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THE ROLE OF SOCIAL BEHAVIOUR AND SPACING IN
POPULATIONS OF THE BUSH RAT, RATTUS FUSCIPES

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RATTUS FUSCIPES
To Honey and Dad.
This thesis describes original research unless otherwise acknowledged. The work was carried out in the Department of Zoology at the Australian National University from March 1976 to December 1979.

Dedee P. Woodside
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ABSTRACT

Social behaviour and social spacing was studied in natural and enclosed populations of the bush rat *Rattus fuscipes*. The aim of this study was to elucidate the role of social behaviour in the population biology of this species. The approach taken involved the manipulation of resources and spatial environments of rats in enclosures in order to reveal details on the relationship between social behaviour and resource availability (primarily resource distribution) and to reveal the behavioural mechanisms responsible for the partitioning of resources among conspecifics. A trapping and tracking study in the field was used to reveal aspects of the social structure of natural populations and changes in spacing associated with natural changes in resource distribution.

A comparison of information from three widely separated populations (from Kioloa, N.S.W., Lees Creek, A.C.T. and Mt Glorious, Qld.) was used to establish the general demographic and social characteristics of the species (using similarities in the data) and to establish the range of social responses to varying environments (differences in data).

The similarities in demography of rats in the three areas were as follows: (a) there was an annual cycle in abundance of animals and annual turnover of membership in the population, (b) the sequence of life history events (mating, births, emergence, dispersal, death) in each cohort resulted in similar timing of peaks and depressions in population size in all study areas; (c) mating took place in spring and early summer, young emerged and became trappable in mid-summer, (d) populations peaked in late summer and autumn and
reached lowest levels just before juveniles appeared, (e) males showed lower residency than females and experience high turnover and typically disperse in spring; (f) females showed high residency and were probably responsible for the overall predictability of population size from cohort to cohort.

The three populations differed primarily in density and stability of numbers over the study periods. While the population at Kiola declined dramatically the populations at Lees Creek and Mt Glorious showed only the typical annual oscillations described above. Both of these latter two populations were consistently more dense than the population at Kiola.

A more detailed study of one population (at Kiola, N.S.W.) provided information on the relationship between resources and the density of individuals and thus helped to explain the observed decline in the size of the local population. A combination of deterioration in patches of appropriate habitat and physical isolation of the population from other sources of R. fuscipes contributed to the decline in numbers and lack of immigration. Spring immigration of males and the availability of sufficient resources for overwintering of resident animals (particularly females) may be essential to stable population size in this species.

Five measures of animal dispersion and one measure of social relationship based on spacing were applied to trapping data from all three field populations and revealed the following general characteristics regarding R. fuscipes: Animal dispersion and animal associations varied seasonally and with the sex and age of the individuals. In particular, adult females maintained discrete spacing in all seasons and showed seasonal association with other types of individuals. In winter some subadults (particularly females)
overlapped with adult females and shared complex burrow systems. Consequently, there was a significant difference in clumping of females in winter compared with their dispersion in other seasons. Males consistently showed a spring increase in movements associated with the onset of breeding. The social associations of males was highly variable through the year.

Information on the use of resources and the diet of R. fuscipes showed that it has a diverse food base with seasonal preferences and that in general both the food resources and potential shelter of bush rats were patchily distributed. At Kiolea it ate and cached the highly toxic seeds of cycads in autumn but did not appear to suffer ill effects. The bush rats dug burrows in autumn and winter and use shallow nests in log hollows for shelter in other seasons. In all seasons and particularly in winter, the bush rats make use of runways which were sometimes clearly discernable.

Enclosure experiments were designed to explore the relationship between changes in the availability and distribution of resources and changes in social behaviour and spacing of R. fuscipes. The establishment of the social order which functions to partition resources was observed in enclosures and attempts were made to show that findings from enclosure studies were consistent with observations in natural populations.

The behavioural mechanisms by which the social structure was maintained were largely revealed by using large outdoor enclosures for short-term (6 week) experiments involving variables such as season (breeding and non-breeding), the number of potentially interacting individuals, and the distribution of food resources (central and scattered). Dominance hierarchies and the use of runways emerged as the key behaviour mechanisms.
The maintenance of spacing and some of the effects of spacing behaviour were studied in semi-natural outdoor enclosures. Linear dominance hierarchies were quickly established and shown to be related to space use patterns of the animals of different social rank. The relationship was more distinct in breeding season when dominance was generally attained by a female and not necessarily the largest individual. She was extremely intolerant of the presence of others in her space and attempted to exclude them. Their attempts to escape were prevented by the walls of the enclosure and the consequence of avoidance behaviour led to an increase in the complexity of the runway system to which all movements were restricted. Intolerant behaviour, and the patrolling of space using runways showed peaks during oestrus and pregnancy. Since breeding and social dominance were correlated, it was postulated that being first to enter oestrus contributed to the probability of being socially dominant and being the first and only female to breed.

Observations in smaller indoor enclosures (called "pools") confirmed the findings from outdoor enclosures that the dominant animal was usually a female and was the only individual to breed successfully, and that socially dominant animals affect the use of space and resources by subordinates. The use of space was linked with development of a runway system and relocation of these runways by changing the positions of specially designed floor tiles revealed that animals rely on olfactory cues to locate the runways. Disturbance of the runways led to a significant drop in social interactions and animal movements remained infrequent until runways were reestablished. Since runways were marked with urine it was postulated that the runways may bear some information about the dominant individual, her ownership of space and reproductive condition, and behavioural state.
Bush rat spacing is probably the consequence of avoidance responses by individuals encountering the fresh odours of dominant animals, (space owners) on runways, and is a means of avoiding direct encounters. In the field secondary cues may be only occasionally reinforced through overt social behaviour, thus accounting for the lack of stylized agonistic behaviour in this species.

Long-term experiments in the pools showed that there are incidental effects on rats living at high density. When confined populations to pools for several months populations stopped growing and young animals which remained confined with a dominant female experienced suppressed growth. Social behaviour may be responsible for impaired fitness of individuals which cannot disperse.
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CHAPTER 1

INTRODUCTION

1.1 THE ROLE OF SOCIAL BEHAVIOUR IN POPULATION BIOLOGY

It is widely accepted that social behaviour plays an important role in population biology serving as a link between changes in environmental resources and changes in population density or size (Ebling & Stoddart, 1978; Krebs, & Perrins, 1978; Wynne-Edwards, 1978). It is often assumed that social behaviour somehow limits population density below the level at which resources are threatened (Lidicker, 1962), yet the causal mechanism in this relationship remains obscure. Instead, the function of social behaviour is largely inferred from field studies. Neither the relationship between social behaviour and the environment (specifically resources such as food and shelter) nor the relationship between social behaviour and population density is fully understood, although the voluminous literature in this area reflect the enormous effort that has been directed toward this problem.

Most studies which set out to illustrate how aspects of social behaviour could affect population density have been confined to
establishing correlations such as those between levels of aggressive behaviour and density (Southwick, 1955a,b; Healey, 1967; Lloyd and Christian, 1967; Archer, 1970; Gipps et al., 1981), between the tendency to aggregate and population size (Terman, 1980), between the tendency to disperse and population density (Myers and Krebs, 1971; Lidicker, 1975) and between dispersal rate and rate of population growth (Myers and Krebs, 1971; Krebs et al., 1976). While these studies have been helpful in revealing aspects of social behaviour which may influence natural populations, the machinery that would make them effective is largely unresolved. Speculation on the nature of the mechanism is embroiled in a controversy which stems partly from the difference in approach taken by those who seek a single causal mechanism such as physiological stress or population genetics (for review see Krebs and Myers, 1974; Tapper, 1976; Krebs, 1978a,b; Tamarin, 1978) and those who think that it involves a network of factors working simultaneously (Lidicker, 1973).

Attempts to reveal the details of how certain behavioural mechanisms could hold a population in check have shown that the physiology of an animal can be affected by the presence of neighbours, and specifically, that the behaviour of the neighbours may cause neurophysiological or neuroendocrine changes which affect reproduction and survival (Houlihan, 1963; Christian and Davis, 1964; Christian, Lloyd and Davis, 1965; Pinter and Negus, 1965; Terman, 1965, 1969, 1979; Lloyd and Christian, 1967; Gerber, 1973; Clark, 1978; Delong, 1978). The influence of one animal on another may be mediated through secondary tactile or pheromonal stimuli which have been shown to inhibit growth and reproduction and sexual maturity (Christian, 1957, 1961; Bruce, 1960, 1961; Myers, 1964; Terman, 1968, 1979, 1980; Rogers and Beauchamp, 1976; Batzli et al., 1977; Bediz and Whitsett, 1979)
and through direct aggressive interactions which might also affect
growth and reproduction (Smollen and Keller, 1979) or result in
infanticide (Armitage et al., 1979; Labov, 1980 and in part Boonstra,
1980) or injury and death in other age groups (Chitty, 1955; Sadleir,
For the most part, the conclusions of these studies have not been
adequately tested. Conclusions reached from experiments carried out in
enclosures should be tested in the field, while the information gleaned
from field studies may be usefully scrutinized by studying enclosed
populations.

Thus far, most studies cited have dealt with the
relationship between social behaviour and population processes and
have not considered the link between social behaviour and changes in
resources such as food and shelter. Surprisingly little has been done
to investigate this relationship given its importance in understanding
population biology (Wynn-Edwards, 1962; Watson and Moss, 1970;
Flowerdew, 1972). Although the relationship between social behaviour
and food was considered an integral part of the model upon which Krebs
and his co-workers based much of their study of population changes in
microtines (Krebs, 1979, p.63), it has been tested in only a few of
their experiments. In general these studies focused on the effect of
food availability by supplementing the food on a trapping grid, but
did not control for the effects of changing food distribution. For
example, Taitt (1981) and Taitt and Krebs (1981) supplemented the food
of two species and found that density increased and reproduction was
prolonged. They concluded that these were consequences of changes in
spacing behaviour (changes in sizes of home ranges) which are limited
by food availability, but did not address the question of how changes
of food distribution may have also affected the spacing behaviour in
the population. Similarly, Fordham (1971) showed that supplementing
the food of Peromyscus maniculatus caused the density of animals to
increase, but noted that the change in density was restricted to
females. He suggested that this reflected a difference in the social
relationships held by males and females and in the relationship of
their social behaviour to resources, but he did not distinguish
between changes in quantity or distribution of resources. Experiments
on enclosed populations of mice revealed an intimate relationship
between the distribution of resources, social behaviour and the degree
of access to resources that mice of different social status were able
to gain (Stueck and Barrett, 1978). Animals of lower social status
were unable to assimilate their food efficiently thus indicating that
a combination of certain types of food distribution and the spacing
behaviour of socially dominant individuals might be responsible for
the impaired fitness of subordinates. The study by Stueck and Barrett
(1978) demonstrated the value of taking such an experimental approach
to investigate the relationship between social behaviour and resource
partitioning.

This thesis explores the relationship between changes in the
availability and distribution of resources, and changes in social
behaviour and spacing of Rattus fuscipes. It attempts to elucidate
this relationship by observing individuals as they establish a social
order which functions to partition resources and attempts to show that
the findings of studies in enclosures are consistent with observations
on natural populations.
1.2 BACKGROUND ON THE STUDY OF SOCIAL SPACING

To some degree all mammals exhibit a dispersion pattern which is actively maintained by individuals. This dispersion pattern is a response to the presence of other animals as well as to the distribution of critical resources (Calhoun, 1963; Eisenberg, 1981). The distance between animals may reflect their mutual efforts to avoid each other or to defend a patch of resource for their own exclusive use. It is possible that the spatial pattern maintained by members of a population is a compromise between avoidance behaviour of individuals on one hand and their mutual attraction on the other (Taylor and Taylor, 1978). The overall pattern of dispersion, therefore, depends both on properties of the individuals involved (their genotype, age, experience, neuroendocrine state etc.) and on properties of their environment (weather, amount, kind and distribution of food and cover) (Chitty, 1967).

It has been argued that social structures, as revealed by dispersion patterns, arise because they provide an optimal context within which an individual can carry out vital functions (Crook et al., 1976). These functions include resource exploitation, predator avoidance, mating and rearing of young. Most of these functions involve some ‘contest’ among individuals, the consequence of which is an unequal distribution of resources or access to mates. The competitive ability of the individual may be expressed through space ownership and social status and maintained through overt behaviour or territorial marking which is negatively reinforced through agonistic encounters (Eisenberg, 1981). The emphasis is therefore placed on the outcome of interactions between individuals to establish their
relative social status or their right to gain access to resources. Thus the social relationships reflected in spacing patterns which develop in this way may be compromises between the individual’s competitiveness and the benefits it gains from being sociable (e.g. protection from predators and information on the whereabouts of resources).

The study of animal spacing involves the measurement of two different phenomena, including spacing patterns and spacing behaviour. Spacing patterns can only be measured at the level of a population (Taylor & Taylor, 1978) and is a description of animal dispersion with respect to critical resources and conspecifics. In contrast, spacing behaviour can only be measured at the level of the individual when it interacts with its environment or conspecifics. It is at this second level that useful manipulations can be made to test the way animals respond to changes in their physical and social environment.

This study of spacing behaviour in Rattus fuscipes was designed to investigate both natural dispersion patterns among groups of animals and the behaviour of individuals which is responsible for maintaining the dispersion patterns. The study was pursued at three levels, each one permitting a different degree of manipulation and observation of the animals involved.

The first level (Chapter 2) was concerned with natural populations of Rattus fuscipes and describes natural changes in population size, density, spacing patterns and social structure. The second and third levels (Chapters 3 and 4 respectively) involved enclosed populations with contrived social structure and artificial distribution of resources. The outdoor enclosure used in the second level permitted study of patterns of space use, the establishment of social rank among individuals and how this affected each animal’s use
of space and resources. The indoor enclosures used in the third level provided a completely controlled environment and the development of new methods for the study of individual interactions and their consequences on the use of resources on breeding success and on survival of each individual.

These three levels constitute an integrated approach to the problem of social spacing and provide an ecological context in which behaviour studies may be interpreted.

1.3 THE STUDY ANIMAL: RATTUS FUSCIPES (Waterhouse)

The bush rat, Rattus fuscipes (Waterhouse) is an indigenous murid rodent and one of six species of Rattus found in Australia. It is one of the most common small mammals of the coastal woodlands with a particular preference for wet sclerophyll forest (Ride, 1970; Wood, 1971; Freeland, 1972), and for areas where the climate is predictable (Taylor and Horner, 1973a). It is not known from the hot and dry parts of northern Australia whilst it is abundant in the cooler and moister habits further south, a possible consequence of the thermophysiology of this species (Collins, 1973) and its inability to go without water even over short time periods (Baverstock, 1976).

There are three recognised subspecies of R. fuscipes (R. f. coracius, R. f. assimilis and R. f. greyi) that occupy the forests of Australia’s east coast and one additional subspecies (R. f. fuscipes) in similar forests in south-western Australia (Figure 1.1). While all of these subspecies have been shown to interbreed under laboratory conditions (Horner and Taylor, 1965), they rarely do so in the wild and only R. f. greyi and R. f. assimilis are known to overlap in their distribution. This study concerns only R. f. assimilis which occurs
along the eastern coastline from the subtropical rainforests of Queensland, to the sub-alpine woodlands and sclerophyll forests of New South Wales and Victoria.

1.3.1 Life History

Breeding in *R. fuscipes* is highly seasonal but is more so in the southern part of its range than in the north. In the south breeding tends to be confined to the summer months (December to February) (Warneke, 1971; Robinson, 1976; Braithwaite and Lee, 1979) while in south-eastern Queensland the timing of the onset of the breeding is more variable and often begins in early November (Wood, 1971), reaches a peak in December and January and continues to occur sporadically throughout the autumn months (March, April and May). The amount of breeding that occurs outside of the summer months varies from year to year and appears to coincide with moderate temperatures at that time (Wood, 1971; Robinson, 1976), rather than rainfall patterns.

Young are born about 23 days after mating (Taylor and Horner, 1972) and are weaned approximately one month later. Consequently, there is a major influx of new animals into the population between mid-summer, and early autumn of each year. In northern populations, juveniles also appear in all other seasons but are less common (Wood, 1971). The new cohort of bush rats reaches sub-adult weight (males between 61-120 g, females between 51-110 g) before the onset of winter. While they are theoretically capable of breeding at this stage (Taylor and Horner, 1971), they rarely mate. Instead most animals emerge from winter as sexually mature adults weighing approximately 120 g for females and 140 g for males.
Adult females are promiscuous and are capable of postpartum oestrus (Taylor and Horner, 1972) but in general produce only one or two litters (Robinson, 1976). The litter size is small, being only four or five young, though this number may range from two in the field (Robinson, 1976) to six in the laboratory (Taylor and Horner, 1972).

While the sex ratio in litters is generally parity, the adult portion of the population can experience seasonal fluctuations in sex ratios as a consequence of differential survival of sexes. For example, adult males show low winter survival (Wood, 1971; Robinson, 1976) and this declines further throughout the mating season to reach a minimum in summer before the emergence of the new cohort. Female adults, however, experience relatively higher survival rates than males in winter and early spring, although there is generally some decline in the numbers of females during this time. Those females that survive through to spring have a high probability of surviving through the breeding season but experience another decline in numbers in mid to late summer (Warneke, 1971; Wood, 1971; Robinson, 1976). Consequently, populations contain fewest individuals just before the new cohort of rats enter the trappable population.

Young rats of both sex have a low survival and there is a mortality of subadults that varies from year to year (Wood, 1971). Young rats disperse in autumn and few establish as residents. The overwintering population consists of a few individuals born in the area, a larger number of immigrants and a few surviving individuals which bred in the previous season (mostly females) (Warneke, 1971; Wood, 1971, Robinson, 1976).

Populations of R. fuscipes experience an almost complete annual turnover since the average lifespan is about one year (Taylor, 1961; Warneke, 1971; Wood, 1971; Robinson, 1976). In the field,
females usually live longer than males but few survive through a second breeding season. Each cohort therefore experiences a seasonally synchronized sequence of events.

1.3.2 Resources

*Rattus fuscipes* is omnivorous, taking a wide range of foods including invertebrates, plants, plant seeds and fungi (Warneke, 1971; Robinson, 1976; Watts and Braithwaite, 1978). Within any season, the diet is less catholic and there is a tendency to concentrate on certain food items such as insects in spring, seeds in summer, and fungi in winter (Watts and Braithwaite, 1978). Whether or not this selective dietary restriction results from choices made by the bush rats or whether it is a consequence of availability and quality of the food available is not certain. Some authors (Warneke, 1971; Watts and Braithwaite, 1978) suggest that the bush rat is entirely opportunistic and eats whatever is most readily available.

*Rattus fuscipes* is generally associated with moist microhabitats (Braithwaite, Cockburn and Lee, 1978) and prefers sites which have dense ground cover (Warneke, 1971; Barnett, Howe and Humphries, 1978; Braithwaite et al., 1978; Press, 1979; Fox, 1980). Within these sites it may take refuge in hollow logs, shallow nests or shallow burrows (Warneke, 1971; Robinson, 1976), but little is known of these habits.

