	E2	5	17	1.18	0.92		
	E3	5	11	1.01	0.86		
	E4	5	12	1.00	0.84		
July 1980	E1	3	16	0.71	0.78	0.75	14.96* (5)
	E2	5	17	0.94	0.73		
	E3	5	19	1.13	0.86		
	E4	5	20	0.96	0.72		
August 1980	E1	5	11	1.08	0.92	0.74	14.89* (5)
	E2	3	14	0.70	0.79		
	E3	4	13	0.89	0.82		
	E4	5	14	1.05	0.85		
September 1980	E1	4	16	0.84	0.75	0.75	14.96* (5)
	E2	4	26	1.09	0.91		
	E3	5	19	1.16	0.88		
	E4	5	22	1.20	0.90		
October 1980	E1	5	26	1.23	0.90	0.74	14.82* (5)
	E2	4	39	1.07	0.86		
	E3	5	22	1.22	0.91		
	E4	6	24	1.25	0.84		
November 1980	E1	4	31	0.76	0.62	0.78	25.05** (8)
	E2	7	95	1.00	0.55		
	E3	7	40	1.24	0.73		
	E4	6	32	1.29	0.84		
December 1980	E1	6	85	1.06	0.64	0.78	21.92** (7)
	E2	5	52	1.00	0.68		
	E3	6	55	1.26	0.78		
	E4	5	22	1.18	0.88		

Appendix 6. Components of prey size diversity: pitfall trap samples.
(d) Open

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
December 1979	E1	10	274	1.47	0.66	0.98	35.11*** (9)
	E2	9	300	1.61	0.75		
	E3	10	248	1.62	0.73		
	E4	9	285	1.49	0.70		
January 1980	E1	9	120	1.29	0.63	0.81	29.05*** (9)
	E2	10	166	1.67	0.76		
	E3	6	79	1.29	0.77		
	E4	7	91	1.46	0.80		
February 1980	E1	8	96	1.30	0.67	0.77	27.68** (9)
	E2	5	85	1.37	0.91		
	E3	9	72	1.58	0.79		
	E4	9	92	1.32	0.65		
March 1980	E1	6	34	1.26	0.81	0.89	28.40*** (8)
	E2	7	40	1.32	0.78		
	E3	6	49	1.08	0.67		
	E4	6	37	1.11	0.71		
April 1980	E1	5	56	1.09	0.74	0.79	18.96** (6)
	E2	4	100	0.98	0.75		
	E3	4	59	1.00	0.78		
	E4	7	84	1.32	0.73		
May 1980	E1	7	20	1.37	0.89	0.66	21.08** (8)
	E2	4	89	0.95	0.72		
	E3	5	17	1.08	0.84		
	E4	7	32	1.14	0.69		
June 1980	E1	5	36	1.01	0.71	0.92	18.43** (5)
	E2	4	14	0.86	0.79		
	E3	4	12	0.72	0.68		
	E4	4	11	0.87	0.83		
July 1980	E1	5	34	0.98	0.69	0.45	7.15 (4)
	E2	3	10	0.71	0.86		
	E3	4	14	1.02	0.94		
	E4	4	13	1.05	0.98		
August 1980	E1	5	21	1.14	0.86	0.35	8.46 (6)
	E2	4	13	0.95	0.89		
	E3	3	3	0.60	1.00		
	E4	2	2	0.35	1.00		
September 1980	E1	5	63	0.96	0.65	0.84	16.75** (5)
	E2	5	45	0.64	0.44		
	E3	4	40	0.83	0.66		
	E4	5	50	0.95	0.65		
October 1980	E1	7	45	1.39	0.81	0.75	24.08** (8)
	E2	7	87	0.94	0.52		
	E3	5	22	1.05	0.78		
	E4	4	24	0.74	0.62		
November 1980	E1	6	13	1.19	0.90	0.80	28.88*** (9)
	E2	8	89	1.38	0.72		
	E3	8	58	1.48	0.79		
	E4	7	22	1.35	0.86		
December 1980	E1	6	85	1.02	0.61	0.82	23.08** (7)
	E2	5	60	0.89	0.61		
	E3	6	50	1.03	0.64		
	E4	5	48	1.15	0.79		

Appendix 6. Components of prey size diversity: pitfall trap samples.
(e) Slopes.