1.3.3 Social Behaviour

There are marked changes in the social behaviour of *R. fuscipes* that are related to phases of the life history, notably the onset of breeding and the establishment of residency by subordinates before winter. In autumn sub-adults begin to disperse and both
immigration and emigration (which may also include less due to mortality) rates show a sharp increase (Woods, 1971; Robinson, 1976). This increase in dispersal coincides with re-sorting of space among residents and immigrants as the latter establish their residency, presumably by establishing some degree of space ownership before the onset of winter (Robinson, 1976). Most individuals that manage to survive winter show evidence of having been attached to a home range throughout that season. In spring (September to November) the males, as sexually mature adults, undergo a marked change in behaviour. This change is indicated by a substantial increase in the average length of movements between captures and by a significant increase in the number of transient males captured on the trapping grid (Wood, 1971; Robinson, 1976). At the same time adult females remain relatively immobile and maintain discrete home ranges in which they remain until their young emerge from their nest (Robinson, 1976).

The timing of the changes in spacing and space ownership coincide with changes in the nature of social interactions as observed in contrived dyadic encounters. For example Robinson (1976) found a peak in antagonistic behaviour between subadults and adults, especially female adults, in autumn, while in spring there was an increase in male-to-male antagonism and tendency for females to avoid each other. Adult females showed a general intolerance of conspecifics throughout all seasons, but male behaviour fluctuates from over antagonism to amicability between seasons. By mid-summer for example, males that had engaged in conflict during spring become more amicable. Robinson (1976), indicated a peak in intolerance among bush rats of all classes from late winter to early summer (August to November) and Braithwaite (1978) extends this to include a period from late autumn to winter (May to August). It is possible that this
seasonal change in intolerance between conspecifics may provide some explanation for the seasonal changes in the social structure of *R. fuscipes* as inferred by field data on natural populations.
FIGURE 1.1: Location of the three study areas.
(1) Kioloa, (2) Lees Creek, and (3) Mt Glorious.
Map insert shows distribution of Rattus fuscipes subspecies R.f. assimilis (R.f.a),
R.f. coracius (R.f.c), R.f. greyi (R.f.g) and R.f. fuscipes (R.f.f).
CHAPTER 2

SOCIAL SPACING IN NATURAL POPULATIONS OF R. FUSCIPES:
A COMPARISON OF RESULTS FROM THREE STUDY AREAS

2.1 INTRODUCTION

Animal spacing in natural populations is typically non-random (Taylor, Woiwod & Perry, 1978) and the dispersion pattern depends upon features of the populations such as density and social structure, as well as features of the environment such as weather and resource distribution. The relationship between animal spacing and these variables is best determined through experimental manipulation. Before performing such experiments, however, it is important to establish the natural range of each variable. Relevant information can be collected from unmanipulated natural populations so that experiments involving manipulation may be designed to remain pertinent to the species in nature.

In this chapter I deal with natural populations of Rattus fuscipes and try to extract from them some information about their demography, social structure and the way they use spatially distributed resources such as food and shelter. I try to determine the range of social structures found in Rattus fuscipes populations as revealed by spacing patterns and I attempt to identify the basis for similarities and differences in social structure between populations.

At first I had planned to obtain this information from a population at Kioloa, NSW, making comparisons between years and between seasons. However, this initially dense population declined in abundance to the point where only two animals were captured in the
area. Reasons were sought for this population decline and its subsequent recovery, and data from other previously studied populations were used to meet my original objectives. The three study areas referred to differ greatly in climate, vegetation and population density. They therefore provide material suitable for determining the range of demographic, social and resource features of the species.

The observations are presented in the following order: First, a comparative study of the demography of the populations; second, a comparison of social structures determined from spatial distribution of animals; and third, a detailed analysis of one population and its resources in an attempt to elucidate resource exploitation and some of the factors that influence animal dispersion.

2.2 METHODS AND MATERIALS

2.2.1 Study Site Description

2.2.1.1 Kioloa Study Area

The main population study was conducted at the Australian National University field station at Kioloa, NSW (35°33'S, 150°23'E). The trapping grid was established on a small, semi-isolated piece of indigenous vegetation (Fig. 2.1) on flat land which was surrounded by a creek and small lagoon to the southeast and by a bitumin road and a well-mowed caravan park on the other sides. The total area was about 3.4 hectares and maximum relief was about 3 m above sea level.

The vegetation in the study area was mainly an alliance of spotted gum (Eucalyptus maculata) with blackbutt (E. pilularia) and a dominant understorey of cycads (Macrozamia communis). In addition, there was an abundance of Banksia serrata and some localised occurrence of swamp mahogany (E. botryoides) associated with sword
grass (*Gahnia clarkei*). The post-fire regrowth areas were scrubby and included some weedy species. Along the edge of the lagoon there was a wide band of soft fine soils supporting a growth of *Casuarina gleuca*, coastal broom *Viminaria juncea*, and a mixed grassy ground cover. This area was subject to frequent flooding and was often waterlogged. The ‘wispy’ growth here contrasted with the sturdy and aged tree stands throughout the rest of the study area. The study area appeared to consist of a minimum of three vegetation zones: the flood zone, the old forest and the regrowth area.

The woodlands and heath close to the study grid had experienced regular routines of control burning, slashing, agricultural practices and logging. In particular, some burning and slashing for electricity lines on the west side of the road in late 1976 rendered that area uninhabitable to *Rattus fuscipes* until there was sufficient regrowth in 1979. As recently as 1975, the southern portion of the study area also experienced control burning.

General information regarding soils, geology and vegetation of the district is available from Gunn (1978). In general, the climate is mild with fairly dependable rainfall and temperatures rarely dropped to freezing. Details on rainfall and temperature are given in Section 2.2.6 of this study.

2.2.1.2. Lees Creek Study Area

This area was trapped by C.R. Dickman between 1978 and 1980 and occurred in a long narrow valley in the Brindabella Mountains near Canberra, ACT (35°25′S, 148°50′E) (Figure 1.1). It was on the western slopes of the Cotter River Catchment at an altitude of approximately 800 m above sea level.
The habitat of the valley floor was a wet sclerophyll alliance of brown barrel *Eucalyptus fastigata* with narrow-leaved peppermint gum *E. radiata* and ribbon gum *E. viminalis*. Beneath this canopy was a dense cover of fishbone water fern (*Blechnum nudum*), bracken fern (*Pteridium esculentum*) with blackberry (*Rubus fructicosus*) and nettle (*Artica incisa*) along the edges.

The trapping area was bound by a road on one side and steep granitic slopes on the other (Figure 2.1). Growing along these slopes was a plantation of pine (*Pinus radiata*). In the valley there was a slow flowing creek littered with logs, branches and other debris, used as cross-over points by animals. While many of the natural 'bridges' were removed at the beginning of the study, bush rats continued to cross over the creek regularly and could move freely in or out of the trapping area.

Temperatures in the Lees Creek area were highly seasonal and generally fell well below freezing during winter. Details on the rainfall which was both unpredictable and unseasonal are provided by Stewart (1979).

2.2.1.3 Mt Glorious Study Area

This study area was trapped by D.H. Wood between 1963 and 1966 and is described in Wood (1967, 1971). It was located in the middle of 60.5 ha parcel of rainforest northwest of Brisbane (27°30'S, 152°40'E) (Figure 1.1), at an elevation of 610 m above sea level. The traps were set in an area of steep slopes covered with a variety of rainforest species. Notophylls and microphylls were most common, with lianas, epiphytes and large buttrous root trees occurring throughout. Soils were deep and rich. Ground cover was low or absent, although the ground was littered with boulders in some places and palm leaves
and branches elsewhere. There were no major barriers to animal movement in or out of the area and no definite physical boundaries to the study site.

Temperatures in this area never fell below freezing and rainfall patterns provided a predictable and mildly seasonal environment. A more detailed description of rainfall and temperature readings are given by Wood (1967, 1971).

There are four main differences between these three study areas: 1) large differences in seasonal climate (altitude, latitude effects); 2) differences in the type and amount of understorey; 3) differences in the degree of patchiness of the habitat and 4) differences in the degree of isolation from other populations of Rattus fuscipes, as well as other types of barriers to rat movement.

2.2.2 Trapping and Tracking Techniques

2.2.2.1 Kioloa Study

A combination of trapping and tracking techniques was used at Kioloa. A main study grid with 234 trap locations (18 x 13) set at 5 m intervals was established at the north end of the study area and two perpendicular and intersecting index lines were set at the south end of the grid. One line ran east-west and the other north-south (see Figure 2.1). The use of index lines is described by Pettigrew and Sadleir (1970) and Hansson (1967). Clusters of four traps were set within 2 m of a focal point and the interval between clusters was 15 m. The edge of the grid was surveyed using perimeter lines of traps set at 2.5 or 5 m spacings. The remaining study area, including the flood zone and regrowth areas, was surveyed during alternate trap sessions using 10 m intervals throughout.
A grid was used initially as it was considered the best method for obtaining information on animal spacing (Delany, 1974). After some pilot studies, it was found that a 5 m spacing was the best compromise between economic use of traps and maximising data on spacing between animals. As with any trapping regime, there are a conflicting series of compromises which must be made (Begon, 1979). In this case, I have assumed that tight spacing of traps would not affect the determination of home range boundaries (c.f. Hayne, 1949; Brant, 1962) as used later in this Chapter to describe the seasonal distribution of individuals (Section 2.3.2.2).

The trapping regime changed during the study as it became necessary to continually re-locate the population. As the population activity centres drifted south, the trap effort expanded accordingly. More time was spent surveying the area for bush rats and trying to track the rats with smoked-sheets to find areas of greatest use. The regular trapping regime consisted of 340 regular trap locations and a total of 26,520 trap nights were spent sampling at regular sites while a further 15,480 trap nights were spent surveying the surrounding area for potential source populations or refuges.

Both the grid and index lines described above were trapped for a minimum of 2 to 3 nights each month. On the final night of each session, only the index lines were set to find out whether all animals could eventually be caught in the southern part of the study area where regrowth vegetation was relatively dense.

Elliott small mammal traps were baited with the standard mixture of peanut butter, rolled oats and honey. Early attempts to pre-bait, as suggested by Tanton (1965) and Wood (1971), failed owing to 'competition' for bait by brushtail possums and ants. It became
necessary to trap and hold the brushtail possums during the trap sessions because of their systematic disturbance of the trap lines. During wet or cold periods, traps were padded with cotton wool and protected with plastic bags.

In addition to trapping, smoked sheets were used to track the small mammals on the ground (Justice, 1961; Fulk, 1972). Some modifications of the tracking technique used by others helped to save a great deal of time and effort and thereby increased the number of tracking sheets that could be used during a trap session. Two-litre orange juice cartons (9.5 x 9.5 x 33.0 cm) were fitted with two sheets of smoked cardboard (9.0 x 33.0 cm), top and bottom. The cards were held in place by paper clips at either end of the open carton, so that the unit could simply be turned over for a second use. The carton was held rigid by a square wire ring. Removal of this ring allowed the cartons to be collapsed to form a flat and rigid rhomboid shape and to be stacked tightly in bags for carrying. The smoked sheets were easily removed for examination or re-smoking (using an acetylene torch) and were protected from marking while in storage and from the weather in the field. The use of open-ended cartons ensured that animal movement was not impeded, while the size of the carton ensured that the probability of encounter by an animal was approximately the same as for a similar sized Elliott trap. To preserve animals' tracks, either hair spray or artists' varnish were used. However, it was possible to record all necessary information from the tracks in the field using a reference photo of tracks for each species and a simple code for species, age class (if determined), pattern of movement and intensity of use. In addition to the five ground dwelling mammals, there were other visitors such as brushtail possums, sugar gliders, skinks, ants, snakes and echidnas and all of these
could be easily distinguished. Tracks of some of these species are shown in Plate 2.1.

Animals caught in traps were identified to species, sex, individual number and age class, by the system used by Wood (1971). Weight was measured to 1.0 g with a Pesola spring balance. Head length was measured using calipers. Faeces were collected on first encounter with each individual in every trap session and observations were made regarding reproductive condition. Information regarding scarring, tail wounds, ectoparasite load and general condition was also recorded. Animals of all species were individually identified by toe clipping and rats were also ear-tagged using Hauptner fish fingerling tags (10 x 3 mm).

Interference with traps by possums, cats or kangaroos was noted and closed traps were excluded from any calculations that involved the total number of traps available.

2.2.2.2 Lees Creek Study

The population at Lees Creek was usually sampled once every month and fortnightly during autumn and winter. Elliott traps were rotated each day of a four-day session, so that every fourth trap line was set on consecutive nights. Each trap site was therefore sampled only once per session. Trap points were on a 10 m grid and trap placement varied within 2 m of each marked point (Figure 2.1). Traps were baited using the same mixture as that used at Kioloa and bedding was provided regularly. All animal records and individual identification were the same as defined for Kioloa.

The trapping results provided by C.R. Dickman for Lees Creek study area are based on approximately 13,000 trap nights and included
information on two cohorts of *R. fuscipes* caught between March 1978 and July 1980. These results had not been analysed previously.

### 2.2.2.3 Mt Glorious Study

Full details on the trapping scheme used at Mt Glorious are given by Wood (1971). In general, the trapping scheme used was similar to the grid trapping used at Kioloa and at Lees Creek (Figure 2.1). The spacing between traps was, however, 15 m. The trapping results extracted from this study and reanalysed here include a single cohort born in late 1963 and surviving to the beginning of 1965.

### 2.2.3 Analysis of Trapping Data

#### 2.2.3.1 Survival Rates

Minimum monthly survival rates were estimated by direct enumeration of the number of individuals known to be alive in one month and the number of these individuals known to have survived to the following month (Krebs, 1966; Wood, 1971). Age-specific events and survivorship rely on the weight-age class relationship established by Wood (1967).
2.2.3.2 Weight Classes

Though live weight is a poor indicator of exact age in *R. fuscipes* (Taylor, 1961; Warneke, 1971; Wood, 1971) weight criteria of the age classes used here are convenient in that they correspond roughly to those established by Robinson (1976) based on eye lens weight on southern Victorian populations and Warneke (1971) using tooth-growth patterns on another Victorian population. As a result these age classes permit comparison of age-related population phenomena (e.g., survival, social behaviour, dispersive) between studies.

Age classes could also be separated on more subjective criteria than body weight. Juveniles for example, were defined as those animals which had newly emerged from the nest to become trappable and were generally less than 60 days old. At 50 days females have rarely ovulated and males are aspermous (Taylor and Horner, 1971) and thus juveniles are sexually immature. Females generally have unperforated vaginal openings at this stage and males have undescended testes. Subadults were those animals between two and approximately five months of age. At five months the individuals generally enter a lull in growth associated with the onset of winter (Warneke, 1971; Wood, 1971). Prior to this, their growth is rapid and although they are capable of breeding, very few animals do so. Scrotal sacs of subadult males are generally small and testes are abdominal. Breeding was generally restricted to adults whose post winter weights were over 110 g for females and 120 g for males. Adult females were generally perforate and males showed fully descended testes and large dark scrotal sacs.
<table>
<thead>
<tr>
<th>Weight of Males (g)</th>
<th>Weight of Females (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juveniles  &lt; 60</td>
<td>&lt; 50</td>
</tr>
<tr>
<td>Subadults  60-120</td>
<td>50-109</td>
</tr>
<tr>
<td>Adults  &gt;120</td>
<td>&gt;110</td>
</tr>
</tbody>
</table>

2.2.3.3 Interspecific Relationships

Interspecific relationships were investigated (i) by correlating the number of individuals of each of the three native species known to be present during each session, and (ii) by using a competition coefficient based on values of habitat overlap (MacArthur, 1972) as follows:

\[ \alpha = e^{-\frac{d^2}{2(\sigma_1^2 + \sigma_2^2)}} \]

where \( \alpha \) = competition coefficient
\( d \) = difference between mean habitat scores of two species
\( \sigma_1 \) and \( \sigma_2 \) are standard deviations of respective mean habitat scores where habitat scores are between 1 and 5 for increasing complexity.

This method was applied to the spatial and temporal/spatial overlaps of the species at Kioaloa and Lees Creek by Dickman and Woodside (1982).

Association of two species in the presence or absence of a third species is calculated by Cole’s index of partial association (Cole, 1957). The index values can range between \(+1\) and \(-1\) so that an association between species is negative when the index is negative and
positive when the index is greater than zero. Values close to zero represent very weak or no association.

2.2.4 Habitat Analysis (Kicloa)

2.2.4.1 Floristics and Habitat Structure

Collection of information regarding vegetation type, structure and relative abundance of plant species was based on the methods described by Gullan et al. (1976), Gullan (1977) and Braithwaite and Gullan (1978). Floristic and structural data were obtained for 69 sites. Each site was a 5 m x 5 m quadrat separated by 20 metres from the next site so that one out of every five trap sites was assessed. The resulting grid pattern for vegetation sampling was considered ideal or maximizing vegetation information in small areas (Williams, 1971). All plants in each quadrat were recorded and assigned a visual estimate of cover/abundance (Gullan et al., 1976).

From the floristic information obtained in each quadrat, an index of floristic similarity or floristic heterogeneity was determined by the formula of Grant and Morris (1971). The cover and abundance scores for each species were compared for each pair of quadrats resulting in a three dimensional matrix. The equation used to summarise the comparison is:

\[ E_s = 100 \left( \frac{\Sigma Y_i}{\Sigma X_i} \right) \]

where \( E \) is the index of similarity

\( Y_i \) is the lower cover/abundance score for a given species at the two sites being compared and

\( X_i \) is the higher of the two cover/abundance scores

A computer program was written in Fortran to accommodate this analysis (Appendix 2.1a). A lower limit of 5% was set for
cover/abundance scores so that any species with scores of < 5% were eliminated. The means and standard deviations were calculated for E from all quadrats. A high mean E indicates a uniform vegetation while a low mean E indicates a non-uniform vegetation which could either be patchy or evenly-mixed.

The study area was divided into vegetation zones based on plant species and used a simple ordination and clustering technique on the floristic data described above. Only the presence or absence of plant species was used to sort the quadrats and species into similar floristic zones. This was done with the aid of a computer, programmed for the Braun Blanquet method as described by Moore (1962) and Bridgewater (1976). This is a simple approach when compared to the more complicated polythetic agglomerative non-hierarchical clustering techniques suggested by Braithwaite and Gullan (1978) for simultaneous use of values for species cover and abundance.