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
December 1979	E1	10	260	1.62	0.73	0.94	33.74*** (9)
	E2	8	388	1.42	0.70		
	E3	10	299	1.42	0.64		
	E4	10	169	1.28	0.59		
January 1980	E1	10	108	1.40	0.66	0.71	25.42** (9)
	E2	9	69	1.44	0.72		
	E3	8	63	1.46	0.78		
	E4	8	71	1.68	0.89		
February 1980	E1	10	310	1.14	0.51	0.83	30.05*** (9)
	E2	7	255	0.97	0.52		
	E3	10	125	1.64	0.76		
	E4	10	159	1.49	0.68		
March 1980	E1	8	85	1.18	0.61	0.73	26.21** (9)
	E2	7	61	1.15	0.65		
	E3	10	85	1.72	0.82		
	E4	10	90	1.72	0.82		
April 1980	E1	5	47	1.01	0.70	0.75	27.03** (9)
	E2	7	166	1.08	0.58		
	E3	7	60	1.31	0.75		
	E4	8	43	1.43	0.79		
May 1980	E1	3	23	0.74	0.78	0.59	19.02* (8)
	E2	6	32	0.92	0.60		
	E3	3	13	0.61	0.70		
	E4	8	17	1.49	0.94		
June 1980	E1	3	36	0.82	0.82	0.75	6.00* (2)
	E2	3	30	0.70	0.72		
	E3	3	37	0.73	0.73		
	E4	3	29	0.77	0.79		
July 1980	E1	4	14	0.93	0.86	0.74	14.75* (5)
	E2	4	17	0.93	0.82		
	E3	5	18	1.01	0.78		
	E4	4	16	0.82	0.73		
August 1980	E1	6	45	1.06	0.67	0.83	16.54* (5)
	E2	5	43	0.92	0.64		
	E3	4	26	1.00	0.83		
	E4	5	24	0.96	0.71		
September 1980	E1	7	59	1.07	0.61	0.69	24.78** (9)
	E2	6	41	0.87	0.55		
	E3	6	27	1.19	0.79		
	E4	7	31	1.20	0.73		
October 1980	E1	8	45	1.07	0.62	0.83	29.76*** (9)
	E2	9	46	1.25	0.68		
	E3	7	28	0.95	0.63		
	E4	8	15	1.35	0.93		
November 1980	E1	6	87	1.09	0.66	0.76	25.52** (9)
	E2	6	47	1.14	0.71		
	E3	9	74	1.34	0.67		
	E4	9	48	1.41	0.73		
December 1980	E1	6	84	1.16	0.70	0.88	28.07*** (8)
	E2	6	75	1.27	0.76		
	E3	7	64	1.34	0.76		
	E4	8	51	1.43	0.78		

Appendix 7. The diversity of prey types obtained by litter sampling.

Notes for this Appendix are the same as for Appendix 5, except that "slopes" habitat was not sampled, and only 40 types of prey were recognised. Ephemeroptera, Odonata, Plecoptera, Phasmida, Trichoptera and Platyhelminthes were never captured during litter sampling.