The structure of the vegetation was also assessed for each of the 69 quadrats. Three types of measurement (i.e. M1, M2 and M3) were taken and are described below. For the analysis of habitat preference by all species of small mammals in the study area (Section 2.3.3.3.), these complex measures were reduced to a single value indicating the relative degree of structural complexity of the vegetation of each site (MacArthur, 1972; M'Closkey and Fieldwick, 1975). First, a quantified analysis of the structural profile was determined by counting intercepts of the canopy with a pole marked off at 30 cm intervals. Four samples were taken in each quadrat in the manner described by Braithwaite and Gullan (1978) (i.e. M1, = mean intercepts where i = 1 to 69). Secondly, a subjective analysis involving another seven structural categories was carried out. Each of these categories was scored (see Newsome and Catling, 1979) from 0
to 4 with 4 as the highest possible rating for the presence of a
certain structural feature. These features were: 1) the relative
amounts of bare ground, 2) the density of small seedlings, 3) the
density of large trees, 4) the availability of homesites (logs, litter
etc.,) 5) the amount of available herbage (monocot and dicot), 6) the
amount of cycad cover and 7) the presence of ants' nests (i.e. M2i =
mean rating for 7 structural categories, where i = 1 to 69). Thirdly,
the effectiveness of the lower canopy in casting shade was measured.
To do this, two photographs were taken at each site; one at ground
level and the other at 60 cm above the ground, using a 21 mm super
wide angle lens on a Nikon camera. No light filters were used,
although recommended by Anderson (1964). An overlay with 1504 squares
was applied to each photograph and the number of squares were counted
in which sky was obscured by more than 25% canopy cover. An index of
shading due to lower canopy versus upper canopy was determined by
using a ratio of the counts for the two photograph levels at each site
(i.e. M3i = ratio of number of obscured squares in lower canopy photo
to higher canopy photo where i = 1 to 69). These were compared with
Kipp solarimeter values at each level but this was not found to be a
useful method (see Fox, 1979; Wiena, 1967; Getz, 1968, for discussion
of light measurements in different habitats).

The maximum and minimum values of M1, M2 and M3 were used to rank each
of the 69 sample quadrats and to calculate a relative rank score
between 1 and 5 for each (i.e. S1i, S2i, S3i, where i = 1 to 69).
These 3 scores were averaged to provide one value representing the
relative structural complexity of each quadrat.
2.2.4.2 Soils

Data on soil structure and soil moisture content were collected with a soil-core auger, to a depth of 10 cm at 36 locations in the study area. Soil was placed in air-tight containers and returned to the laboratory for weighing, sieving and drying. The four sieve sizes used to separate the soil into different particle classes and are:

- Particles > 1200 um (S₁) (litter and humus)
- 212 um (S₂) (medium to coarse)
- 106 um (S₃) (fine granules of sand)
- 106 um (S₄) (very fine sand, soil)

The relative proportions of each particle size were determined. The soil was then dried until it reached a stable weight and the percentage moisture content per unit dry weight was determined (Chapman, 1976, Chapter 7).

The relationship between soil moisture and particle size was determined by fitting a simple binomial model to the data to adjust for transformed values (percent soil moisture and proportion of each particle size) and applying an F-test to the result. A statistical package entitled GLIM was used in this analysis and the format follows that used by Gregg (1981).

The various values for soil moisture were divided into five equally-sized classes (lowest value was 0.032 % dry weight and highest value was 0.6186 % dry weight). These classes were used by a second computer package SYMAP, to develop a proximal (or interpretive) map of soil moisture for the study area. This map was then used to interpret the location of burrows, and the boundaries of vegetation zones.
2.2.5 Diet Analysis (Kioleo)

Faecal pellets were collected from inside each visited trap and preserved in 70% alcohol. In the laboratory, each sample of faeces was washed through a fine sieve (mesh size 0.1 to 0.2 mm). It was then stained with haematoxalin and aliquots were mounted on two slides. Food particles were identified and an estimation of percentage volume of each food item made by modification of the points method (Watts and Braithwaite, 1978). The results of the two slides were averaged for each individual and combined averages were taken to provide values for the percent volume of the different food items eaten by the entire population at the time of sampling. Slides of unwashed and unsieved faeces were also examined. Because endosperm of some seeds such as Macrozamia are soluble, the washing procedure was eliminated. Estimates of content made in this way were not included in the above calculations. The faecal analysis was undertaken by C.H.S. Watts and the technique is described in detail by Watts (1968) and the results by Woodside and Watts (in preparation).

2.2.6 Determination of Environmental Predictability and Seasonality (Kioleo)

In some regions of Australia it is difficult to allocate the months to the four normal seasons (e.g. Braithwaite and Lee, 1979). By comparing the predictability of rainfall patterns when the months are grouped differently, it is possible to determine the most 'reliable' definition for each season. As seasons often form a framework in which population changes are described (e.g. seasonal changes in behaviour, spacing, reproduction etc.), the seasons should be clearly defined according to relevant changes in environmental
conditions (weather and consequently plant growth) which can affect the population.

A quantitative measure of environmental predictability was determined by the method developed by Colwell (1974) and used by Inger and Colwell (1977). Predictability has two additive components: constancy ($C$) which is the degree of 'sameness' in the measure of some environmental phenomenon, and contingency ($M$) which is the degree of reliable oscillation in the measure of an environmental phenomenon ($P = C + M$). Both of these measures of predictability have profoundly different implications in ecology (Colwell, 1974) and are therefore considered important in this study. It is possible that two seasons may be equally predictable from year to year but that one season is predictable because temperatures or rainfall vary in the same way each year while the other season experiences constant conditions each year.

Periodic rainfall patterns are associated with high contingency ($M$) values, while uniform rainfall is associated with high constancy ($C$) values. The determination of constancy and contingency values rely on the mathematics of information theory and in particular on the Shannon information statistic. Tests of significance for each of these measures involve the G-statistic and appropriate $X^2$ tables.

In this analysis of rainfall measurements from Kioloa were transformed by log$_2$ functions in order to adjust for the linear relationship between the standard deviation of precipitation and the mean precipitation for each month which would otherwise dramatically alter the index of predictability.

The predictability of rainfall was determined for two time periods at Kioloa: (i) the five years encompassing the study and (ii) the previous 24 years. The relative contributions of periodicity and constancy in determining the predictability of seasons at Kioloa are
shown in Figure 2.2 and statistical significance for each value of 'c' and 'm' is provided in Appendix 2.2. A graphic profile of rainfall and temperature for the six-year period is shown in Figure 2.3. The interpretation of this analysis follows. At Kiolea, there was a practical problem with defining the length of summer. Predictability was not significantly altered, however, by allocating either three or four months to this season (indicated by e and u for 'even' and 'uneven' divisions of months respectively in Figure 2.2) and for convenience, summer was maintained as a three month season.

Accordingly, the winter (JJA) can be seen as having a predictable periodic rainfall (highest M) while the spring (SOND) has a predictable but constant rainfall. The trend is similar for both the five year and twenty-four year summaries of rainfall at Kiolea. In both cases, winter involves the most dramatic changes in rainfall and may be an ecologically important season. There is predictable decline in conditions to become colder and drier in winter (Figure 2.3).

2.2.7 Analysis of Spatial Distribution and Movements (Kiolea)

Dispersion and clumping of individuals was measured by Morisita's index of dispersion (see Morisita, 1962; Southwood, 1966; Batzli, 1976). The index normally involved a ratio of the number of individuals caught, to the number of possible captures in a defined sample space. A modified version of this was also used here. In this case a ratio of the number of times traps were re-visited to the total number of traps visited any number of times was determined. This enabled a measure of extreme clumping and multiple use of only a few traps. The standard form of Morisita's index concerns the ratio
between the number of traps visited against the total number available.

Calculation of home range size was attempted by several methods, but was abandoned in favour of a diagrammatic assessment of distribution. Home ranges are drawn by the maximum polygon method used by Wood (1971). There is a host of methods available but this one involves the fewest assumptions.

The average maximum distance moved in each session (AVM) was calculated for each individual (Southwood, 1966; Flowerdew, 1976b) and a comparison of AVM for different classes of individuals was made by the Mann-Whitney U-test for ranked scores.

2.2.8 Analysis of Social Structure (all three study areas)

The social structure of each population was examined during each season. Associations between individuals and types of individuals (e.g. male, female; adult, immature) were determined by applying a type of nearest neighbour analysis to the centres of activity of individual bush rats in each season. The analysis used here was adapted from Koeppi et al. (1979) and slightly modified.

The modifications included a calculation of seasonal rather than sessional centres of activity where the centre of activity is defined as the weighted mean X and mean Y coordinates for all captive locations for a given individual. Seasonal centres of activity were a necessary compromise to accommodate the various trapping regimes used at each of the three study areas. They were not all trapped at similar or equal time intervals. Simberloff (1979) criticizes the use of central points and favours the use of circles of activity. The calculation of central points was fundamental to the present analysis of social spacing and to overcome some criticisms of this technique.
the standard deviation and standard error of each centre of activity was also calculated. The reliability of each centre of activity could therefore be tested. In addition all animals caught only once were excluded from this analysis. Low numbers of captures made it difficult to test the model of bivariate normality in the spatial data, an assumption which should be considered in the use of centres of activity.

Using the centres of activity to describe the position of individual bush rats, the Euclidian distance between each pair of individuals was calculated for each season. The distances were ranked and the five closest neighbours were determined for each base individual. These five neighbours (henceforth referred to as 'levels of neighbouredness') consisted of four 'classes' of individuals from two age classes (adults and immatures) and two sexes. The likelihood with which a base individual of one class would have a neighbour of any of these four classes can be determined. This results in a 4 x 4 matrix of possible associations between classes of individuals. There would be five such matrices (one for each level of neighbouredness) in each season. The likelihood of association between types of individuals at each level of neighbouredness was determined and compared with the actual frequency with which different classes of individual associated. The G-test suggested by Koepl et al. (1979) for calculating the significance of each association was substituted here by a $X^2$ test. Low observed values and frequent zero classes invalidated the G-test while in these circumstances $X^2$ measures are more robust (Kohler and Larntz, 1980). Deviation from expected $X^2$ values were assigned a number of plus (+) or minus (−) signs according to relative deviation size in each cell of the matrix (Appendix 2.3). The intensity and direction of observed associations was deduced from
these tables and summarised diagrammatically using the format provided by Koeppel et al. (1979). Large circles represent adults and small circles represent immature animals. Arrows represent the presence and direction of associations between each category of individuals (either a positive association using a solid lined arrow or a negative association using a broken line). No arrowhead means the association is mutual and a blank means there is no associations between certain groups. Lines within each circle indicate that a given group of animals associate or disassociate with their own kind and asterisks indicate statistically significant associations (X² values).

2.2.9 Justification of Approach and Some Assumptions

The present analysis of mark-recapture data is aimed at answering two types of questions. The first type concerns the demographic trends of a population and asks how the numbers of animals and the structure of the population changes in time. The second type of question deals with distributional information on the population from which dynamic aspects of individual associations are inferred. Mark-recapture data, however, relies on two variables: (1) the efficiency and reliability of the trapping technique and (2) whether or not all individuals can be trapped. The actual number of individuals is rarely known and thus all conclusions are based only on those individuals which appear on the calendar of captures (Petrusewicz and Andrezewski, 1962). Furthermore, some individuals are caught frequently and others infrequently, and thus a tally of animals known to be alive at any one time can only be made in retrospect. The revival of some individuals assumed to be dead for several months sheds some doubt on conclusions drawn from spatial or demographic analyses of a trappable population. The assumption made
here requires some faith that the trappable population is representative of the whole. This familiar problem with trap-recapture studies has been considered throughout the interpretations of the following results.

2.3 RESULTS

2.3.1 Comparative Demography of the Three Study Populations

2.3.1.1 Fluctuations in Numbers

Profiles of the three study populations are shown in Figure 2.4. In each population the numbers fluctuated seasonally and showed a pattern of oscillations which were consistent between years. Typically, there was a population low in mid-summer and a population peak in late summer or autumn. This peak represented the accumulation of young animals of a new cohort born during the summer and surviving adults of the previous cohort in the trappable population. The lowest population size occurred at a time when there was poor survival among adults, particularly male adults, shortly after breeding (Section 2.3.1.2). A less dramatic decline in numbers occurred in late autumn and early winter when subadults as well as adults facing their second winter suffered poor survival (Section 2.3.1.2). Spring (September to November) was marked by a small increase in numbers due to an influx of immigrant males prior to breeding. This secondary peak was most noticeable at Mt Glorious and Lees Creek but was virtually absent in some years at Kieloa.

There are three other major features held in common by each of these three populations. First was the tendency for there to be an almost complete annual turnover of individuals, a feature which is
typical of this species in population throughout its range (Watts and Aslin, 1981). While some individuals were known to survive into their second year in each population, most individuals were replaced on an annual basis. The turnover was less abrupt for females than for males because of the greater longevity of females and hence more overlap between generations. To illustrate this the annual turnover of the males and females at Kioloa is shown by a modified calendar of catches (Figure 2.5).

The second feature common to all three populations is the tendency for the number of females to reach approximately the same maximum each year. For example the maximum number at Kioloa was 9 females and was attained each autumn. In contrast the maximum number of males showed considerable variation although the differences between sexes in this regard was less noticeable at Lees Creek.

The third feature in common to all three populations is the overall decline in total populations size during the course of each study and may indicate that in each case animals were disturbed by regular trapping.

Generally, Mt Glorious and Lees Creek retained the highest and most similar numbers of animals. The study of the population at Kioloa began with numbers of animals in approximately the same order as the other two areas but experienced a steep decline by the end of the first year and a continued decline over the following two years. By the winter of 1978 the males had disappeared entirely from the population and the females reached an all-time low of two individuals. The following breeding season saw a marginal recovery in numbers of both males and females during 1979.

At Kioloa the pattern of replacement shown by the males during the population decline was not as consistent as that of the
females and there was a decay in replacement in the second year. The decay was complete by the winter of the third year by which time the males had become extinct. Subsequent renewal of the male component of the population occurred entirely through immigration the following year. In each spring previous to this, immigration had not occurred and probably reflected the lack of source populations outside the bounds of the study area.

Trapping surveys in all neighbouring habitats revealed that there was only one area which could serve as a source of immigrants to the study grid. This area was situated across a road, which may have served as an effective barrier to bush rat movements (Barnett et al. 1978). Trapping results indicated the presence of a relatively dense population of rats (30 individuals/ha) in the other area living among vegetation that had been undergoing post-fire regrowth for approximately two to three years. Only two of the individuals tagged there during survey trapping migrated across the road in the spring of 1978 and were able to establish themselves in the study area. As these were the only two males known to be alive during breeding on the grid, the juveniles of that breeding season were assumed to be sired by either of them.

Male and female bush rats showed a high degree of residency at Kioloa (Figure 2.6); a feature which is also common to other bush rat populations elsewhere (Wood, 1971; Robinson, 1976). Females, however, more likely to remain in an area for a longer period than males and this characteristic together with greater longevity contributed toward the greater stability of the female component of the population. A combination of high residency for both sexes and an annual replacement of individuals suggests that at any time of year (except autumn) there will be a relatively uniform size and age
structure in the population (i.e. see Figure 2.7), and that the same group of residents will be undergoing age-related behaviour and life history events somewhat synchronously.

In summary:

1. All three populations of R. fuscipes show an annual pattern of oscillations with a peak population in late summer and autumn as a result of the influx of a new cohort and a population low in mid-summer just before juveniles begin to emerge from the nests and become trappable.

7. All populations showed a decline in numbers during the period of study, a trend which is common to populations studied elsewhere (Robinson, 1976; Wanneke, 1971). Only the Kioloa population showed signs of increase in numbers at any stage during the study and this was a partial revival of a population which had virtually crashed during the third year.

3. There is a tendency in all populations for the numbers of individuals to reach, but not exceed a certain level each autumn.

4. The numbers of males in each population tend to fluctuate more than females and vary between years. This trend was more marked in the populations at Kioloa and Mt Glorious than at Lees Creek.

5. There is an annual turnover in animals which is almost complete for each population.
6. There is a high degree of residency in bush rats although females are more apt to remain in an area for a longer period than males. Males become nomadic in spring and summer.

7. The main difference between populations was in total numbers of individuals. Kioloa had the smallest population in terms of the total number of individuals known to be alive while Lees Creek had the highest.

8. The population at Kioloa was the only one to experience a dramatic decline in numbers that was marked by extinction of resident males and very low numbers of females.

9. Only the population at Kioloa showed a lack of immigration of adults in spring and summer. At Lees Creek and Mt Glorious there was a marked increase in influx of new males each year at this time.

2.3.1.2 Survivorship in Relation to Population Size

Adult, subadult and juvenile survival rates, along with the numbers of individuals in each of these age classes are shown separately for the three study areas in Figures 2.8a, b and c. The survival rates of the various age classes do not appear to be consistently related to their density although there are some indications of an inverse relationship between adult density and survival of immatures. This relationship could not be tested statistically because of low numbers and is therefore an unquantified
interpretation of the visible trends in these figures. A brief summary of these trends in each population follows.

At Kioloa, the numbers of adults and the minimum survival rate of subadults were, with one exception, not related (Figure 2.8a). The exception was in the autumn of 1977 when the female subadults showed a high survival rate at a time when there were no adult females in the population. If the adult females disappeared as a result of some environmental factor, then it is interesting that subadult survivorship was not affected in the same way. Instead, female subadults showed an increase in both number and survivorship at that time.

The survival rates of the sexes also differed at Kioloa. Adult females, but not males, survived well in winter each year. This trend was reversed for subadult males and females during the first two years.

The dense rat population at Mt Glorious had distinctly related patterns of adult and subadult survival (Figures 2.8c). Consistently, the minimum survival rate of female adults was lowest in autumn and was followed by an increase in the number of subadult females which survived. On the other hand, many adult males died or disappeared in autumn. Evidently, the survival rates of both males and females were lowest when the numbers were highest. For each sex and age class, the larger the numbers the higher the death rate.

The Lees Creek population was as dense as that of Mt Glorious and showed similar trends in survival (Figure 2.8b). In the more severe and seasonally variable environment at Lees Creek, the probability of subadult males surviving to become an adult in spring was low and the probability of surviving to the end of summer was very low. The female survival pattern did not show such a dramatic change
over this period. However, subadult females showed a higher winter survival than do adult females, while adults were more apt to survive in spring. These patterns of survival are similar to those found by Stewart (1979) in a nearby population.

In summary:
1. Survival is not apparently related to density.

2. It is hard to separate density-related survival from other causes because of the relative synchrony of the life-history of individuals of the same cohort.

3. There is some evidence of differential survival rates with respect to sexes and age classes in all populations.

4. Juveniles of both sexes experience low survival in late summer and early autumn and few became subadults. Of the female subadults that survived until the beginning of winter most generally survived through to spring as well. As adults, most of these females experienced a survival period in mid-summer followed by a second low in autumn. Any females that survive until their second winter were rarely found again in the following spring. Male adults showed their lowest survival in winter and again in mid-summer.

5. There is a stronger winter decline in males and females at Kioloa than either Mt Glorious or Lees Creek.
6. Differences between populations lie mainly in size of fluctuation in survival, especially when the Kioloa population reached minimum levels in 1978. The general trends for age classes and sexes are similar.

2.3.1.3 The Relationship Between Body Weight and Winter Survival and Breeding.

Male and female bush rats were divided into two weight classes: heavy and light. For females a prewinter weight above 115 g was considered to be 'heavy' while 'heavy' males were those greater than 120 g. Any animals with weight below this were considered to be 'light'. The number of males and females of each weight class which survived winter in all three study areas is shown in Table 2.1.