Appendix 7. Components of prey type diversity: litter samples
(a) Ribbon Gum

Date	Site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
Oct. 1978	E1	20	(2)	202	(12)	2.43	(2.32)	0.86	(0.86)	0.76	87.71*** (23)
	E2	23	(3)	343	(32)	2.47	(2.31)	0.83	(0.81)		
	E3	22	(3)	229	(24)	2.48	(2.33)	0.86	(0.84)		
	E4	21	(3)	335	(29)	2.11	(1.94)	0.72	(0.70)		
	C1	18	(2)	236	(15)	2.16	(2.03)	0.79	(0.77)		
Jan. 1979	E1	16	(2)	175	(36)	2.17	(2.08)	0.83	(0.85)	0.72	57.34*** (16)
	E2	16	(1)	225	(4)	2.07	(2.03)	0.79	(0.79)		
	E3	12	(0)	290	(0)	1.94	(1.94)	0.81	(0.81)		
	E4	18	(1)	220	(5)	2.26	(2.21)	0.83	(0.83)		
	C1	17	(2)	265	(15)	2.17	(2.04)	0.80	(0.79)		
Apr. 1979	E1	19	(3)	261	(30)	2.31	(2.10)	0.83	(0.80)	0.74	85.19*** (23)
	E2	22	(3)	302	(26)	2.37	(2.22)	0.81	(0.79)		
	E3	21	(1)	224	(16)	2.40	(2.32)	0.84	(0.83)		
	E4	24	(3)	266	(21)	2.43	(2.28)	0.81	(0.79)		
	C1	17	(1)	279	(23)	2.20	(2.10)	0.81	(0.79)		
July 1979	E1	18	(3)	200	(21)	2.19	(2.04)	0.81	(0.80)	0.73	69.12*** (19)
	E2	16	(1)	336	(7)	1.31	(1.24)	0.49	(0.48)		
	E3	18	(2)	130	(8)	1.80	(1.66)	0.68	(0.65)		
	E4	18	(2)	170	(12)	2.06	(1.94)	0.76	(0.75)		
	C1	16	(2)	188	(9)	1.93	(1.82)	0.74	(0.73)		
Oct. 1979	E1	16	(1)	268	(5)	1.64	(1.59)	0.62	(0.61)	0.69	69.42*** (20)
	E2	19	(1)	174	(4)	2.27	(2.22)	0.84	(0.83)		
	E3	16	(1)	144	(3)	2.07	(2.00)	0.81	(0.80)		
	E4	18	(0)	154	(0)	1.89	(1.89)	0.70	(0.70)		
	C1	19	(1)	217	(2)	1.85	(1.82)	0.67	(0.67)		
Feb. 1980	E1	17	(1)	197	(7)	2.13	(2.06)	0.80	(0.79)	0.73	76.62*** (21)
	E2	18	(1)	298	(2)	1.36	(1.33)	0.49	(0.49)		
	E3	17	(1)	144	(2)	2.10	(2.06)	0.80	(0.80)		
	E4	17	(1)	438	(4)	1.69	(1.65)	0.61	(0.62)		
	C1	22	(1)	336	(11)	1.95	(1.87)	0.66	(0.64)		
Apr. 1980	E1	22	(3)	246	(31)	2.28	(2.10)	0.83	(0.80)	0.77	89.10** (23)
	E2	17	(2)	206	(26)	2.03	(1.91)	0.81	(0.79)		
	E3	21	(3)	311	(11)	2.36	(2.21)	0.76	(0.74)		
	E4	23	(3)	381	(18)	2.21	(2.09)	0.78	(0.76)		
	C1	20	(2)	284	(34)	1.97	(1.72)	0.80	(0.77)		
July 1980	E1	17	(1)	223	(18)	2.18	(2.10)	0.81	(0.77)	0.71	70.56*** (19)
	E2	19	(3)	314	(31)	2.01	(1.87)	0.63	(0.60)		
	E3	16	(1)	158	(12)	2.05	(2.01)	0.80	(0.79)		
	E4	19	(3)	210	(6)	2.15	(2.07)	0.81	(0.80)		
	C1	18	(2)	184	(15)	1.99	(1.90)	0.76	(0.74)		
Oct. 1980	E1	16	(1)	180	(2)	2.02	(1.96)	0.78	(0.77)	0.85	97.63*** (21)
	E2	21	(1)	217	(12)	2.36	(2.30)	0.88	(0.86)		
	E3	18	(2)	188	(5)	2.14	(2.09)	0.81	(0.81)		
	E4	17	(2)	159	(16)	1.89	(1.83)	0.77	(0.76)		
	C1	19	(1)	228	(3)	1.76	(1.73)	0.70	(0.70)		
Jan. 1981	E1	20	(2)	343	(33)	2.23	(2.11)	0.86	(0.84)	0.75	73.28*** (19)
	E2	18	(1)	281	(6)	2.15	(2.10)	0.81	(0.80)		
	E3	17	(1)	212	(12)	2.20	(2.13)	0.82	(0.82)		
	E4	19	(2)	233	(5)	1.98	(1.93)	0.69	(0.69)		
	C1	18	(1)	194	(18)	2.31	(2.26)	0.87	(0.86)		