Only males and females living in the moderate climate of Mt Glorious showed a relationship between prewinter weight and winter survival. The heavier females were more likely to survive winter than were the lighter females (exact $X^2 = 6.84$, $P = 0.01$) and heavier males also had a higher probability of survival (exact $X^2 = 3.28$, $P = 0.35$). In contrast, bush rats living in the more seasonally variable climates at Lees Creek and Kioloa did not benefit in the same way from larger body weight. In addition, the Mt Glorious population had the highest population of adult animals surviving for two breeding seasons (Table 2.1), although most of these older individuals did not survive the third winter (Table 2.1). The death of these adults caused a major increase in the proportion of heavy animals that did not survive. Consequently, the real advantage of being heavier may have been masked by the inclusion of individuals from more than one cohort. While small body size and prewinter weight loss may be adaptive in a seasonally variable environment (Iverson and Turner, 1974; Stewart,
1979), the advantages of larger body size for animals living in the mild and reasonably stable environment of Mt Glorious was not known.

The population at Mt Glorious was unique in another sense. The heavier females at the start of winter were not only the best survivors but also the best breeders ($X^2 = 8.96 \ P < .005$). Pre-winter weight was not a good indicator of breeding success at Kiolea or Lees Creek, although they showed the same trend as Mt Glorious (Table 2.1). In both, most of the heavy animals bred (at Kiolea 6 out of 6 and at Lees Creek 7 out of 8). In addition, light females that survived winter had a lower probability of breeding. A light animal did not usually breed, however, until a minimum weight of 120 g was reached during the spring or summer. Unfortunately, the latency experienced by these breeding females, as a result of having lower body weights, could not be tested in the populations as their numbers were very small.

In all three populations, males assumed breeding condition before females. Males had descended testes in late winter and early spring while females did not become pregnant until late spring.

In summary, animals in the Mt Glorious population showed relationship between body weight and winter survival and survival to breed successfully. This was not evident in other populations.

2.3.1.4 Breeding Patterns

Some females did not breed during the breeding season in all three populations (Figure 2.9). At Lees Creek many of the non-breeder were adults by age but subadults by weight. At Mt Glorious, non-breeder occurred only in early spring months after which all members of the subadult weight class either disappeared or became adults. The remaining adult females, though few in number, all
bred during the breeding season.

At Kioloa, 5 of the 32 individual females known to be born on the grid during the study survived their first adult summer without breeding or attaining adult weight. None of these individuals survived to their second breeding season. On the other hand, all of the 39 males which survived to the breeding season had fully descended testes and were apparently reproductively active.

Juvenile bush rats usually first appeared in the trappable populations in mid-summer months in all populations, but this was not precisely synchronized within any one year so that young appeared over a period of 30 days or more. The date for the appearance of the first members of a new cohort also varied from year to year.

At Kioloa, young appeared in February in the first two years and in January in the last two years. Only in the 4th year was there any evidence of winter breeding when two young appeared in mid-July (winter). At Lees Creek, juveniles first became trappable in January of each year and there was no evidence of winter breeding. At Mt Glorious, young appeared in all seasons but a peak in emergence of juveniles occurred in early February in the first two years and late January in the third year.

2.3.2 Measures of Mobility and General Dispersion Patterns

2.3.2.1 The Reliability of Seasonal Centres of Activity

The reliability of the calculated centres of activity for males and females in different seasons can be related to sex differences in mobility and in general space use. The standard errors were determined for both the X and Y coordinates of the seasonal centre of activity for each individual. The mean standard errors for males and females for the same seasons were compared using a
Hann-Whitney U test. At Lees Creek and at Mt Glorious, males had greater standard errors than females, along both X and Y axes. That is, the centres of activity were less reliable for males than for females. This difference did not occur at Kioloa. A summary of the U-tests is provided below and a list of standard errors is given in Appendix 2.4.

<table>
<thead>
<tr>
<th></th>
<th>X Coordinate</th>
<th>Y Coordinate</th>
<th>n₁</th>
<th>n₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lees Creek</td>
<td>U = 20 p &lt; .025</td>
<td>U = 26 p &lt; .05</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Mt Glorious</td>
<td>U = 7 p &lt; .02</td>
<td>U = 6 p = 0.0</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Kioloa</td>
<td>U = 99</td>
<td>U = 67</td>
<td>13</td>
<td>13</td>
</tr>
</tbody>
</table>

While the reliability of the centre of activity indicates whether or not an individual is associated with a specific site habitat, the deviation or dispersion about the individual centre of activity indicates the size of the space used by that individual and provides indirect information regarding mobility. This measure of dispersion is not to be confused with Morisita’s index used later to describe the distribution of the entire population at Kioloa. The standard deviations about the mean are presented in scattergrams for males and females at all three study areas (Figure 2.10). The dispersion represented in this way was generally higher for males than for females, and this trend was most pronounced at Lees Creek.

At Kioloa, the females used more space in the second and third years and particularly during the winter of 1978. This
dispersion pattern coincided with a drop in population size. At all three areas there is some indication of seasonal variation in individual use. For example at Lees Creek, males appeared to occupy larger areas in spring and summer when compared to autumn and winter. Females were more consistent in the amount of space occupied throughout the year at both Lees Creek and Mt Glorious.

2.3.2.2 Home Ranges

A complete series of diagrams of home ranges in three study areas appears in Figure 2.11. The pattern is similar for all three study areas regardless of population size and climate. The characteristic features of male and female home ranges for each season is summarised in the table below.

<table>
<thead>
<tr>
<th></th>
<th>Comparison of Overlap of Home Ranges</th>
<th>Home Range Size</th>
<th>Spatial Pattern of Home Ranges</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M vs F</td>
<td>Ad vs Imm</td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>M &gt;&gt; F</td>
<td>-</td>
<td>F: ranges discrete and in similar locations as in winter. M: nomadic</td>
</tr>
<tr>
<td></td>
<td>F: little overlap</td>
<td>M &gt; F</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M: reestablish ranges</td>
</tr>
<tr>
<td>Summer</td>
<td>M &gt; F</td>
<td>increased overlap for M &amp; F</td>
<td>larger for both M &amp; F (M &gt; F)</td>
</tr>
<tr>
<td></td>
<td>M overlap with F</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn</td>
<td>M &gt; F</td>
<td>some overlap M = F</td>
<td>M: smaller F: unchanged (M=F)</td>
</tr>
<tr>
<td>Winter</td>
<td>M &gt; F</td>
<td>much overlap M = F</td>
<td>M = F smaller for both</td>
</tr>
</tbody>
</table>

Ranges for males were large in spring and summer and contracted in winter. Female ranges were less seasonally variable.
Home range overlap was more common among adult males than females. An important trend that emerged earlier is confirmed here, that is, the tendency toward cohesion in the population in winter. There was an increase in overlap of adult and subadult ranges in winter as well as a reduction in the size of adult home range.

2.3.2.3 Movements

Comparison of movements in the different populations was not possible since the spacing between trap sites was not the same. The seasonal trends within each study can, however, be compared.

The average movement made by an individual rat during a single trap session is referred to here as AVM. A mean AVM was determined for each sex and for each season. A summary is given in Table 2.2 for male and female movements at Kioloa and Lees Creek. The same information for the Mt Glorious population is given by Wood (1967). A comparison of movements made by males and females indicates that there is no sex-related difference at either Kioloa or Lees Creek but a large difference in the movements of males and females at Mt Glorious. The results of the Mann-Whitney U test for each population are given below:

<table>
<thead>
<tr>
<th></th>
<th>U</th>
<th>n₁</th>
<th>n₂</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Kioloa</td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>n.s.</td>
</tr>
<tr>
<td>Lees Creek</td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>n.s.</td>
</tr>
<tr>
<td>Mt Glorious</td>
<td>2</td>
<td>5</td>
<td>5</td>
<td>P = 0.016</td>
</tr>
</tbody>
</table>
Variation in movements between breeding (spring and summer) and non-breeding season (autumn and winter) was also considered for each sex. Female movements showed little variation between seasons at Kioola and Mt Glorious. At Lees Creek, however, movements of females were smaller in the non-breeding season ($t = 5.05$, $df = 5334$ $P < 0.001$). Male movements were similar in all three study areas and were consistently greater in the breeding season. The $t$-test results are shown below:

<table>
<thead>
<tr>
<th>Location</th>
<th>$t$</th>
<th>$df$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kioola</td>
<td>13.36</td>
<td>207</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Lees Creek</td>
<td>5.15</td>
<td>3008</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Mt Glorious</td>
<td>3.36</td>
<td>188</td>
<td>$&lt; 0.05$</td>
</tr>
</tbody>
</table>

2.3.2.4 Distance to Conspecific Neighbours

Distances between the centres of activity of each possible pair of individuals (all individuals were paired against each other) were compared between sexes and seasons. Distances were calculated between pairs of males (M-M), pairs of females (F-F) and between males and females (M-F). A frequency distribution of distances maintained by each class of individuals was determined for each season and for all seasons combined. A comparison of these distributions made use of the $X^2$ homogeneity test (Table 2.4) and thus established whether there was or was not a difference between distributions but did not establish the direction of the differences that existed.
The distribution of distances combined for all seasons, between males (M-M) differed from that of females (F-F), both at Mt Glorious (P < 0.001) and at Kio-loa (P = 0.05). Similarly, the distance maintained between males and females (M-F) at Mt Glorious differed from those maintained by either males or females (P < 0.001). At Kio-loa, however, the distribution distances maintained between males and females was similar to that maintained by females but differed from that of males (P < 0.01).

The comparison of the distribution of inter-animal distances between seasons can be summarised as follows: none of the study areas showed a change in inter-female distances between seasons; inter-male distances varied between seasons at all three areas; and distances between males and females varied at Kio-loa and Mt Glorious. While inter-male distances were variable, inter-female distances remained constant.

Plots of the mean distances to the first five nearest neighbours for males and females of two age classes are given in Figure 2.12. In the Kio-loa population (Figure 2.12a) there was a marked increase in distances during the period of population decline 1978-1979. A feature common to both the Kio-loa and Mt Glorious (Figure 2.12c) populations was a trend toward increased adult neighbour distance in spring and a shortening of the distances in autumn and winter. This pattern was not as clear at Lees Creek (Figure 2.12b). No distinction was made in this analysis between the 'type' of neighbours, so that the five nearest neighbours to an individual in any season could be of either sex or any age class.
2.3.2.5 Seasonal Social Structure Based on Neighbour Types

For the first five levels of neighbourliness the frequencies with which males and females of two age classes were associated were determined. The likelihood of these associations was tested by an \( X^2 \) statistic. Positive and negative deviations from expected frequencies helped to determine positive and negative associations between neighbour 'types' (Appendix 2.3). Some of the more significant associations are summarised below for each study area and the details of seasonal changes in bush rat associations are represented by sociograms (Koepli et al., 1979) (Figure 2.17).

Kioloa

The seasonal trends for four years were similar so that frequencies and expected values could be combined to provide larger sample sizes in each class and thus to generate a single seasonal profile of associations. As a result the sociograms presented here (Figure 2.13a) are an indication of average associations and are probably conservative. In spring there were associations between different age classes and sexes. While male adults associated with female adults, the relationship was not reciprocal. Immature males also associated with female adults, but not with male adults. Immature females showed no strong associations of any kind and female adults were negatively associated with each other.

In winter there was a consistent tendency for positive association between females of different age classes. Male immatures also associated with both classes of females, and male adults associated with members of their own age class but not with other age classes.
In both summer and autumn male immatures had few consistent neighbour relationships with other males but may be associated with female immatures in autumn. The latter tended to associate with adult females while adult females tended to show weak or negative associations with all groups. Again, female adults were the most consistent in all seasons.

Lees Creek

The association between different categories of neighbours changed considerably with season (Figures 2.13c, d). There were well-defined associations in winter, spring and autumn. In winter of both years there were positive associations within sexes due mainly to neighbourliness of adults and subadults of the same sex while members of the same age class disassociated. Interestingly, there was no association between sexes; males and females were separated.

In the spring, there was a positive association between adult males and a negative association between males and females. The associations within females varied over the different levels of neighbourliness (Appendix 2.3). This was due mainly to changes in the degree of adult-subadult overlap. There was, however, little or no association among adult females in springtime.

In the autumn, there was a strong relationship between male adults and female immatures and between female adults and male or female immatures. Female adults however, did not associate with each other.

The sociograms (Figure 2.13) show some of these trends as well as some of the anomalies between years. Only the degree of association within females and between female adults and others remained consistent. Female adults tended to disassociate or at
least, not associate throughout all seasons. They were found near immatures in autumn and winter and had a particularly strong tendency to overlap with subadult females in winter. This tendency for females to disassociate in all seasons is typical of all three populations.

Mt Glorious

The observations taken from Wood (1967) cover one sequence of four seasons and thus cover associations within one cohort between late 1963 and early 1965. As for the other study areas, spring and winter at Mt Glorious showed an association between some sex-age groups (Figure 2.13b). In the spring, male adults associated with other male adults but departed from immature males. The association of females with male adults was positive but male adults did not associate with females. Again, adult females showed a weak or negative association with each other.

The winter associations were reminiscent of the trends in the Lees Creek population. There was a negative association between males and females and a strong tendency for female subadult-adult association. Adult females were not close neighbours.

In autumn the relations between the four possible types of neighbours were weak and variable. The trend, however, was for adult males to freely associate with all types of neighbours whereas adult females consistently disassociated with other adult females. This adult disassociation continued through autumn, although there was a general trend for adults and subadults of the same sex to be close neighbours.
2.3.2.6 Summary of Measures of Spacing, and Social Relationships

A summary of the five measures of bush rat spacing described above and one measure of social relationship among bush rats based on nearest neighbours is given in point form below.

1. Measures of dispersion using the standard deviation of the centre of activity:
   
   (a) males were much more dispersed than females.
   
   (b) females showed less seasonal variation in the degree of dispersion than do males.
   
   (c) both males and females became more dispersed as the population at Kiolea declined.

2. Seasonal home ranges:
   
   (a) there was a marked change to winter cohesion in home ranges of both males and females.
   
   (b) there was an increase in sub-adult/adult overlap of ranges in winter but no increase in overlap among female adults.
   
   (c) male home ranges increased in spring and summer
   
   (d) male home ranges contracted in winter
   
   (e) the size of female adult home ranges did not vary seasonally.
   
   (f) female adult home ranges were generally discrete and non-overlapping.
   
   (g) male home ranges generally showed some overlap with ranges of females and other males.
   
   (h) subadult males and females form home ranges by the
end of autumn.

3. Average movements:
   (a) there is no difference in the average movements made by males and females at Kioloa or Lees Creek, but a strong difference at Mt Glorious ($M > F$).
   (b) female movements did not vary seasonally at Kioloa or Mt Glorious but the movements of females were smaller in the non-breeding season at Lees Creek.
   (c) In all study areas the average movement of males was greatest in breeding season.

4. Distance between all neighbours:
   (a) the distribution of distances between males differed from that of females at Mt Glorious and Kioloa.
   (b) the distribution of distances maintained between individuals of the same sex differed from that maintained by males in relation to females at Mt Glorious. At Kioloa the distance maintained by males in relation to females was similar to the distribution of distances maintained between females.
   (c) the distribution of distances between females did not vary seasonally.
   (d) the distribution of distance between males and between females varied seasonally in all populations.

5. Distance to the five nearest neighbours:
(a) there was a marked increase in distance between neighbours at Kioloa as the population declined in the second and third years.

(b) there was an increase in distances between adult neighbours in spring at Kioloa and Mt Glorious.

(c) there was a decrease of adult neighbour distances in autumn and winter at Kioloa and Mt Glorious but not at Lees Creek.

6. Animal associations using sociograms based on the type of nearest-neighbour:

(a) In spring male adults positively associated with female adults but not the converse. Male immatures positively associated with female adults and male adults. Female immatures showed highly variable associations while female adults retained neutral associations with others of their kind.

(b) In summer and autumn, associations and disassociations were similar. Immature males strongly associated with adult females and immature females (in autumn), but not necessarily with adult males. Female adults dis-associated or remained spaced out so that they did not appear to associate with each other.

(c) In winter female adults and immatures associated with each other but adult females disassociated with other adult females.

(d) In general the most consistent find between study areas and seasons was the tendency for adult females to
disassociate with each or at least they never associated positively with each other.

2.3.3 Kioloa Population - Changes in Abundance and Dispersion

2.3.3.1 General Description of the Changes in the Population

In the autumn of 1976 a total of 29 bush rats were captured on a grid of 0.3 ha (a density of 96.7 rats/ha) situated at the northern end of the Kioloa study area. This was the highest density recorded during the four year study. By the end of autumn of 1977 it had fallen by 73% to 243 rats/ha when 17 animals were trapped in 0.7 hectares. The values declined by a further 64% during the next year to 8.7 rats/ha when a total 13 animals were trapped in 1.5 hectares. In the fourth year (1979), however, numbers had increased again to reach a density of 11.3 rats/ha when 17 animals were trapped in 1.5 hectares. These changes in density reflect both a dramatic drop in the total size of the population and a gradual change in the distribution of animals each year of the study (Figure 2.14). As the total number of animals in the population and the area used by each individual rat increased so that the population became more dispersed and more difficult to locate.

To cope with this changing rat distribution, the trapping grid was progressively enlarged to encompass more of the peripheral traps. By the end of 1977, the regularly trapped area had increased by seven-fold. Periodic tracking and trapping surveys were used over the entire 3.4 ha in order to monitor any changes in distribution, but unmarked animals were seldom discovered. It seemed that the animals caught and marked comprised the total population living in the study area. Both at its maximum size of 29 animals in the first year and a
its nadir of 2 animals in the third year, the trapped population represented the total inhabitants of the area.

This large increase in trap effort was profitable in that it enabled a study of a decline in a population of *R. fuscipes* and how this was related to changes in local resource levels and distribution.

The bush rats at Kioloa experienced changes in their distribution which were both long-term (over the 4 year study) and short-term (seasonally) and which were related to gradual change and seasonal cycles in the distribution of resources including food and shelter, respectively. Throughout the study, the distribution of rats was patchy and began (March 1976) by being concentrated at the north end of the study area in a mature stand of spotted gum with a dense cycad and fern undergrowth; later (end of 1977) rats were trapped in the southern end of the study area, where the vegetation that had been dug up and burnt three years earlier was undergoing rapid and dense regrowth. Six trap sites continued to catch rats throughout the duration of the study. These sites were situated in the central part of the study area where dense cycad growth mixed with banksia, eucalypt, sword grass and various tree and shrub species undergoing regrowth and thus resulted in a dense and layered vegetation.

The changes in distribution and the location of the most productive trap sites are shown for each year in Figure 2.14. The details on the various floristic zones in the study area are shown in Figure 2.15 and explained in detail in Section 2.3.3.2.