Appendix 7. Components of prey type diversity: litter samples.
(b) Fern

Date	Site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
Oct. 1978	E1	20	(1)	268	(11)	2.38	(2.31)	0.84	(0.83)	0.88	100.68*** (23)
	E2	23	(3)	247	(21)	2.51	(2.39)	0.85	(0.85)		
	E3	22	(2)	211	(13)	2.56	(2.45)	0.88	(0.87)		
	E4	23	(4)	212	(12)	2.11	(1.98)	0.72	(0.72)		
	C1	21	(2)	295	(15)	2.09	(1.98)	0.72	(0.70)		
Jan. 1979	E1	18	(1)	215	(21)	2.09	(1.98)	0.77	(0.74)	0.76	68.06*** (18)
	E2	16	(2)	308	(36)	2.14	(1.95)	0.81	(0.77)		
	E3	16	(2)	237	(21)	2.02	(1.86)	0.77	(0.74)		
	E4	17	(2)	249	(16)	2.10	(1.96)	0.78	(0.76)		
	C1	17	(2)	282	(40)	1.98	(1.78)	0.73	(0.69)		
Apr. 1979	E1	18	(3)	208	(27)	2.27	(2.13)	0.84	(0.84)	0.85	102.55*** (24)
	E2	24	(3)	320	(40)	2.35	(2.18)	0.78	(0.75)		
	E3	25	(3)	230	(22)	2.57	(2.42)	0.85	(0.84)		
	E4	22	(2)	209	(23)	2.32	(2.18)	0.80	(0.78)		
	C1	21	(2)	208	(15)	2.17	(2.03)	0.76	(0.74)		
July 1979	E1	14	(2)	95	(13)	1.93	(1.71)	0.81	(0.76)	0.73	65.81*** (18)
	E2	16	(2)	130	(23)	1.94	(1.76)	0.76	(0.73)		
	E3	14	(2)	255	(9)	1.68	(1.58)	0.67	(0.66)		
	E4	18	(2)	425	(8)	1.21	(1.14)	0.43	(0.42)		
	C1	18	(2)	297	(10)	1.63	(1.51)	0.58	(0.57)		
Oct. 1979	E1	17	(1)	119	(7)	2.28	(2.21)	0.88	(0.87)	0.80	88.78*** (22)
	E2	19	(1)	237	(11)	2.37	(2.30)	0.85	(0.84)		
	E3	23	(3)	140	(11)	2.40	(2.26)	0.84	(0.83)		
	E4	17	(1)	163	(5)	2.19	(2.13)	0.83	(0.83)		
	C1	19	(2)	134	(5)	2.15	(2.06)	0.79	(0.79)		
Feb. 1980	E1	25	(3)	503	(127)	2.43	(2.41)	0.78	(0.81)	0.81	93.19*** (23)
	E2	24	(2)	361	(81)	2.50	(2.52)	0.83	(0.87)		
	E3	24	(3)	406	(70)	2.36	(2.27)	0.77	(0.78)		
	E4	23	(2)	395	(64)	2.56	(2.48)	0.85	(0.85)		
	C1	22	(3)	314	(37)	2.54	(2.44)	0.86	(0.87)		
Apr. 1980	E1	19	(2)	251	(15)	2.34	(2.26)	0.84	(0.83)	0.78	88.64*** (23)
	E2	21	(3)	212	(38)	2.14	(2.00)	0.75	(0.73)		
	E3	24	(2)	281	(29)	2.61	(2.51)	0.89	(0.89)		
	E4	19	(2)	193	(14)	2.32	(2.20)	0.84	(0.83)		
	C1	20	(3)	212	(25)	2.28	(2.11)	0.82	(0.81)		
July 1980	E1	17	(2)	118	(18)	1.96	(1.77)	0.77	(0.74)	0.77	70.25*** (18)
	E2	19	(2)	239	(17)	1.78	(1.70)	0.63	(0.61)		
	E3	18	(1)	208	(37)	2.09	(1.98)	0.78	(0.75)		
	E4	15	(2)	247	(21)	2.00	(1.89)	0.76	(0.73)		
	C1	16	(2)	169	(12)	1.85	(1.75)	0.71	(0.69)		
Oct. 1980	E1	20	(2)	156	(4)	1.92	(1.87)	0.72	(0.71)	0.86	85.36*** (22)
	E2	17	(1)	128	(5)	2.23	(2.17)	0.86	(0.85)		
	E3	19	(1)	179	(7)	2.20	(2.14)	0.82	(0.81)		
	E4	18	(2)	208	(18)	2.14	(2.04)	0.79	(0.77)		
	C1	22	(3)	243	(27)	2.48	(2.32)	0.84	(0.82)		
Jan. 1981	E1	20	(2)	216	(17)	2.39	(2.29)	0.83	(0.82)	0.80	73.4*** (19)
	E2	18	(1)	198	(19)	2.11	(1.99)	0.79	(0.76)		
	E3	21	(1)	236	(22)	2.41	(2.31)	0.85	(0.84)		
	E4	17	(3)	281	(29)	2.14	(1.98)	0.77	(0.74)		
	C1	19	(2)	273	(31)	2.07	(1.95)	0.76	(0.74)		

Appendix 7. Components of prey type diversity: litter samples.
(c) Under log

Date	Site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
	E1	21	(2)	189	(8)	2.42	(2.34)	0.85	(0.85)		
Oct.	E2	24	(2)	224	(9)	2.29	(2.21)	0.77	(0.76)		
1978	E3	25	(3)	242	(7)	2.11	(2.02)	0.70	(0.70)	0.73	91.15***
	E4	21	(2)	150	(7)	2.22	(2.12)	0.79	(0.78)		(25)
	C1	19	(1)	159	(7)	2.23	(2.16)	0.82	(0.81)		
	E1	16	(1)	201	(7)	2.34	(2.28)	0.90	(0.89)		
Jan.	E2	16	(3)	304	(129)	2.02	(1.83)	0.76	(0.76)		
1979	E3	15	(2)	226	(11)	1.80	(1.69)	0.70	(0.69)		
	E4	18	(2)	333	(52)	1.92	(1.76)	0.69	(0.66)	0.72	68.65***
	C1	20	(1)	241	(61)	2.20	(2.20)	0.78	(0.80)		(19)
	E1	20	(2)	278	(11)	2.19	(2.09)	0.77	(0.76)		
Apr.	E2	22	(3)	243	(8)	2.31	(2.23)	0.79	(0.80)		
1979	E3	23	(2)	313	(5)	2.17	(2.12)	0.73	(0.73)	0.85	106.65***
	E4	24	(3)	309	(19)	2.48	(2.36)	0.82	(0.81)		(25)
	C1	22	(2)	326	(11)	2.08	(1.99)	0.71	(0.70)		
	E1	13	(1)	121	(3)	1.88	(1.83)	0.79	(0.79)		
July	E2	19	(2)	223	(6)	2.19	(2.12)	0.79	(0.79)		
1979	E3	21	(2)	180	(5)	2.11	(1.04)	0.75	(0.74)		
	E4	18	(2)	266	(5)	1.94	(1.88)	0.71	(0.71)	0.75	71.28***
	C1	20	(2)	220	(6)	2.27	(2.20)	0.81	(0.81)		(19)
	E1	19	(1)	171	(3)	2.10	(2.05)	0.77	(0.76)		
Oct.	E2	23	(2)	174	(10)	2.05	(1.94)	0.71	(0.69)		
1979	E3	14	(1)	117	(2)	2.12	(2.08)	0.87	(0.88)		
	E4	19	(1)	173	(10)	2.11	(2.02)	0.77	(0.75)	0.76	71.85***
	C1	17	(1)	135	(8)	1.67	(1.55)	0.64	(0.61)		(19)
	E1	22	(2)	141	(4)	2.37	(2.31)	0.84	(0.84)		
Feb.	E2	23	(2)	276	(9)	1.94	(1.85)	0.65	(0.64)		
1980	E3	21	(1)	274	(3)	2.44	(2.41)	0.84	(0.85)	0.63	69.22***
	E4	21	(1)	236	(5)	1.77	(1.71)	0.62	(0.60)		(22)
	C1	23	(1)	391	(8)	1.97	(1.92)	0.66	(0.65)		
	E1	22	(2)	301	(17)	2.09	(1.98)	0.74	(0.73)		
Apr.	E2	20	(1)	233	(32)	2.18	(2.10)	0.81	(0.79)		
1980	E3	18	(2)	269	(29)	2.30	(2.19)	0.84	(0.84)	0.71	79.47***
	E4	21	(3)	178	(21)	1.89	(1.72)	0.66	(0.64)		(22)
	C1	18	(2)	456	(41)	1.29	(1.14)	0.46	(0.44)		
	E1	15	(2)	167	(90)	1.90	(1.91)	0.63	(0.72)		
July	E2	19	(2)	235	(7)	2.13	(2.04)	0.77	(0.76)		
1980	E3	16	(1)	197	(21)	2.01	(1.93)	0.84	(0.82)	0.73	70.89***
	E4	20	(1)	248	(15)	2.28	(2.23)	0.80	(0.79)		(19)
	C1	17	(2)	294	(18)	1.94	(1.83)	0.74	(0.70)		
	E1	16	(1)	176	(7)	2.15	(2.04)	0.82	(0.81)		
Oct.	E2	19	(1)	212	(10)	1.90	(1.86)	0.69	(0.69)		
1980	E3	22	(2)	193	(3)	2.31	(2.26)	0.81	(0.81)	0.79	82.31***
	E4	20	(2)	261	(6)	2.24	(2.20)	0.79	(0.79)		(21)
	C1	17	(2)	163	(10)	1.73	(1.63)	0.65	(0.63)		
	E1	19	(2)	245	(18)	2.18	(2.10)	0.80	(0.78)		
Jan.	E2	20	(2)	198	(9)	1.92	(1.83)	0.68	(0.65)		
1981	E3	21	(1)	210	(6)	1.84	(1.78)	0.65	(0.63)	0.82	95.68***
	E4	20	(1)	173	(24)	2.13	(2.03)	0.79	(0.76)		(23)
	C1	24	(3)	148	(38)	2.41	(2.23)	0.83	(0.82)		