The dispersion pattern of the bush rats has already been described with respect to the position and type of other individuals and has been compared with the patterns observed in two other populations (Section 2.3.2.6).
Information from Kioloa was also analysed using Morista’s index of dispersion and showed that the population was generally clumped (Figure 2.16); that is, some traps are more regularly visited by rats than others. The values given for this index are far higher than those that might normally be expected and the extreme variability of the index in this case makes it very difficult to interpret. A modified index of dispersion (Figure 2.14a) however, indicated that traps at certain locations regularly caught more than one individual and that the multiple use of these sites by rats varied with season. Clumping measured in this way was consistently a winter (in June and July) phenomenon where as clumping only occasionally occurred in spring (in September and October), a season during which there were substantial changes in patterns of space use by adult males (Section 2.3.2.3).

The seasonal trend in clumping was largely the result of changes in associations among females. A comparison showed that females were significantly seasonal in their multiple use of traps \( (X^2 = 27.00 \ P < .001) \) whereas males were not \( (X^2 = 7.07 \ P > .05) \). Females overlapped more in autumn and winter and were less likely to overlap in spring and summer (Table 2.4). This change in distribution of females corresponds to the autumn and winter associations between adult females and subadult females described in Section 2.3.2.5 by using sociograms. During that same period adult females continued to disassociate.

2.3.3.2 Changes in Vegetation

During the four years of trapping at Kioloa the vegetation in the southern end of the study area underwent marked changes in terms of the degree of dense undergrowth that was available. By the
end of the study a floristic analysis of the entire area showed that there were six different vegetation types and four major vegetation zones that could be easily defined. The mean index of floristic similarity ($E_1$) for the 69 sample sites was 0.24 (SD = 12, n = 2211) and this confirmed the observation that the distribution of plant species was patchy and the study area was highly heterogeneous. A low mean index value indicated a non-uniform vegetation and a high standard deviation indicated a patchy distribution of the species (Grant and Morris, 1971).

The floristic units which could be separated are described in a two way table (Table 2.5), in which sample quadrat and plant species are grouped according to their similarity. Information on plant associations common in coastal vegetation was taken from Beadle et al. (1972) and Ingerson (1976) and used to establish otherwise arbitrary boundaries between the floristic groups. The species of plants were grouped into categories indicated by numbers 1 to 6 while the letters A to D were used to indicate spatial vegetation zones based on the vegetation found in each sample quadrat.

Plant species in categories 1, 2 and 3 were characteristic of quadrats grouped under B and C. These species were weeds, herbs, grasses or creepers and were typically found in recently disturbed or burnt areas. The sites in area B had been regularly control-burned and area C largely consisted of sites which border the old public access path through the area. Species of categories 5 and 6 were ubiquitous and may represent elements of the pristine situation. In particular category 5 contained some opportunistic species (such as cycada) which typically take advantage of natural regular firing or disturbance, while category 6 is indicative of associations in a secondary or senescing forest where the canopy is high and even. The
species in category 8 thrive on well-drained sandy soils and are rarely found in the wetter soils at areas B and C. In contrast, plants in category 7 do well in moist soils and represent a native association common to areas B and C. The quadrats which fall into Areas A and D are the least disturbed and may differ slightly from each other because of age or soil moisture. The level of detail and number of quadrats sampled are insufficient to distinguish fine differences between some groups. Plant categories 2, 6, 7 and 8 were essentially transition zones between more distinct plant associations.

In summary, the study area can be described as a floristic mosaic (Figure 2.15) of variously aged natural patches of vegetation and vegetation that has experienced disturbance. This is illustrated by photographs of each of the major types of vegetation contained in Plates 2.2, 2.3, 2.4, 2.5.

A comparison of Figure 2.14 and Figure 2.5 shows that, at the beginning of the study bush rats were most frequently caught in the mature forest zones with native vegetation dominated by cycad plants (Areas A and D) at the beginning of the study. The cycads provided dense cover and seasonal food resource (Section 2.3.3.4) not found in the southern end of the study area at that time. By 1978 vegetation areas A and B in the southern end of the study, consisting of native plant associations on most soils with three-year old regrowth of shrubs and trees, area were harbouring most of the resident population. Most of the resident rats continued to live in this area until the end of the study in 1980. The least consistent trap success was in areas with ephemeral or weedy species such as areas with plant categories 1, 2 and 3. This information confirms earlier statements that R. fuscipes is a habitat specialist.
(Braithwaite et al. 1978, Fox 1980) and requires dense undergrowth preferably where conditions are moist.

2.3.3.3 The Effect of Other Mammals on Bush Rat Distribution

In this study of the spacing between conspecifics it is important to consider the possibility that some of the measures of spacing are confounded by the effects of interaction with other species of small mammals.

At Kioloa there were four species of ground dwelling small mammals, in addition to R. fuscipes. There were two species of antechinus, stuartii (A. st.) and A. swainsonii (A. sw) as well as two other murid rodents, R. rattus (R. r) and Mus musculus (M. m), both of which are introduced. All five occurred in suitable patches of habitat throughout the study area. The appearance of R. rattus and M. musculus was however, infrequent and spatially scattered. Consequently, they have not been considered as important in this study and have not been included in the analysis of species associations. The spatial distribution of captures for all species and the degree of spatial overlap between species is shown in Figure 2.17a, while their relative abundance is shown in Figure 2.17b. A large proportion of the study area revealed some species overlap but sites were rarely used by as many as four or all of the small mammals present.

Rattus fuscipes is the dominant species in terms of numbers, in the community, although A. stuartii and A. swainsonii were also resident throughout the study. The numbers known to be alive for each of these species were not inversely correlated as would be expected if these were competing species (MacArthur, 1972; Grant, 1972). The partial correlation coefficients for numbers known to be alive were as
follows: for R. fuscipes with A. swainsonii, $r = -0.2173$; for R. fuscipes with A. stuartii, $r = +0.266$; and A. swainsonii with A. stuartii, $r = +0.176$; $P < 0.05$ in each case. In the absence of an inverse numerical association, the oscillations in bush rat numbers at Kioloa cannot be explained by interspecific competition. The numbers of all resident species tended to rise and fall somewhat synchronously which indicated a common response to seasons and a similar timing of life history events.

A comparison of the degree of overlap between species and within species at each trap site indicates that conspecifics of any species are more likely to overlap than any other during a three-day trap session; there were only 77 interspecific overlaps as opposed to 153 intraspecific overlaps. This discrepancy may indicate one of three things: that each species chose slightly different microhabitat, that the individuals were attracted to traps containing the odour of conspecifics which had been caught the night before or that the individuals were repelled by the odour of the other species and were therefore not caught in the same trap. The number of each type of species overlap is given below:
At a coarse level of analysis of spatial separation of species, using an index of vegetation cover (see M'Closkey and Fieldwick, 1976) it is evident that all three species show a marked preference for the same type of habitat (Table 2.6). This means that trapping and tracking sites surrounded by vegetation which has an index of cover around 2.5 (intermediate between a value of 1 which is most dense and 5 which is least dense) will be suitable for either species. The results from both trapping and tracking reveal similar cover selection at Kioloa.

Finer levels of overlap and separation may, however, be indicated by use of Coles' index of association (Coles, 1957). The results show that while species may choose the same habitat-type they may not associate within a given patch of that habitat. Part of this analysis for Kioloa is shown in Table 2.7 and involves a test of the effect of the presence of a third species on the spatial association between the remaining two species. Information from Lees Creek, is included for comparison.
From trapping results there is no evidence of spatial association between any pair of species. The possibility of any association is unaffected by the presence of the third species both at Kioleta and at Lees Creek. There is, however, a significantly high level of association between all three species shown by the tracking data at Kioleta. In particular, these results show that when bush rats are present, the two dasyurids are less negatively associated. That is, the three species are more likely to overlap altogether than are the two Antechinus. However, the low frequency with which the overlaps occur at Kioleta prevents further interpretation of these results (Dickman and Woodside, 1982).

The presence of other mammal species in the habitat used by R. fuscipes, is therefore of little consequence. There is no evidence that the distribution or behaviour of this species is affected by the presence of any other.

2.3.3.4 The Use of Resources

Burrows, Soils and Runways

The bush rats of the Kioleta area used three different types of burrows and homesites. The type of homesite used varied with season. For example animals were found to live in hollow logs (Plate 2.6a) or in shallow burrows under the litter, during the spring and summer. These homesites were particularly difficult to find as the entrances were often blocked with leaves or other debris. By using radio transmitters, some individuals were followed to these burrows.

In the autumn, digging activity became very noticeable as burrow entrances, marked by round holes and mounds of dirt, occurred virtually anywhere. The entrances appeared at the base of cycads,
trees or logs or in the face of sandy mounds covered with grassy growth (Plate 2.6b). The entrances were generally very tidy and often surrounded by a scattering of seeds, eucalypt buds, or pieces of plant stems and leaves (Plate 2.7a). One of the most common items was cycad seeds collected from ripened cycad cones (Plate 2.7b) and carried to the burrow. Burrows constructed in autumn and winter were either simple or complex. Simple burrows were most common and had one or two entrances, contained a couple of small chambers and were usually occupied by a single tenant. Plaster casts of two of these simple burrows are shown in Plate 2.8. In contrast, complex burrow systems were not common; only six were located in the study area, although several others were found during survey trapping elsewhere. A large number of entrances (up to 13) were found to connect to a network of chambers and tunnels (Figure 2.18). The tunnels had minor slopes and the chambers were parallel to the soil surface. The maximum depth attained by these burrows was 50 cm from the ground surface. The regular use of some entrances was monitored by tracking, trapping and sets of infrared light beams and photoreceptors. The results indicated that several of the entrances were regularly used and maintained by more than one individual. Multiple use was confirmed by trapping. In two cases, this included one female adult, one male adult and one female subadult as well as juveniles born during the autumn. In two other cases, burrows were shared by a female adult and two subadult females. A third burrow contained a mixture of 4 male and female subadults and one adult female. Adult females were never found together.

Previously, *R. fusipes assimilis* has been described as constructing only shallow burrows (Warneke, 1971), but has also been considered not to burrow (Robinson, 1976). This study suggests that
burrowing is a common and seasonal event at Kioloa. Burrows were also noted at Lees Creek (C.R. Dickman, personal communication). The communal burrows systems found in this study were similar to those described only once before, for a different subspecies, *Rattus fuscipes grevi* on Kangaroo Island (Wheeler, 1970).

The distribution of burrows did not appear to be related to soil characteristics such as soil moisture or soil structure. The structure of the soil was clearly correlated with soil moisture (Table 2.8). Humus content was positively correlated with moisture levels \( F = 8.74 \) \( P < 0.25 \) as was the presence of fine soil particles \( F = 4.59 \) \( P < 0.05 \), while the more granular soils had a lower moisture content, but neither soil moisture nor soil structure was sufficient for determining the presence or absence of burrows. A map of soil moisture and burrow locations is provided in Figure 2.19. The majority of burrows were, however, found in the vegetation zones described as A and D (Section 2.3.3.2). The associations of native plants were least disturbed and included some species (plant category 7) which favour slightly moister soils.

In winter, burrows were often marked by two or three radiating runways (this contrasts with descriptions given by Warneke, 1971) made obvious by the flattened vegetation or litter, depression in bare soil and foot prints in loose soil near the burrow. Runways were particularly distinct in tall grass or among dense stands of sword grass (*Cahnia clarkei*). It was difficult to determine the full length of any runway or its end point and it is therefore impossible to state whether runways served as direct links between burrows and food resources. This would be most likely when food resources were predictably clumped as suggested by Braithwaite and Lee (1978) in their description of space and resources by *Rattus lutreolus*. 
In order to ascertain whether or not runways were a seasonal phenomenon or just seasonally more apparent, animals were systematically released near or away from points thought to be part of their marked path. The pathways were determined on the first day of each trapping session by tracing each rat's movements upon release at the point of capture. It soon became apparent that animals released away from runways, would go through the same behavioural sequence, freeze their stance, flick their tail, hop in several different directions around a small area and then suddenly run, presumably after locating a pathway. In contrast, animals released directly on the path ran immediately.

Only in late autumn and winter were runways clear enough to be recorded without first observing the movements of an animal released from a trap. During spring and summer runways were indistinct and animals that were followed would run along logs, up tree trunks and even along tree branches up to one metre above ground. These pathways, although complex and convoluted, were used repeatedly.

In addition to *R. fuscipes* both dasyurids (*A. stuartii* and *A. swainsonii*) used these runways on some occasions although *A. swainsonii* was far more regular in this use than *A. stuartii*.

The use of runways by other species and the frequency of use of certain runways by *R. fuscipes* was determined using the light beams and smoked tracking sheets described earlier. This method was only applied in winter when runways were obvious. Light beams were placed off and on runways, but no animals passed through the beams away from clear runways. Some runways were used more than others with one runway on one occasion accounting for 93% of the beam interceptions (representing a total of 84 animal passes). The most frequent user was always *R. fuscipes*, although *A. swainsonii* and *A. stuartii* foot
prints were found on the smoked sheets or runways on 9 out of 11 trials.

Seasonal Diet and Seed Caching

In addition to digging burrows, the bush rat also dug to bury seeds, to uncover previously cached seeds and to search for fungi. This behaviour occurred between late autumn to the end of winter. *R. fuscipes* has not previously been known to cache-food stuffs, nor to attend to these caches at a later date, but caches of fresh and aged cycad seeds were found each year in this study (Plates 2.9a and b) and rats were sometimes observed to transport seeds from cycads to a nearby cache.

Caches which were created in autumn when the seeds of the cycads ripened, were either visited regularly thereafter or completely neglected. There were no instances where all seeds in a cache were consumed by the end of winter. Occasionally, a large number of eucalypt buds and capsules were found hidden in the same manner and many of these also remained undisturbed through the winter. Any gnawing or disturbances of the caches by brushtail possums was easily recognised; claw marks or tooth imprints left on the seeds, and smoked tracking sheets were used to verify frequent visits by bush rats.

Tracking sheets also revealed that, during fall and winter, *Rattus fuscipes* dug small shallow pockets in the soil surface, presumably in search of fungi. Shredded pieces of mushrooms, other fungi and small twigs were often found scattered at the lip of the hole. The location of these holes was correlated with soil moisture (moist soils) and were particularly frequent in areas where there was sword grass, rotting logs or friable soil around the base of trees,
all of which were found in vegetation types A and D (Figure 2.15 and Section 2.3.3.2).

Both cycad and fungi featured strongly in the winter diet of *Rattus fuscipes* at Kiooa. The occurrence of these and other food items, as determined by faecal analysis, is shown in Figure 2.20, and an estimate of importance of each item is given as percentage volume (see also Appendix 2.5). As commonly found for this species (Watts and Braithwaite, 1978), the diet was that of a general omnivore, showing strong seasonal shifts in the dominant food items. Whether these changes reflected seasonal availability, the ease with which the food item was obtained, seasonal preference or nutritional demands, is not known.

In addition to cycad seeds, flowers, seeds and stems were important dietary components. These were generally taken in spring and summer when consumption of cycads and fungi was low. During the same period, insects were also eaten. They may be, however, overrepresented in the dietary analysis because of their indigestible exoskeleton. The higher incidence of insects in summer coincided with higher insect activity which supports previous statements regarding the bush rats' varied and opportunistic diet (Watts and Braithwaite, 1978; Watts and Aslin, 1981).

Cycads as Food

The consumption of cycads is both interesting and significant. There are four reasons for this: (i) the use of cycad seeds by bush rats has not been reported before, (ii) it is a dominant food item in autumn and winter, (iii) there are seasonal changes in behaviour related to this food resource, particularly that of seed caching, and (iv) it is highly toxic and acts as an acute toxin, a
neurotoxin and a cumulative carcinogen (Hirono, 1972; Kirkland, 1972; Zedeck et al., 1972); it is also a powerful chromosome breaker (Whitty, Spatz and Matsumoto, 1966). Moreover, the toxic actions are most marked if the seed is ingested and the toxin exposed as a result of enzymatic action (Druckrey and Lange, 1972). A single dose is sufficient to induce tumors in six different tissues (Hirono, Laquer and Spatz, 1968). On the other hands, cycad seeds are potentially a good source of food. The outer husk, which is also toxic (Yang and Mickelsen, 1968) is sweet and has a high sugar content. The composition of the endosperm has been calculated as 48% H2O; 0.7% fat; 11.5% protein, 28.4% starch; 3.8% sugar, 6.6% cellulose and some ash (J. Beaton, personal communication: analysed by Australian Government Analyst, ACT in 1973).

At Kioloa, cycads, along with fungi and some stem and leaf tissue, constituted the main food of Rattus fuscipes throughout the winter at a time when food resources are supposedly limited (Warneke, 1971).

There was no evidence that cycad consumption affected the survival of bush rats at Kioloa and no effects were found on the reproductive fitness of females which were known to eat cycads during the winter before breeding. Further evidence of the tolerance to the toxic food was gained from field and laboratory feeding trials in which short and long-term effects were investigated (Woodside and Monahan, in preparation). In both the field and the laboratory, animals from Kioloa readily consumed husks and endosperm, sometimes in preference to other foods presented at the same time (Woodside and Watts, in preparation).
Summary

In summary, the way in which *R. fuscipes* uses its resources (food, shelter and space) generally changes with season, is generally opportunistic and involves some manipulative behaviour on the part of each individual. This behaviour includes the storing of seeds and fruit in caches, the digging of burrows and the development and use of runways.

The use of food resources is seasonal and opportunistic in that rats will eat a wide variety of food items but show a seasonal trends in the type of food most frequently taken. Food such as fungi and cycads are taken in autumn and winter and both resources are clumped. Fungi is associated with moist soils and cycads with a specific vegetation type; cycad seeds are collected and cached away. During this season animal distribution is also clumped (Section 2.3.3.1) and simple or complex burrow systems are developed and shared. Burrows are not necessarily located in moist soils where fungi is found, but they do occur most frequently in vegetation containing cycads and other native plants such as *Gahnia*, a seed producer. Runways which become more apparent in winter may represent frequently used pathways between shelter and clumped food resources although this cannot be substantiated at present. Runways exist but are less apparent when the population is more dispersed in other seasons.

2.4 DISCUSSION

Even though the three bush rat populations described in this chapter differed widely with respect to certain attributes such as the
habitat and climate, and average density, they showed similar
demographic trends and differed only in the magnitude of these.
Similarly, many aspects of the social structure, spacing patterns and
seasonal changes of the spatial associations of certain categories of
individuals were common to all three populations. The similarities
probably reflected intrinsic characteristics of the species, while the
differences between populations emphasized the effects of local
environmental conditions on demography and distribution. Changes in
the social spacing between seasons and differences between populations
also reflected the range of responses of spacing behaviour that could
be expected to occur naturally. In order to understand what
conditions are most important in influencing R. fuscipes in general,
it is, therefore, important to consider both the similarities and
differences of widely spread populations as well as consider temporal
changes within each population. These points will be dealt with
below.