Appendix 7. Components of prey type diversity: litter samples.
(d) Open

Date	Site	Numbers of prey types represented		Numbers of prey		Diversity H		Evenness J		W	χ^2(d.f)
	E1	17	(2)	290	(25)	1.99	(1.84)	0.73	(0.71)		
Oct.	E2	22	(2)	165	(15)	2.21	(2.09)	0.77	(0.76)		
1978	E3	18	(1)	262	(19)	1.75	(1.62)	0.64	(0.60)	0.86	81.65***
	E4	17	(1)	244	(31)	2.04	(1.91)	0.76	(0.73)		(19)
	C1	17	(2)	244	(13)	1.95	(1.83)	0.72	(0.71)		
	E1	15	(2)	311	(52)	2.16	(1.94)	0.83	(0.79)		
Jan.	E2	15	(1)	288	(11)	1.73	(1.64)	0.67	(0.65)		
1979	E3	11	(1)	357	(1)	1.57	(1.57)	0.67	(0.67)		
	E4	11	(1)	371	(11)	1.51	(1.42)	0.65	(0.64)	0.71	64.16***
	C1	16	(2)	196	(30)	2.08	(1.89)	0.80	(0.76)		(18)
	E1	15	(1)	278	(5)	1.98	(1.93)	0.77	(0.76)		
Apr.	E2	18	(3)	230	(48)	2.36	(2.13)	0.86	(0.83)		
1979	E3	22	(3)	232	(28)	2.48	(2.31)	0.85	(0.83)	0.80	83.74***
	E4	20	(3)	205	(20)	2.29	(2.12)	0.82	(0.80)		(21)
	C1	20	(2)	294	(11)	2.08	(1.99)	0.73	(0.72)		
	E1	13	(1)	118	(7)	1.71	(1.59)	0.72	(0.70)		
July	E2	14	(2)	163	(16)	1.91	(1.76)	0.77	(0.76)		
1979	E3	17	(2)	195	(17)	1.87	(1.70)	0.70	(0.67)		
	E4	15	(2)	175	(11)	1.87	(1.73)	0.74	(0.72)	0.82	57.69***
	C1	14	(2)	260	(17)	1.58	(1.43)	0.62	(0.60)		(14)
	E1	20	(2)	401	(7)	1.78	(1.71)	0.61	(0.61)		
Oct.	E2	15	(1)	94	(5)	2.06	(1.97)	0.84	(0.83)		
1979	E3	19	(2)	222	(15)	1.84	(1.71)	0.66	(0.64)		
	E4	17	(1)	303	(38)	1.61	(1.42)	0.59	(0.54)	0.80	76.26***
	C1	15	(1)	311	(3)	1.26	(1.23)	0.49	(0.48)		(19)
	E1	13	(1)	78	(1)	1.64	(1.61)	0.71	(0.72)		
Feb.	E2	17	(2)	236	(6)	1.75	(1.67)	0.65	(0.65)		
1980	E3	19	(2)	300	(7)	1.89	(1.80)	0.67	(0.66)	0.69	65.20***
	E4	17	(1)	849	(4)	0.90	(0.87)	0.32	(0.32)		(19)
	C1	19	(2)	333	(6)	2.16	(2.10)	0.76	(0.77)		
	E1	16	(1)	193	(12)	2.03	(1.96)	0.79	(0.78)		
Apr.	E2	21	(2)	262	(6)	2.18	(2.08)	0.78	(0.75)		
1980	E3	18	(2)	269	(11)	2.13	(2.02)	0.76	(0.74)	0.71	72.09***
	E4	18	(1)	303	(28)	1.93	(1.85)	0.68	(0.67)		(20)
	C1	19	(3)	219	(9)	2.27	(2.12)	0.83	(0.81)		
	E1	14	(2)	164	(18)	1.81	(1.67)	0.73	(0.71)		
July	E2	19	(2)	113	(9)	2.00	(1.90)	0.75	(0.75)		
1980	E3	13	(2)	209	(21)	1.89	(1.75)	0.77	(0.75)	0.75	66.88***
	E4	18	(1)	231	(24)	2.14	(2.06)	0.79	(0.78)		(18)
	C1	16	(2)	147	(3)	2.07	(1.98)	0.82	(0.83)		
	E1	14	(1)	231	(19)	1.73	(1.63)	0.70	(0.68)		
Oct.	E2	18	(1)	268	(22)	2.08	(1.98)	0.74	(0.71)		
1980	E3	18	(2)	398	(33)	2.11	(1.95)	0.77	(0.75)	0.70	54.75***
	E4	16	(1)	193	(4)	1.85	(1.81)	0.75	(0.74)		(16)
	C1	17	(1)	178	(10)	1.97	(1.90)	0.77	(0.75)		
	E1	18	(1)	186	(8)	2.10	(2.01)	0.79	(0.77)		
Jan.	E2	22	(2)	617	(17)	1.19	(1.12)	0.41	(0.40)		
1981	E3	17	(1)	241	(1)	1.88	(1.86)	0.71	(0.71)	0.83	88.12***
	E4	19	(2)	412	(2)	1.63	(1.57)	0.57	(0.59)		(19)
	C1	18	(1)	177	(7)	1.94	(1.89)	0.69	(0.69)		

Appendix 8. The diversity of prey sizes obtained by litter sampling.

Notes for this Appendix are the same as for Appendix 6.

Appendix 8. Components of prey size diversity: litter samples.
(a) Ribbon Gum.

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
October 1978	E1	9	202	1.55	0.73		
	E2	10	343	1.32	0.59		
	E3	10	229	1.59	0.72	0.94	42.14***
	E4	10	335	1.49	0.66		(9)
	C1	10	236	1.38	0.63		
January 1979	E1	7	175	1.21	0.65		
	E2	8	225	1.33	0.66		
	E3	6	290	1.34	0.77	0.77	34.71***
	E4	10	220	1.47	0.67		(9)
	C1	10	265	1.27	0.57		
April 1979	E1	10	261	1.62	0.73		
	E2	8	302	1.41	0.70		
	E3	8	224	1.27	0.63	0.92	41.19***
	E4	7	266	1.01	0.54		(9)
	C1	7	279	1.25	0.66		
July 1979	E1	8	200	1.39	0.70		
	E2	6	336	1.18	0.67		
	E3	6	130	1.32	0.77	0.88	39.73***
	E4	8	170	1.43	0.72		(9)
	C1	6	188	1.23	0.71		
October 1979	E1	7	268	1.04	0.55		
	E2	9	174	1.46	0.70		
	E3	8	144	1.54	0.78	0.93	41.66***
	E4	8	154	1.41	0.71		(9)
	C1	9	217	1.65	0.78		
February 1980	E1	7	197	1.28	0.68		
	E2	8	298	1.04	0.51		
	E3	8	144	1.16	0.59	0.86	38.57***
	E4	6	438	0.90	0.51		(9)
	C1	9	336	1.16	0.55		
April 1980	E1	8	246	1.41	0.69		
	E2	7	206	1.12	0.60		
	E3	9	311	1.36	0.64	0.88	39.81***
	E4	9	381	1.20	0.58		(9)
	C1	8	284	1.27	0.63		
July 1980	E1	7	223	1.26	0.67		
	E2	8	314	1.38	0.68		
	E3	6	158	1.32	0.76	0.91	35.88***
	E4	8	210	1.45	0.72		(8)
	C1	7	184	1.11	0.58		
October 1980	E1	5	180	1.31	0.90		
	E2	9	217	1.09	0.51		
	E3	8	188	1.62	0.84	0.84	33.80***
	E4	7	159	1.47	0.80		(8)
	C1	8	228	1.23	0.60		
January 1981	E1	8	343	1.33	0.65		
	E2	9	281	1.26	0.58		
	E3	8	212	1.41	0.71	0.90	40.56***
	E4	6	233	1.20	0.69		(9)
	C1	9	194	1.29	0.61		