Comparative Demography and Use of Resources

In general trends in abundance in populations of R.
fuscipes are predictable from year to year. While the number of
trappeable individuals appears to decline over the period of study for
all populations examined so far (Wood, 1971; Warneke, 1971; Freeland,
1972; Robinson, 1976; Press, 1979 and this study), there is a late
summer and autumn peak in numbers which is approximately the same each
year. This peak results from the number of offspring successfully
reared by resident adults and modified to some extent as a result of
migration in and out of the study area combined with the number of
surviving resident adults. These predictable yearly peaks may be
related to the seasonal carrying capacity of the area and particularly
limited by the carry capacity in winter (Robinson, 1976). This idea has not been adequately tested but may help to explain why populations from the subtropics (Mt Glorious), temperate zone (Lees Creek) and south-coastal inlands (Robinson, 1976) reached a certain size each year and rarely grew beyond that. Most of the fluctuations in animal numbers that occur within the annual cycle are primarily as a result of changes in numbers of males which experience periodic low in survival and season peaks due to immigration while the female experience less dramatic drops in survival and very low immigration rates and thus tend to remain fairly constant throughout most of the year (Wood, 1971; Robinson, 1976 and this study).

All populations of R. fuscipes showed an almost complete annual turnover of both sexes and the events that occur during the year show similar timing throughout the entire range of this species. An increase in numbers trapped occurs only twice for each cohort and represent the summer influx of juvenile animals of both sexes and the spring immigration of adult males prior to breeding. The exact timing and duration of these events varies only slightly from across the range of the species. Breeding for example, can be up to two months earlier in Queensland (Mt Glorious) than at Lees Creek and last for two months longer under the mild subtropical climatic conditions. The populations peaks however, occur around the same time. The populations decline during winter, experience a new influx of males in spring and decline again in summer to reach an annual low in mid-summer just before the influx of young. Summer is therefore the time of greatest population oscillations.

As long as the number of adult females entering the breeding season is the same each year, so also is the number of juveniles recruited (Robinson, 1976; this study). This suggests that the size
of the new cohort may be the consequence of events that occurred before breeding and not necessarily a reflection of the conditions current during mating, lactation and weaning. Robinson (1976) went so far as to suggest that animals (presumably females) that successfully established a home range prior to winter will be more apt to survive until spring for breeding. The process of establishing residency for subadults in autumn will therefore be a major influence on the size of the breeding populations. Consequently, autumn and winter become critical seasons in the interpretation of demographic trends.

The idea that winter survival of bush rats is related to the availability of food in that season was tested by Wheeler (1970) who supplemented the food of a bush rat population throughout winter. He found that he could increase the survival of males but not females in that season. If, as Robinson (1976) suggests, females have already established themselves before winter, then they may have already secured sufficient resources to see them through that period. Males, however, are less site tenacious (Wood, 1971; Robinson, 1976; this study) and may benefit from supplemental food during their foraging forays. This would result in an increase in male but not female survivorship over winter.

Each spring males showed a sharp increase in numbers at Mt Glorious, Lees Creek and at localities in southern Victoria (Robinson, 1976), but not at Kioloa. Most of these new males are transient, and this is a prominent characteristic of males during the spring mating period. Females generally remained resident and numbers were constant over this period. At Kioloa both males and females experienced low winter survival in 1977 (Figs 2.4 and 2.8a) and male immigration was restricted to one individual during that spring (Figure 2.5), the combination of which may have been enough to caused the decline in the
size of subsequent cohorts.

It is possible that the low survival of animals in the winters of 1977 and 1978 is a reflection of the harsh conditions. Autumn rains were low in 1977 and may have resulted in poor prewinter plant growth and poor resources over winter. While female survival may not be improved by augmenting winter food under normal conditions, it may be affected by the decline in resources under more harsh conditions. Poor winter rain in both 1977 and 1978 were probably responsible for drier soils and less fungi, a major part of their winter diet (Section 2.3.3.4). Low rainfalls in spring and summer of those years may have affected lactation and subsequent survival of young in summer. While the appearance of juvenile rats was spread over a period of 30 or more days in most years, it was restricted to a short period in January of 1978 (Figure 2.7). The survivorship of these young was particularly low and of the males known to be born in the study area that year, none survived the following winter. Prewinter rainfall of 1978 was higher than in 1977 and was thus more typical (Figure 2.3) and three of the six females that entered winter were able to survive to breed in the following spring. Those that survived were in good condition after winter and experienced very little weight loss during that period (Figure 2.7). In late spring (November 1978) two immigrant males appeared in the study area and were undoubtedly responsible for siring the entire cohort of that breeding season.

The two male immigrants were marked individuals from a population across the highway. This population was monitored for 2 years from the time when its habitat had been slashed and burnt. The regrowth vegetation available by November 1978 supported a rat population of approximately 30 animals ha and was therefore a likely
source for immigrants to the study area. However, very few immigrants succeeded in crossing the road that served as a boundary to one side of the study grid. While roads are known to be effective barriers to rat movements, entry was also effectively barred along other sides of the study area due to the presence of other barriers such as an estuary and an open area with cut grassy lawns. For the most part the habitat beyond these barriers was not adequate for rats and therefore could not serve as regular sources of immigrants to the study population.

Recruitment of immigrants appears to be a critical factor in breeding of rats as it serves to replace males lost from the population through winter attrition. A combination of poor winter survival in females in one year resulting in a small breeding population and low probability of males surviving winter, as well as impaired immigration may have been sufficient to cause the population of bush rats to become almost extinct.

The populations at Mt Glorious and Lees Creek were not as physically isolated as at Kieloia. Both of these other populations were part of much larger populations in each area. Immigration and emigration were possible since the habitat available in the trapped areas was also available nearby. At Lees Creek the same vegetation grew along the creek so immigrants could enter at either end of the grid and at Mt Glorious migration was possible in any direction. A combination of higher numbers of females surviving winter and free movement of males in spring meant that neither Lees Creek nor Mt Glorious suffered a similar population decline.

The demographic similarities between the three study areas can be summarized as follows: (a) there was a typical annual turnover of membership in the population; (b) the sequence of life history
events (mating, births, emergence, dispersal, death) in each cohort resulted in similar timing of peaks and depressions in population density in all study areas; (c) mating took place in spring and early summer, young emerged and became trappable in mid-summer; (d) populations peaked in late summer and autumn and reached lowest levels just before juveniles appeared; (e) males did not remain resident in the area for as long as females and as a result showed a higher turnover; typically there was an influx of male migrants each spring; (g) female numbers were relatively stable and are probably responsible for the overall predictability of population size from cohort to cohort; (h) life history events of *R. fuscipes*, relatively synchronous over much of its range but events as breeding are extended over longer periods, in areas which experience milder weather conditions such as those at Mt Glorious.

The predictability of climate and habitat resources of a population can influence the degree to which individual animals will develop habitat specializations or seasonal behaviour patterns. This is particularly true where resources show spatial heterogeneity and temporal predictability (Waser and Wiley, 1979) and for the most part, the habitat of *R. fuscipes* has both of these characteristics. The population at Kioloa provided a good opportunity for studying the effect of seasonal changes in spatial distribution of resources on the dispersion patterns of individuals and the effects of long term deterioration of a habitat on the seasonal behaviour patterns.

The habitat at Kioloa was found to be a mosaic of plant alliances showing high spatial and temporal variation (Section 2.3.3.2). The bush rats showed a preference for mature forest habitat type A and D which were primarily native plant associations. The greatest density of rats was found in habitat A where patches of
Cahnia clarkei infringed on mature forest and where they regrowth of native vegetation formed a dense and structurally complex canopy which was 1 to 2 metres high.

The bush rat requires structurally complex habitats (Barnett et al., 1978; Cockburn, 1980). R. fuscipes is late to colonize and breed after fire situations (Fox, 1980, 1982; P. Catling, personal communication), and may only be able to persist for as long as there is sufficient undergrowth in its habitat (P. Catling, personal communication). There is a general tendency for R. fuscipes to 'wait' until at least 1½ or 2 years before invading a regrowth dry sclerophyll forest recovering from fire and there is a period of about 5 years before it attains peak density. The population then begins to plateau and decline in numbers (Newsome et al., 1975; Christensen and Kimber, 1975; Fox, 1980). The rats at Kioloa fitted this pattern; they began to use the southern part of the study area about two years after disturbance and use of the more open and older Eucalypt stands began to decline during this period.

During the decline in numbers, the individuals that remained continued to show normal weight and normal growth of rats, but were more dispersed and used larger home ranges (Section 2.3.2.1 and 2.3.2.2). This observation leads to a testable hypothesis that states that if there exists a direct relationship between resource availability and maximum population density then it is likely to involve some form of spacing behaviour which is responsible for the partitioning of the resources into units that are adequate to support the animals that remain. The nature of this spacing behaviour and some further comments on the appropriateness of this hypothesis to populations of R. fuscipes follow.
Animal Dispersion Patterns and Social Spacing

Taylor and Taylor (1978) suggest that spacing provides a alternative to intraspecific competition for limited resources. When two or more individuals occupy a patch of the environment, they will either space themselves or partition the resources and thus an unequal partitioning of the resources may reflect individual competitive ability (Lomnicki, 1978). Individuals living in a familiar habitat are, therefore, faced with only three choices: to stay and compete for resources, to space out in order to share resources or to move away completely and find new resources.

If a group of individuals stay in a patch and partition the resources, then the associated behaviour patterns must adjust to changing distributions of resources in each season. For example, they may need to account for the seasonal change in resources which are evenly dispersed in summer and clumped in winter. In winter they eat stored caches of cycad seeds and fungi found in moist soils (Woodside and Watts, in preparation) both of which have clumped distributions. If more than one of the resident rats has access to the same cache then this may stimulate behaviour to partition resources temporarily as well as spatially in order to avoid direct competition and costly encounters. Interestingly, adult females at Kiooa share their home ranges with subadults in winter but not with other adults. If these subadults are the daughters of the associated adult female adult then there would be some advantage to sharing rather than competing for resources which are clumped and probably scarce. The existence of multiple-burrow systems with radiating runways suggests that these animals are sharing shelter and travelling to other areas to forage. Since food and shelter may be distributed independently of each other, it is difficult to whether one or both of these resources is critical
in determining the distribution of animals as shown through trapping. The existence of clear runway systems suggests that during this period, animal spacing may not involve the division of habitat patches by individuals into circular resource areas but may involve division into groups of small patches interconnected by runway systems and consequently a rats perception of its resource space may be more linear than it is 2-dimensional.

While the spacing of individuals reflects both resource distribution and social relationships among conspecifics, it might also be the consequence of interactions with other animal species sharing the same space. At Kioloa and at Lees Creek R. fuscipes overlapped with Antechinus stuartii and A. swaissonii and even occurred in the same traps on successive nights. There was however no evidence for interspecific competition for space or resources (Section 2.3.3.3). Interspecific interactions between R. fuscipes and other small mammals have been previously tested by examining a model of change in niche breadth (i.e., habitat preference) and changes in niche space (i.e., spatial/temporal overlap) when the other species were present or absent (Fox, 1980). Again, there was no evidence that R. fuscipes experienced restricted habitat use in the presence of other species. However, these tests reflected only 'gross habitat partitioning' among species. Since ground dwelling small mammals are more likely to show 'microhabitat separation' (Dueser and Shugart, 1978, 1979), this was also tested for R. fuscipes at Kioloa. Using Colé's (1957) index of association, R. fuscipes was found to be unaffected by the presence of other species in the same microhabitat. In the same community, however, there was evidence of competition and microhabitat separation among other small mammal species, thus
validating the discriminatory power of the tests used (Dickman and Woodside, 1982).

Bush rats and the two dasyurids were able to distinguish each other by odour (Woodside and Dickman, in preparation) and each species is most likely to enter traps occupied by conspecifics. Rats, in particular, are curious of another rat's odour and show very strong response to rat-scented traps. A similar comparison of tracking information shows that rats readily travel where other species have gone but are most likely to associate with other rats (Woodside and Dickman, 1982).

The spacing of bush rats and the association of males, females and immatures in each season was summarized in Section 2.3.2.6. There are few differences between the three study populations in spite of the differences in density of individuals and general availability of habitat. For example, the population at Kilioka continued to show similar social relationships among its few members as among members of the other populations. This consistency may indicate that it is necessary to look within suitable habitat patches at spatial relationships rather than trying to assess relationships of larger areas consisting of several discrete habitat patches. It also indicates the importance of looking at different sex and age categories of neighbours to understand the nature of the spacing behaviour. In contrast, measures of dispersion of the entire population offered more information on animal distribution with respect to resources.

Female adult bush rats show little change in home range throughout their residency and little overlap of home ranges. Koeppel et al. (1979) found similar trends in social spacing of Rattus exulans and concluded that the tendency of females to dissociate from
each other indicates that females of that species must actively maintain and regulate their spacing.

Adult female bush rats rarely have overlapping home ranges and share parts of their range including winter burrows, only with juveniles or subadults (Section 2.3.2.2) and do so only until the end of winter. In contrast males have overlap in space use, show variable associations with other age classes and show relatively little site-attachment. Males show strongly seasonal spacing behaviour; in winter they are sedentary but disperse in spring. It is not surprisingly then that the movements of males exceed those of females in breeding season (spring and summer), as found in earlier studies of *P. fusipes* (Leonard, 1970, 1972; Freeland, 1972; Robinson, 1976), and in other studies of small mammals (Stickel, 1946; Barnett et al., 1978). This increase in male movements during breeding may increase their chances of encountering reproductive females. Males normally live for only one year, and therefore have only one breeding season in which they are able to sire offspring. Since the number of breeding females is fixed at the number that established residency in the autumn, then males are competing for a finite resource during mating. On the other hand, if females actively defend their patches of resources at this time, then it is possible that an increase in male movements is a consequence of them being expelled from defended female territories. While some males may be successful in mating with females, the consequences of a vagrant life style may result in them becoming stressed and they may die as a consequence a phenomenon more commonly described for various species of *Antechinus*. The low summer survival of males in all three study areas (Figure 2.8) supports this concept.
There may also be a third though more speculative explanation. This increase in male movements has also been observed in a dense island population of R. fuscipes (Robinson, 1976) and thus inspires the speculation that moving about does more than increases the chances of inseminating more females as it would in more dispersed populations. There may be a 'Coolidge effect' (Wilson, Keuhn and Beach, 1963; Brown, 1974) involved with these male wanderings. That is, repeated exposure to unfamiliar females may stimulate male reproduction and may also stimulate female receptivity. The females that have established home ranges and have secured adequate resources for rearing a litter may be stimulated to enter oestrus by frequent encounters with wandering reproductive males in addition to a variety of other environmental factors. It is not until a female is in oestrus, however, that she will be receptive to any of the male intruders (Drewett, 1973; Beach, 1976; McClintock and Adler, 1978). Males that have developed fully descended testes during late winter and have begun to wander in early spring would be 'prepared' and available for the first receptive females. This idea is strengthened by the fact that in all three study areas males appeared to be fully reproductive long before females became pregnant.

Social Behaviour

The possibility that social behaviour may influence survival through winter and so determine the number of females present in the breeding season was examined in the three study populations by determining whether heavier bush rats survived, assuming that they may be better competitors when conditions were poor. Higher body weight was not associated with survival of rats living at Kioloa or Lees Creek, but it was a good predictor of survival at Mt Glorious. Males
and females with lower body weight in autumn had less chance than the others of being present in the population at Mt Glorious at the end of winter. Whether they died or emigrated is not known, (see Christian, 1970; Krebs et al., 1973).

In the seasonally variable environment at Lees Creek, low body weight may be advantageous in the survival of bush rats in winter (see Stewart, 1979), although this is not supported by my data. However, at Mt Glorious where winter conditions were less harsh, adaptations to winter survival may be of a different sort. That is, in places where winter survival is not directly affected by climate, it may be affected by social competition, and large body size may be of some advantage. The influx of subadults into the population in the autumn may saturate the available habitat and the density of the animals may signal potential 'resource stress'. Competition for resources before they become critically limiting may be accompanied by the establishment of social hierarchies dominated by heavier animals (Gauthreaux, 1976). The development of hierarchies under similar circumstances has been described for Microtus (Widicker, 1973; Rose and Gaines, 1976) and experimentally tested in some birds (Wiley and Hartnett, 1980). In some R. fuscipes populations such as the one at Mt Glorious, winter survival may therefore be affected by weight-related social dominance.

While pre-winter body weight may help to predict which animals will be present at the beginning of the breeding season, the relationship between body weight and breeding success at Mt Glorious was not as clear. There was a positive association between pre-winter weight and breeding success in the following spring and summer, suggesting that there may be a link between establishment of residency
in autumn to secure adequate resources for overwintering and the
subsequent reproductive fitness of individual rats.

The establishment of residency of home ranges for breeding
and for surviving times of resource shortage may be directly related
to social dominance and competitive ability (Gauthreaux, 1977). It is
difficult to tell what stimulates competitiveness since the shortage
of resources such as food are not always sufficient stimuli to
encourage the expression of social dominance. For example, social
interactions examined in dense populations with unlimited resources,
have been shown to be associated with reproductive suppression of some
subordinate individuals (Christian, 1971; Vandenberg, 1973; Bediz and
Whitsett, 1977; Terman, 1979), starvation of those denied access to
food resources (Stueck and Barrett, 1978; Lomnicki, 1978) and poor
survival of new recruits (Lidicker, 1976). In order to understand the
circumstances under which social dominance is established and how this
comes about as well as how it can ultimately affect individual
fitness, it is important to look at the spatial association of
individuals and to assess the likelihood of certain types of
individuals interacting. Having established in this study that
individual bush rats associate differently according to sex, age and
seasonal resource distribution, it is possible to design useful
experiments in semi-natural enclosed environments that will test these
findings and thus explain the role of social dominance and spacing
behaviour in natural populations.
PLATE 2.1: Footprints on smoke sheets (scale 1cm:2.2cm)
(a) R. fuscipes  (b) Antechinus stuartii
(c) A. swainsonii  (d) Mus musculus
(e) Trichosurus vulpecula
PLATE 2.2: The flood zone

(plant species group 7: see text)
PLATE 2.3:  (a) Vegetation type A; species group 7.
           (b) Vegetation type A; species group 8.
PLATE 2.4:  
(a) Vegetation type B; species groups 2 and 3. 
(b) Vegetation type C; species group 1.
PLATE 2.5:  
(a) Vegetation type D; species group 5.  
(b) Vegetation type D; species group 6.
PLATE 2.6: Homesites of bush rats were found either in logs (a) or appeared as holes in the ground marked by a round mound of sand or dirt at the entrance that was often littered with seeds (b).
PLATE 2.7:  

(a) Cycad seeds and Eucalypt buds accumulated at the entrance to a bush rat's burrow.