Appendix 8. Components of prey size diversity: litter samples.
(b) Fern

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
October 1978	E1	8	268	1.43	0.71	0.89	39.98*** (9)
	E2	8	247	1.29	0.64		
	E3	7	211	1.40	0.75		
	E4	6	212	1.31	0.76		
	C1	9	295	1.33	0.63		
January 1979	E1	6	215	1.28	0.74	0.83	29.22*** (7)
	E2	7	308	1.20	0.63		
	E3	8	237	1.36	0.68		
	E4	8	249	1.34	0.67		
	C1	8	282	1.26	0.62		
April 1979	E1	6	208	1.18	0.68	0.83	37.17*** (9)
	E2	8	320	1.13	0.56		
	E3	6	230	1.33	0.77		
	E4	7	209	1.28	0.88		
	C1	6	208	1.24	0.72		
July 1979	E1	5	95	1.13	0.75	0.90	31.62*** (7)
	E2	6	130	1.40	0.82		
	E3	5	255	1.15	0.73		
	E4	8	425	1.11	0.55		
	C1	7	297	1.30	0.69		
October 1979	E1	9	119	1.53	0.74	0.87	39.07*** (9)
	E2	8	237	1.46	0.73		
	E3	8	140	1.55	0.79		
	E4	8	163	1.49	0.75		
	C1	9	134	1.36	0.66		
February 1980	E1	10	503	1.29	0.57	0.91	40.73*** (9)
	E2	10	361	1.43	0.64		
	E3	10	406	1.35	0.60		
	E4	10	395	1.58	0.70		
	C1	10	314	1.58	0.71		
April 1980	E1	7	251	1.21	0.64	0.79	35.33*** (9)
	E2	8	210	1.42	0.71		
	E3	8	278	1.26	0.62		
	E4	9	186	1.18	0.56		
	C1	7	212	1.37	0.73		
July 1980	E1	6	118	1.23	0.72	0.84	29.86*** (7)
	E2	7	239	1.47	0.80		
	E3	5	208	1.04	0.68		
	E4	7	247	1.12	0.59		
	C1	6	169	1.19	0.69		
October 1980	E1	8	156	1.37	0.69	0.86	34.41*** (8)
	E2	9	128	1.24	0.61		
	E3	7	179	1.16	0.64		
	E4	8	208	1.47	0.74		
	C1	9	243	1.30	0.61		
January 1981	E1	10	216	1.61	0.73	0.92	41.14*** (9)
	E2	8	198	1.30	0.64		
	E3	10	236	1.27	0.58		
	E4	9	281	1.54	0.73		
	C1	9	273	1.20	0.57		

Appendix 8. Components of prey size diversity: litter samples.
(c) Under log.

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
October 1978	E1	8	189	1.43	0.72	0.92	36.64*** (8)
	E2	7	224	1.28	0.68		
	E3	8	242	1.49	0.74		
	E4	9	150	1.39	0.67		
	C1	7	159	1.33	0.71		
January 1979	E1	9	201	1.51	0.72	0.79	35.41*** (9)
	E2	5	304	0.96	0.61		
	E3	9	226	1.19	0.57		
	E4	10	333	1.21	0.54		
	C1	10	240	1.26	0.57		
April 1979	E1	8	278	1.46	0.73	0.91	40.80*** (9)
	E2	9	243	1.47	0.69		
	E3	6	313	0.95	0.54		
	E4	6	309	1.31	0.75		
	C1	8	326	1.30	0.64		
July 1979	E1	7	121	1.33	0.73	0.92	41.20*** (9)
	E2	7	223	1.36	0.73		
	E3	7	180	1.44	0.77		
	E4	9	266	1.17	0.55		
	C1	7	220	1.36	0.72		
October 1979	E1	9	171	1.53	0.73	0.92	41.56*** (9)
	E2	9	174	1.40	0.67		
	E3	7	117	1.46	0.80		
	E4	7	173	1.32	0.71		
	C1	7	135	1.25	0.68		
February 1980	E1	8	141	1.25	0.63	0.88	39.79*** (9)
	E2	7	276	1.15	0.61		
	E3	8	274	1.31	0.65		
	E4	8	236	0.87	0.43		
	C1	10	391	1.20	0.54		
April 1980	E1	7	301	1.48	0.80	0.85	34.51*** (8)
	E2	8	233	1.32	0.65		
	E3	8	269	1.10	0.53		
	E4	9	178	1.21	0.58		
	C1	7	451	1.27	0.66		
July 1980	E1	7	167	1.28	0.68	0.92	32.39*** (7)
	E2	7	235	1.09	0.58		
	E3	6	197	1.36	0.79		
	E4	8	248	1.22	0.61		
	C1	7	294	1.12	0.59		
October 1980	E1	8	176	1.20	0.60	0.89	35.71*** (8)
	E2	7	212	1.17	0.62		
	E3	8	193	1.30	0.64		
	E4	7	260	1.38	0.74		
	C1	6	163	1.49	0.89		
January 1981	E1	8	245	1.06	0.53	0.93	41.78*** (9)
	E2	9	198	1.28	0.61		
	E3	10	210	1.31	0.59		
	E4	7	173	1.20	0.64		
	C1	8	148	1.14	0.57		