(b) Female cycad plant with a ripe cone of seeds. These plants generally ripened in the autumn at which time the bush rats were found to eat seed husks and store the rest in large caches.
PLATE 2.8: Plaster casts of two single burrows found at Kioloa.
PLATE 2.9: (a) and (b) Old cycad caches after being excavated by a bush rat; some seeds eaten, new ones added.
TABLE 2.1: Relationship between body weight, winter survival and spring breeding at Kiooa, Lees Creek and Mt. Glorious

<table>
<thead>
<tr>
<th></th>
<th>Number of Individuals</th>
<th>Breeding performance of animals surviving winter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>surviving winter</td>
<td>not surviving winter</td>
</tr>
<tr>
<td><strong>KIOOA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>heavy</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>light</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>heavy</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>light</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td><strong>LEES CREEK</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>heavy</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>light</td>
<td>13</td>
<td>11</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>heavy</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>light</td>
<td>10</td>
<td>16</td>
</tr>
<tr>
<td><strong>MT. GLORIOUS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>heavy</td>
<td>60(2^s)</td>
<td>14(12^s)</td>
</tr>
<tr>
<td>light</td>
<td>41(1^s)</td>
<td>26(2^s)</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>heavy</td>
<td>88(8^s)</td>
<td>20(10^s)</td>
</tr>
<tr>
<td>light</td>
<td>43</td>
<td>19</td>
</tr>
</tbody>
</table>

superscript 's' refers to number of animals in their second year
Fishers exact test used; \(^*\) \( P < 0.05 \) \(^**\) \( P < 0.01 \)
TABLE 2.2: Mean length of the average movement (AVM) of *R. fuscipes* males and females in each season at (a) Kiooloa and (b) Lees Creek. Results of t-tests comparing movements in the winter and summer, are given for each sex.

### a) KIOLOA

<table>
<thead>
<tr>
<th>SEASON</th>
<th>SEX/AGE</th>
<th>N</th>
<th>AVM (metres)</th>
<th>STANDARD ERROR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn</td>
<td>M All</td>
<td>22</td>
<td>31.8</td>
<td>(6.5)</td>
</tr>
<tr>
<td></td>
<td>F All</td>
<td>21</td>
<td>26.5</td>
<td>(5.9)</td>
</tr>
<tr>
<td>Winter</td>
<td>M All</td>
<td>19</td>
<td>18.4</td>
<td>(2.2)</td>
</tr>
<tr>
<td></td>
<td>F All</td>
<td>22</td>
<td>28.6</td>
<td>(5.5)</td>
</tr>
<tr>
<td>Spring</td>
<td>M Ad</td>
<td>11</td>
<td>25.8</td>
<td>(4.2)</td>
</tr>
<tr>
<td></td>
<td>F Ad</td>
<td>6</td>
<td>19.9</td>
<td>(2.6)</td>
</tr>
<tr>
<td>Summer</td>
<td>M Ad</td>
<td>14</td>
<td>44.4</td>
<td>(10.9)</td>
</tr>
<tr>
<td></td>
<td>F Ad</td>
<td>13</td>
<td>30.9</td>
<td>(11.6)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>df</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>13.36</td>
<td>207</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>Female</td>
<td>0.97</td>
<td>207</td>
<td></td>
</tr>
</tbody>
</table>

### b) LEES CREEK

<table>
<thead>
<tr>
<th>SEASON</th>
<th>SEX/AGE</th>
<th>N</th>
<th>AVM (metres)</th>
<th>STANDARD ERROR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>M Ad</td>
<td>20</td>
<td>110.3</td>
<td>(20.5)</td>
</tr>
<tr>
<td>1978</td>
<td>F Ad</td>
<td>26</td>
<td>50.1</td>
<td>(26.0)</td>
</tr>
<tr>
<td>Winter</td>
<td>M All</td>
<td>32</td>
<td>42.3</td>
<td>(5.3)</td>
</tr>
<tr>
<td>1975</td>
<td>F All</td>
<td>57</td>
<td>37.5</td>
<td>(1.9)</td>
</tr>
<tr>
<td>Summer</td>
<td>M Ad</td>
<td>23</td>
<td>81.5</td>
<td>(8.6)</td>
</tr>
<tr>
<td>1979</td>
<td>F Ad</td>
<td>32</td>
<td>44.7</td>
<td>(5.1)</td>
</tr>
<tr>
<td>Winter</td>
<td>M All</td>
<td>26</td>
<td>47.1</td>
<td>(5.3)</td>
</tr>
<tr>
<td>1979</td>
<td>F All</td>
<td>31</td>
<td>39.8</td>
<td>(3.2)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>df</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>5.15</td>
<td>3008</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>Female</td>
<td>5.05</td>
<td>5354</td>
<td>P &lt; 0.001</td>
</tr>
</tbody>
</table>
TABLE 2.3: A comparison of distances maintained between males and other males (M-M), between females and other females (F-F), and between males and females (M-F). The frequency distribution of distances between seasonal centres of activity was determined for each class of individuals and compared using the chi-square test for homogeneity.

a) Comparison between classes with all seasons combined

<table>
<thead>
<tr>
<th>Distances compared</th>
<th>Kioloa (df = 18)</th>
<th>Lees Creek (df = 59)</th>
<th>Mt. Glorious (df = 26)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M-M vs F-F</td>
<td>28.85*</td>
<td>61.95</td>
<td>123.75***</td>
</tr>
<tr>
<td>M-M vs M-F</td>
<td>34.42**</td>
<td>40.79</td>
<td>66.34***</td>
</tr>
<tr>
<td>F-F vs M-F</td>
<td>15.51</td>
<td>52.15</td>
<td>57.44***</td>
</tr>
</tbody>
</table>

b) Comparison of seasonal distributions within classes

<table>
<thead>
<tr>
<th>Distances compared</th>
<th>Kioloa (df = 24)</th>
<th>Lees Creek (df = 42)</th>
<th>Mt. Glorious (df = 30)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M-M</td>
<td>41.20**</td>
<td>73.62*</td>
<td>72.27***</td>
</tr>
<tr>
<td>F-F</td>
<td>20.90</td>
<td>23.19</td>
<td>22.88</td>
</tr>
<tr>
<td>M-F</td>
<td>50.12**</td>
<td>57.34*</td>
<td>47.49***</td>
</tr>
</tbody>
</table>

(*P < 0.05;  **P < 0.01;  ***P < 0.001)
TABLE 2.4: Seasonal clumping in *R. fusipes* based on the frequency with which members of the same or opposite sex were trapped within 10m of each other during the same trap session.

<table>
<thead>
<tr>
<th></th>
<th>Summer (DJF)</th>
<th>Autumn (MAM)</th>
<th>Winter (JJA)</th>
<th>Spring (OND)</th>
<th>$\chi^2$ (df = 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females trapped</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>alone</td>
<td>18</td>
<td>17</td>
<td>16</td>
<td>21</td>
<td>27.00***</td>
</tr>
<tr>
<td>associated with males</td>
<td>6</td>
<td>30</td>
<td>36</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td><strong>Males trapped</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>alone</td>
<td>16</td>
<td>24</td>
<td>14</td>
<td>17</td>
<td>7.07</td>
</tr>
<tr>
<td>associated with males</td>
<td>10</td>
<td>19</td>
<td>29</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>and females trapped separately.</td>
<td>15</td>
<td>33</td>
<td>32</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>associated</td>
<td>11</td>
<td>10</td>
<td>11</td>
<td>16</td>
<td></td>
</tr>
</tbody>
</table>

(*** P < .001)
Table 2.5: Floristic analysis of the Kioloa study area. Plant species and sample quadrats were sorted using the Braur-Blanquet method described in the text. The grouping of this information (the cover-abundance score for each species in each quadrat) into plant groups 1 to 9 and quadrat groups A to D was subjective and based on criteria set by Bridgewater (1976).

<table>
<thead>
<tr>
<th>PLANT SPECIES</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Echium plantagineum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
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</tr>
<tr>
<td><em>Veronica persicifolia</em></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td><em>Salix caprea</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><em>Ligustrum vulgare</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Populus nigra</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Crataegus monogyna</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Prunus spinosa</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><em>Alnus glutinosa</em></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fraxinus excelsior</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Populus tremula</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 2.6: Habitat overlap as determined by trapping and tracking results at Kioloa. Table (a) gives the frequency of capture of each species at trapsites with differing degree of structural complexity of the covering vegetation. A value of 5 depicts the most and 1 the least complex vegetation. Table (b) gives the competition coefficient determined from these values.

(a)

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Mean</th>
<th>Std. deviation</th>
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</thead>
<tbody>
<tr>
<td><strong>Trapping Results</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. fusipes</em></td>
<td>4</td>
<td>13</td>
<td>78</td>
<td>76</td>
<td>54</td>
<td>3.72</td>
<td>0.95</td>
</tr>
<tr>
<td><em>A. stuartii</em></td>
<td>0</td>
<td>2</td>
<td>26</td>
<td>47</td>
<td>2</td>
<td>3.69</td>
<td>0.58</td>
</tr>
<tr>
<td><em>A. swainsonii</em></td>
<td>1</td>
<td>3</td>
<td>41</td>
<td>9</td>
<td>1</td>
<td>3.10</td>
<td>0.61</td>
</tr>
<tr>
<td><strong>Tracking Results</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. fusipes</em></td>
<td>5</td>
<td>3</td>
<td>87</td>
<td>60</td>
<td>26</td>
<td>3.54</td>
<td>0.96</td>
</tr>
<tr>
<td><em>A. stuartii</em></td>
<td>1</td>
<td>8</td>
<td>26</td>
<td>37</td>
<td>6</td>
<td>2.55</td>
<td>0.83</td>
</tr>
<tr>
<td><em>A. swainsonii</em></td>
<td>0</td>
<td>4</td>
<td>17</td>
<td>38</td>
<td>15</td>
<td>3.86</td>
<td>0.80</td>
</tr>
</tbody>
</table>

(b)

<table>
<thead>
<tr>
<th></th>
<th>Trapping results</th>
<th>Tracking results</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. fusipes</em>/</td>
<td>1.00</td>
<td>0.99</td>
</tr>
<tr>
<td><em>A. stuartii</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. fusipes</em>/</td>
<td>0.86</td>
<td>0.91</td>
</tr>
<tr>
<td><em>A. swainsonii</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. stuartii</em>/</td>
<td>0.82</td>
<td>0.95</td>
</tr>
<tr>
<td><em>A. swainsonii</em></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 2.7: Cole's coefficient of partial association for the three species, *Rattus fuscipes*, *Antechinus stuartii* and *Antechinus swainsonii* determined for trapping and tracking data. Italics denote a difference ($P < 0.05$) in association between pairs of species when the third species is present.

<table>
<thead>
<tr>
<th></th>
<th>Kioloa</th>
<th>Lees Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trapping</td>
<td>Tracking</td>
</tr>
<tr>
<td>3rd species present</td>
<td>A. stuartii/A. swainsonii</td>
<td>-0.420</td>
</tr>
<tr>
<td></td>
<td>A. stuartii/R. fuscipes</td>
<td>-0.917</td>
</tr>
<tr>
<td></td>
<td>A. swainsonii/R. fuscipes</td>
<td>-0.890</td>
</tr>
<tr>
<td>3rd species absent</td>
<td>A. stuartii/A. swainsonii</td>
<td>-0.323</td>
</tr>
<tr>
<td></td>
<td>A. stuartii/R. fuscipes</td>
<td>-0.070</td>
</tr>
<tr>
<td></td>
<td>A. swainsonii/R. fuscipes</td>
<td>-0.070</td>
</tr>
</tbody>
</table>
TABLE 2.8: Relationship between soil structure and moisture content at Kiola: results of a fit of a binomial model to information on proportional occurrence of four particle sizes and water content. The amount of deviation in the pattern of soil moisture at 26 sites accounted for by the occurrence of a given particle size class is tested using an F test on the deviances. The fit was performed using "GLIM".

<table>
<thead>
<tr>
<th>Trend</th>
<th>Source</th>
<th>df</th>
<th>Deviance</th>
<th>Mean Deviance</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humus (+)→H₂O (+)</td>
<td>S₁</td>
<td>1</td>
<td>0.671</td>
<td>0.671</td>
<td>( )</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>24</td>
<td>1.843</td>
<td>0.07679</td>
<td>8.74∗</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>25</td>
<td>2.514</td>
<td>0.10056</td>
<td></td>
</tr>
<tr>
<td>Gravel (+)→H₂O (+)</td>
<td>S₂</td>
<td>1</td>
<td>0.518</td>
<td>0.518</td>
<td>( )</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>24</td>
<td>1.996</td>
<td>0.08317</td>
<td>6.23∗</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>25</td>
<td>2.514</td>
<td>0.10056</td>
<td></td>
</tr>
<tr>
<td>Fine particles (+)</td>
<td>S₃</td>
<td>1</td>
<td>0.404</td>
<td>0.404</td>
<td>( )</td>
</tr>
<tr>
<td>+H₂O(+)</td>
<td>Residual</td>
<td>24</td>
<td>2.110</td>
<td>0.879</td>
<td>4.59∗</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>25</td>
<td>2.514</td>
<td>0.10056</td>
<td></td>
</tr>
<tr>
<td></td>
<td>S₄</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>25</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

where: \( S₁ \) is proportional content by humus ( >1200μm)  
\( S₂ \) is proportional content by large particles (>212μm)  
\( S₃ \) is proportional content by fine sand (>106μm)
FIGURE 2.1: Trapping schemes for the three study areas.
FIGURE 2.2: Predictability of seasonal rainfall at Kiloa over two time periods. The predictability of the annual rainfall pattern was determined for when the twelve months were evenly (e) and unevenly (u) divided into seasons (see text)
FIGURE 2.3: Annual rainfall and temperature profiles for Kioleia. Winter is indicated by a bar.
FIGURE 2.4: Number of individual *R. fuscipes* known to be alive at each of three study areas.
FIGURE 2.5: Modified calendar of catches for *R. fuscipes* at Kioloa showing the overlap between yearly cohorts of animals.
FIGURE 2.6: Number of resident and non-resident individual *R. flavipes* at Kioloa. Residents were defined as those individuals present in the study area for a minimum of three months.
FIGURE 2.7: Weight profiles of male and female bush rats at Kioloa as shown by the proportion of the population in each weight class.
FIGURE 2.8: Minimum monthly survival and the number of individuals in each age class for the population at a) Kioloa, b) Lees Creek and c) Mt Glorious. Each graph includes survival of adults (a), sub-adults (b), and juveniles (c).
KIOLOA

MINIMUM SURVIVAL RATE

1.0
0.5
0.0

1.0
0.5
0.0

1.0
0.5
0.0


(a)
LEES CREEK

MINIMUM SURVIVAL RATE

1.0
0.5
0.0

1978 | 1979 | 1980

(b)
FIGURE 2.9: Proportion of the female population breeding during each breeding season at each study area.
FIGURE 2.10: A measure of dispersion about the centres of activity shown by the standard deviation of the mean $z$-coordinate and mean $y$-coordinate of capture locations of each individual bush rat

a) Kioloa
b) Lees Creek
c) Mt Glorious
(a)
LEES CREEK

○ X-coordinate
○ Y-coordinate

STANDARD DEVIATION OF CENTRE OF ACTIVITY (metres)

A  W  Sp  I  Sm  A  W  Sp  I  Sm  A  W

(b)
MOUNT GLORIOUS

\[
\begin{align*}
&\text{STANDARD DEVIATION OF CENTRE OF ACTIVITY (metres)} \\
&\text{\hspace{1cm} X-coordinate} \\
&\text{\hspace{1cm} Y-coordinate}
\end{align*}
\]

\[\text{Sp 1963} \quad \text{Sm 1964} \quad \text{A 1965} \quad \text{W 1965}\]

\[\text{(c)}\]
FIGURE 2.11: Home ranges of male and of female *R. fusipes* at
a) Kioloa (scale 1cm:0.46m)
b) Lees Creek (scale 1cm:0.39m)
c) Mt Glorious (scale 1cm:0.37m)
FIGURE 2.12: Mean distance between individuals and their first five nearest neighbours during each season. Sexes and age classes are shown separately and the standard error of each mean is indicated by a bar. Sample size is given for each season

a) Kioloa
b) Lees Creek
c) Mt Glorious
MT GLORIOUS

DISTANCE BETWEEN BASE ANIMAL AND NEIGHBOURS [metres]

(c)
FIGURE 2.13: Social associations between different age classes and sexes.
I = immature    A = adult
solid line = positive association
dashed line = negative association
dashed and solid lines together = highly variable association.

Arrows represent the direction of the association and asterisks indicate statistically significant associations
a) Kioloa
b) Mt Glorious
c) Lees Creek (Year 1)
d) Lees Creek (Year 2)
FIGURE 2.14: Distribution of captures of *R. fusipes* for four years at Kiolca.
1976
Number of Individuals

- 1
- 2
- 3
- 4
- 5
- * > 5

1977
Number of Individuals

- 1
- 2
- 3
- 4
- 5
- * > 5
FIGURE 2.15: Floristic mosaic of the Kioloa study area:
Vegetation groups are described in text and
Table 2.1.
FIGURE 2.16: Morisita's index of dispersion for captures of Rattus fuscipes at Kioioa.

a) A modified index that measures multiple use of trap sites.
b) The normal index dispersion for four years.
FIGURE 2.17: Community structure and species overlap at Kiolea.  
a) number of species occurring at each trapsite  
b) number of individuals trapped of each species 
in each trap session.
FIGURE 2.18: An excavated burrow system at Kiolea.
FIGURE 2.19: Distribution of burrows in the study area and a division of the study area at kīolōa into regions with different soil moisture (increasing from 1 to 5). Details regarding theses levels of soil moisture are given in text.
FIGURE 2.20: Foods eaten by *R. fuscipes* at Kioloa.

a) diet analysis involving washing and sieving
b) unwashed faeces used in order to estimate cycad endosperm content
CHAPTER 3

AN EXPERIMENTAL STUDY OF ANIMAL SPACING IN SEMI-NATURAL ENCLOSURES: MANIPULATION OF FOOD DISTRIBUTION AND THE EFFECT OF BREEDING CONDITION.

3.1 INTRODUCTION

There are certain disadvantages in studying spacing in freeliving populations such as those described in Chapter 2. The particular stimuli triggering a change in animal dispersion are difficult to unravel because a number of environmental variables are usually changing at the same time. Any attempt to discern which are the critical variables by experiment are therefore crude and observations are difficult to replicate (for discussion of this see Cohen, Malpass and Klein, 1980, p.xv). These problems can be largely resolved by experiments in semi-natural or enclosed populations provided the experiments are designed to test hypotheses based upon observations of natural populations.

Observations from the field studies (Chapter 2) which suggest that there is a close relationship between bush rat density, spacing, social behaviour and resource distribution include: 1) population density varies seasonally but reaches a predicted maximum each year; 2) animal spacing is different for each sex and age class and varies seasonally; 3) the social relationships assumed from spatial associations of rats in each season were similar in three widely separated populations; 4) bush rat distribution was clumped in
seasons when resources were also clumped but only certain classes of individuals were involved, thus indicating that there may have been some selective sharing (e.g. between mothers and daughters in winter) of critical resources. In order to gain insight into the relationship between bush rat social behaviour and its resources, it is therefore important to include the following variables in any experimental manipulation: resource distribution, season and the numbers and types of individuals that could potentially interact. To do this, groups of rats (including both sexes) were observed in the breeding and non-breeding seasons and were exposed to food resources that were either clumped or scattered.