Appendix 8. Components of prey size diversity: litter samples.
(d) Open

Date	Site	Numbers of size classes represented	Numbers of prey	Diversity H	Evenness J	W	χ^2(d.f.)
October 1978	E1	8	290	1.12	0.55	0.84	37.63*** (9)
	E2	9	165	1.10	0.53		
	E3	9	260	1.31	0.62		
	E4	9	244	1.46	0.69		
	C1	9	244	1.43	0.68		
January 1979	E1	6	311	1.24	0.71	0.85	38.11*** (9)
	E2	8	288	1.05	0.52		
	E3	6	357	1.02	0.58		
	E4	7	371	1.09	0.57		
	C1	7	196	1.26	0.67		
April 1979	E1	6	278	1.16	0.67	0.90	40.40*** (9)
	E2	7	230	1.37	0.73		
	E3	8	232	1.37	0.68		
	E4	7	205	1.37	0.73		
	C1	8	294	1.29	0.64		
July 1979	E1	6	118	1.01	0.60	0.88	35.39*** (8)
	E2	6	163	1.22	0.71		
	E3	7	195	1.24	0.66		
	E4	7	175	1.13	0.61		
	C1	6	260	1.06	0.61		
October 1979	E1	10	399	1.18	0.53	0.86	38.86*** (9)
	E2	9	94	1.52	0.75		
	E3	7	222	1.29	0.69		
	E4	7	303	1.04	0.55		
	C1	7	311	1.15	0.61		
February 1980	E1	8	78	1.21	0.63	0.78	35.27*** (9)
	E2	7	236	0.87	0.46		
	E3	6	300	0.95	0.54		
	E4	6	849	0.37	0.21		
	C1	7	333	0.97	0.51		
April 1980	E1	7	193	1.22	0.65	0.80	36.13*** (9)
	E2	6	262	1.38	0.80		
	E3	6	269	1.20	0.69		
	E4	8	303	1.36	0.68		
	C1	7	219	1.19	0.63		
July 1980	E1	6	164	1.04	0.60	0.86	30.28*** (7)
	E2	5	113	0.98	0.62		
	E3	6	209	1.20	0.69		
	E4	7	231	1.18	0.63		
	C1	6	147	1.27	0.74		
October 1980	E1	7	231	1.23	0.65	0.78	35.02*** (9)
	E2	9	264	1.27	0.60		
	E3	10	398	1.18	0.53		
	E4	7	193	1.19	0.63		
	C1	6	178	1.07	0.62		
January 1981	E1	6	186	1.06	0.62	0.94	42.29*** (9)
	E2	7	611	1.18	0.61		
	E3	8	241	1.24	0.61		
	E4	7	412	1.09	0.57		
	C1	8	177	1.29	0.65		

STUDIES CONCERNG SMALL MARSUPIALS

Appendix I. Studies concerning the small marsupials of Australia and New Guinea.

C. R. Dickman. (Ph.D. thesis, The Australian National University, Canberra.)

Superscripts placed to the left of the first author's name refer to studies that provide evidence suggestive of competition. The numerical value of the superscript (1-4) refers to the maximum number of possible examples of competition between different pairs of species in that study. Unbracketed superscripts refer to studies that provide evidence suggestive of competition among small marsupials, bracketed superscripts to those providing evidence suggestive of competition between small marsupial and eutherian mammals.

Superscripts are omitted if a study discusses or reiterates the findings of a previous study. For example, although Main (1961) discusses possible competition among Macropodidae, his discussion adds little to the original observations of Serventy (1951), and a superscript for this study is therefore inappropiate. Hope (1974) also restates the observations of a previous study (Hope 1973), so again no superscript is provided.

Appendix I.

1. STUDIES CONCERNING THE SMALL MARSUPIALS OF AUSTRALIA

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