Field observations and other studies were used as the basis for predicting the outcome of these experiments. The first of these was that if social behaviour and resource distribution are responsible for the spacing of rats then there should be an unequal partitioning of resources among individuals and this should reflect their relative competitive abilities (Lommicki, 1978) and/or social status (Geathreaux, 1977). Secondly, the types of behaviour involved with the establishment of social dominance should be different for different distributions of resources (Hoss, 1969). Thirdly, the spatial organization of the group should reflect the social relationships and social behaviour among the individuals (Smith, Maza and Wiener, 1980). Fourthly, it was predicted that competition for resources would vary between sexes and would be different in different seasons. These experiments therefore, had two purposes; to reveal details about the relationship between resources and social behaviour and to identify the behavioural mechanisms which maintain the social organization of bush rat populations.
3.2 METHODS

3.2.1. Experimental Design

Three variables were considered to be of importance (food distribution, time of year and the number of potentially interacting individuals), and were incorporated into an experimental design (Figure 3.1). The availability of shelter was not included as a variable in order to reduce the complexity of the experiments. Furthermore, field studies did not reveal any predictable pattern in the availability of this resource.

The populations of animals consisted of two males and two females ($N_i$). After establishing themselves in the separate enclosures, the groups of rats were given an opportunity to intermix with a neighbouring enclosure population through unplugged passageways at the bottom of the enclosure walls. The potential frequency of intraspecific interaction (FIE) increased factorially when the number of rats effectively doubled ($N_s = 2 \times N_i$). There were one half the number of $N_s$ trials as $N_i$.

Four different types of experiments were used in the experimental design. Each was attempted three times. Each experiment consisted of four enclosure replicates, so that a total of 48 individual enclosed populations were required to complete the design. However, the experiments were frequently interrupted by several Rattus rattus that burrowed their way into the enclosures and the subsequent escape of several experimental R. fuscipes. This meant that less than half of the attempted experiments could be used for the analysis intended in this study. The analysis therefore concerned the results of 20 enclosed populations which consisted of 4 replicates of each of five separate experiments. The five experiments differed
according to the food distribution provided and the season in which they were performed. The 20 statistically analysed enclosures, the five sets of experimental conditions are summarised below. For convenience the name of each experiment shown here will be applied throughout the text and each of the 4 replicate enclosures in each experiment will be referred to individually as "Enclosure A, B, C or D".

<table>
<thead>
<tr>
<th>For Regime</th>
<th>Breeding Season</th>
<th>Non-Breeding Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central</td>
<td>&quot;Central-B&quot; (x4)</td>
<td>&quot;Central-A&quot; (x4)</td>
</tr>
<tr>
<td>(N₁ and N₂)</td>
<td>&quot;Central-C&quot; (x4)</td>
<td></td>
</tr>
<tr>
<td>Scattered</td>
<td>&quot;Scattered-A&quot; (x4)</td>
<td>&quot;Scattered-B&quot; (x4)</td>
</tr>
<tr>
<td>(N₁ and N₂)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3.2.2 **Enclosure Design**

A total area of 422 m² (27.4 x 15.4 m) was enclosed using a combination of wire mesh and 26 gauge galvanised metal (see Figure 3.2 and Plate 3.1). The area was divided into four equal sections of 105.5 m². All four enclosures were observed from a centrally located hide which was perched on stilts to a height of 1.5 m above ground.

A reference grid was established in each enclosure. The side walls were marked with fluorescent paint and subdivided into 16 units so that a total of 256 grid locations could be readily
identified in each enclosure during observations of animal activity.

The construction of the enclosures included the following features:

1. Overhead netting to prevent predation on rats.

2. Underground netting to prevent escape by burrowing.

3. Cement edges to prevent burrowing.

4. Smoothed, taped and greased seams to prevent climbing up the metal walls.

5. Metal walls on two sides (1.3 m high) and mesh on the remaining sides with a skirt of metal (1 m off the ground to prevent escape by climbing).

6. Six holes in the bottom of the walls adjoining pairs of enclosures. There were kept plugged until the second phase of each experiment.

7. A generator was used to run 36 red coloured incandescent lights (25 walls each) strung overhead.

8. Nest-boxes made from six white house bricks and a square roof of styrofoam (1.5 x 50 x 50 cm) for protection against sun and frost. Each enclosure contained four nest-boxes each of which was equidistant from the
centre and one side wall and equidistant between the opposite two end walls.

3.2.3. **Animals Used**

Bush rats in these experiments were collected from several localities in the ACT and were thus accustomed to the climatic conditions and day length pattern in the Canberra area.

Animals were wild-trapped and treated for ectoparasites using Malawash. They were then maintained in separate cages for approximately two weeks before being introduced into an enclosure.

Individuals were ear-tagged using Haupner tags (see Chapter 2) and marked with Durafur dye in such a way that individuals could be easily identified from a distance. Groups of four animals, called "populations" in the study, were chosen at random. As a result the groups consisted of animals of unmatched body weights. The two males and two females selected for each enclosure and did not come into contact until the start of each experiment. As much as possible, groups of animals were controlled for age and the possibility of familiarity in the past (i.e. in the field).

3.2.4. **Sampling and Observation**

Experiments were run for 30 days or until any females known to become pregnant gave birth. During that period, several levels of observations were made on each enclosure. Watches occurred on every second night of the experiment for a period of approximately three hours post-sunset. Initially, some extended watches were made in order to determine the activity periods of the animals.

Each watch involved 15 minutes of observation on each of the four enclosures in rotation. During that period, social interactions,
individual behaviour, location and exact time were recorded continuously for all four animals. At the end of each 15 min observation period, all individuals in all enclosures were located. Supplantation (wins) and flight (losses) were scored.

Every day throughout the experiment, the use of nest-boxes or other shelter was recorded. In addition, any indication of food caching, nest building, burrowing or predation on mice was noted. Caches were scored for size and degree of apparent use.

On days 3, 6, 18 and at the end of the experiment, the visible runway systems were mapped in each enclosure. Infrared photography was used to determine the presence of runways and to provide an indication of the amount of traffic on each runway from the extent of wear.

3.2.5 Other Tests

Other tests on animals included: a) trapping experiments to look at general trap response and trap bias, b) attempts to block or cover runways with objects and note response, c) determination of time taken to recognise new objects if placed beside a runway, d) tests of the effectiveness of an electric infrared beam for use in the field for assessing traffic along pathways.

3.2.6 Analysis

Data analysis included the following tests and methods. Where appropriate, the test used is mentioned in the text, together with the results.

1. Simple correlation matrices
2. Pearson's correlation
3. Spearman's rank correlation (and z transformation)
4. Analysis of variance (ANOVA)
5. Chi-squared homogeneity test.

Social interactions are classified according to four categories:
1. Intolerant (threats, chases, bites, squealing etc.)
2. Tolerant (or amicable)
3. Investigatory (sniffing, following or prodding associated with sexual activity)
4. Aloof (within same grid unit in enclosure but not engaged in overt attention)

Throughout the analysis the winner is the name given to the individual which supplants another. Dominance was determined in two ways: 1) by objective assessment of most frequent winner, and 2) by subjective assessment of social and non-social behaviour. Submissive behaviour was interpreted from postures, jerkiness of actions, height at which the tail is held off the ground, tendency to flee before an encounter can occur and amount of time spent out and active in the enclosures. The actions of the dominant animal were more direct and definitive; tail is held low, and the animal was generally the most active.

The frequency of each type of interaction is determined for each watch by calculating the mean number of interactions per minute of observation time. The frequency of each interaction for each of the six unique combinations of individuals in the 4 x 4 matrix was also determined. The actual variable used as "frequency of interaction" in the analysis was:
\[
\sum_{i,j=1}^{4} a_{ij}
\]

duration of the watch

where \((a_{ij} = a_{ji} = 0)\) and \((a_{ij} = \text{frequency of interaction between each pair } i, j)\).

That is, the sum of the frequency of activity of all pairs divided by the length of watch in minutes, gives a rate of interaction which is assumed to be approximately normal.

3.3 RESULTS

3.3.1 General Observations

During the course of the enclosure experiments, several important observations were made regarding some general aspects of rat behaviour. A description of each of these is given below.

1. Severity and duration of social interactions. Interactions can be very long. Some agonistic encounters were seen to last up to 10 minutes while several chases lasted 5 minutes or more.

Social interactions involved a great deal of communication without physical contact, including various threat postures, squealing and chasing. The events were intense and not always decisive. Amicable interactions were generally less obvious, and those which did occur were usually shorter. An active amicable behaviour sequence such as allogrooming or tail sniffing, may last up to 1 minute while huddling, which is a more passive form of amicable behaviour can last hours.
Chases were long and commonly the result of the initiative of the dominant animal. The pattern of the chases was either circular in the open spaces or direct and at higher speeds when they occurred along runways. Tail-biting was observed during chases. Both amicable and intolerant interactions resulted in supplanting of individuals. The approach by one animal was often a sufficient stimulus to induce avoidance or flight by another. The approaching animal then occupied the vacant spot (also seen in rabbits; Fullagar, Davey and Malafant, 1981).

2. Patrolling Activity. The individual classified as dominant was regularly seen to patrol the runways system of the enclosures. This animal was often active early in the evening and appeared to make deliberate excursions over most runways as well as visits to each nest-box. This activity was particularly obvious in enclosures where females were dominant and reproductively active.

Dominants commonly sat and waited at main runway intersections. These sites became worn and stained by continuous use and frequent marking with urine. In the case of pregnant females, these sites were vantage points from which she would rush at other individuals and interrupt their activities.

Similarly, socially dominant males would sit at intersections and would often interrupt the behaviour of other rats. Whereas dominant males would return to sitting at a runway intersection, dominant females would regularly patrol the enclosure. A dominant animal would appear to track down another by apparently following its scent along the runways.

3. Use of Runways. Generally, individual activity and interactions
were restricted to runways. The bush rats became so accustomed to using certain pathways that they seemed to run blindly, and would sometimes even collide with each other or objects placed across their path. For example, some animals were caught as they ran into Elliott traps placed on a runway regardless of whether it was closed or already occupied. Pursued animals sought protection by hiding in the grass beside a runway. Animals which jumped off the runway during chases generally went unnoticed by the pursuing rat.

Runways developed early in each experiment. Patterns of space-use were clear by the end of the first watch and were consistent with the runways which later became physically apparent (Plate 3.3) by the end of the third or fourth watch. The runway system became more complex with time.

4. Locomotion. In familiar space, animals ran or walked. There was, however, a distinct difference in three forms of this gait. Animals were either seen walking or running with their tail in a horizontal attitude, raised high off the ground or they were seen dragging their tails. Tail marks and imprints of belly fur left on smoked tracking sheets scattered around the enclosures confirmed a difference in the degree of body contact between the animals and the ground in each of these situations.

Hopping was a gait observed under two sets of conditions:

a) when an animal first entered a foreign space or b) when one animal was avoiding another during a chase. During a chase, the hopping gait became shorter and erratic.

5. Nest-box Defence. Nest-boxes were treated as safe retreats by animals being pursued. Once inside the shelter they could defend
themselves against intrusion by others. On some occasions, however, harassment of one animal inside the nest-box by another animal on top of the nest-box would continue for several minutes. Most attempts to invade an occupied nest-box failed.

6. Burrowing and Nest Building. Both burrowing and nest building were more common in enclosures where females were breeding or when temperatures were low. In the non-breeding season, all enclosures showed a higher incidence of scattered burrowing and tunnelling under the nest-boxes. Nests found in burrows or home sites of pregnant females were large and included cut grass and debris such as paper, sticky-tape, string and pieces of plastic. Pregnant females tended to build large mounds of dirt and grass around their nests which were often littered with food cubes (Plate 3.4).

Males also built nests. Generally the nests were made of grass which had been cut and gathered by the rats. The entrances to the nest-boxes were often filled in with dried grass during the day and reopened each evening.

7. Food Hoarding. Food hoarding was very common, and usually occurred just after new food was added to the food tray in the central food experiments, and continuously in the scattered food experiments.

8. Stealing Food. On four occasions, animals were seen to steal food from one another. Food was not scarce at the time. One animal would approach another and grab the cube or cause it to drop the food. The stolen cube of food was then nibbled and discarded or snatched by a third rat. On one occasion a single cube was passed between all four individuals within 15 min of observation.
9. **Predation.** *R. fuscipes* were seen to capture, kill and eat *M. musculus* which freely wandered through their enclosure. Carcasses of mice were found on numerous occasions with their stomachs and part of the anal region missing.

10. **Cannibalism.** In two enclosure experiments, a female from one population killed litters from another. On both occasions, a dominant female crossed into the adjoining enclosure when the holes between them were first unplugged, and then after smelling the intersections to several runways followed one until she encountered a nest-box which she entered and immediately killed the litter inside. The mother, on both occasions, was out patrolling and was periodically occupied by other social interactions with other resident bush rats. On return to the nest, the mother either attacked the lingering intruder or followed the pathway taken by the intruder back to the enclosure.

11. **Interactions between Enclosure Populations.** Animals took a long time to respond when the holes between enclosures when they were unplugged and often waited beside the open holes for periods of up to 30 minutes before venturing out. There was no correlation between social status and readiness for venture into the new enclosure as both subordinates and dominants eventually crossed the boundary. Most animals returned to their home enclosure by morning and rarely managed to establish a regular nesting site in the new area. This is discussed later in the section concerning nest-box use.

12. **Sex Differences in Behaviour.** There are several important points regarding the performance of each sex.
a. Dominant males and females showed similar social behaviour patterns except while patrolling the runways or when the dominant female entered breeding condition. The observations could therefore be pooled for all dominants, regardless of sex, to give one profile of a dominant animal during social interactions under non-breeding conditions.

b. Individual or non-social behaviour is, however, very different between males and females. Postures, locomotion, position of tail, jerkiness or smoothness of actions inevitably established the sex of individuals even before their identity could be determined from fur-dye markings.

c. Males tended to sit in corners or at runway intersections more often than females. Females tended to patrol runways.

d. Dominant males dragged their hind quarters and walked slowly. Female held their tails horizontal and generally moved faster.

e. Male subordinates were more likely to approach other animals, even if they had lost encounters with these animals, than female subordinates. Female subordinates appeared to avoid confrontations.

f. The intensity and nature of female interactions were variable, they appeared to change with time and changed dramatically with oestrus or pregnancy. In contrast,
male interactions were more consistent between the breeding and non-breeding seasons. Males generally interacted only on encounter with another male while females in breeding season sought out other animals and then interacted.

g. Male-female interactions were often shorter and more decisive than intra-sexual interactions, but inter-sexual interactions were more common than either male-male or female-female interactions.

3.3.2 Classification and Description of Social and Non-Social Behaviour.

The behaviour observed in the enclosures fell into three distinct categories. Social, non-social and those which are both social and non-social. These are listed in Table 3.1. Each behaviour was not looked upon as a single motor response to stimuli, but as a sequence of actions and signals such that each behavioural unit described here is a typical action pattern accompanied by predictable responses. This behaviour may otherwise be classified with respect to the mechanisms involved with signalling to other animals. There are four such classes of behaviour; tactile, visual, olfactory and auditory (Barnett, 1975). In this study, each of these signal classes is variously combined and classified according to the function rather than the mechanism of the behaviour. Hence the classification given in Table 3.2.

Some of these behaviour are described in more detail in Table 3.2 and illustrated in Figure 3.3. Where these postures or behavioural sequences have been previously described or used by other
authors, a reference is given. Throughout this study an attempt has been made to use unambiguous terminology. Hence "intolerant" behaviour is used where possible to classify certain types of interactions rather than "aggressive" behaviour, which is accompanied by a long history of different applications (Barnett & Marples 1981). In particular, this avoids implications of a "tendency" on the part of animals to attack (Scott and Frederickson, 1951). Use of the definition of aggression by Barnett (1964), where it is described as "not only attack but all activities which tend to repel others of the same species," avoids needless interpretation of tendencies or intentions of the animals being observed.

3.3.3 Association of Four Types of Interaction

The frequencies with which each of the four major classes of social behaviour occurred in all experiments showed a strong positive correlation with each other. The matrix of correlation coefficients is given below:

<table>
<thead>
<tr>
<th></th>
<th>Intolerant</th>
<th>Amicable</th>
<th>Investigatory</th>
<th>Aloof</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intolerant</td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amicable</td>
<td>0.0339</td>
<td>1.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Investigatory</td>
<td>0.3042</td>
<td>0.3705</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>Aloof</td>
<td>0.4019</td>
<td>0.5215</td>
<td>0.3939</td>
<td>1.0</td>
</tr>
</tbody>
</table>

With 136 degrees of freedom, a correlation coefficient of 0.2500 is significant at the 1% level. Intolerant and amicable behaviour are the only two variables which are not positively correlated at that level, nor are they negatively correlated as might
be expected. The tendency is for all types of behaviour interactions to decrease or increase synchronously except in the case of intolerant and amicable behaviour.

The uniform change in the frequency of different types of interaction is confirmed by a test for the independence of each type. Independence is strongly rejected, indicating that these groups cannot be treated separately in subsequent analyses. The test for independence (Morrison, 1976) given the correlation matrix $R$ of $p$ types of interactions is as follows (where $N$ is the number of observations and $r_{ij}$ is an element in the matrix):

$$\chi^2 = \frac{N}{6} (2p+5) \sum \sum r_{ij}^2$$

In this case $\chi^2 = 112.5$ ($df = 6; p \ll 0.001$).

The lack of independence indicates that any further analysis should involve multivariate techniques. However, to avoid some of the problems of dealing with statistical techniques such as multivariate analysis of variance, the following information was reconsidered. Although there was a lack of statistical independence among all behaviour classes only amicable and intolerant behaviour were negatively correlated. Any independent analysis of the frequency of intolered behaviour would therefore provide some indication of the trends occurring in investigatory and aloof behaviour but would be the opposite of trends for amicable behaviour. A simple analysis of variance (ANOVA) for frequency of intolerant behaviour by the rats is therefore useful for interpreting the general changes in social behaviour among rats during the experiment. The various interpretations of this statistic test have been applied carefully to this group of related behaviours.
3.3.4 Analysis of Variance on Experiments, Enclosures and Watches

To satisfy the criteria for ANOVA both "Experiment-type" (or treatment) and "Enclosure" (or replicate) were treated as fixed conditions and "Watches" (or time) was treated as a random variable.

A summary of the results for intolerant behaviour follows and reveals that a strong experiment (treatment) effect exists and that watches within experiments vary significantly as well. The four enclosures within experiments, however, show little variation and can be treated as statistical replicates. For example, the variance ratio determined for Enclosure effect in Experiment Central-C was 0.849 and for Scattered-A was 1.909.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>VR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment</td>
<td>4</td>
<td>4.86 P = 0.01 (F = 15)</td>
</tr>
<tr>
<td>Residual</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Experimental Watch</td>
<td>30</td>
<td>2.482 P = 0.01 (F = 0.04)</td>
</tr>
<tr>
<td>Residual</td>
<td>88</td>
<td></td>
</tr>
</tbody>
</table>

Both the Experiment and the Watch effect were investigated further. The mean frequencies of intolerant interactions for each experiment were compared using the t-test:

\[ t \ (\text{SED}) \ \text{where} \ t = 1.96 \ \text{and} \ \text{SED} = 0.02326 \]

Using 95% confidence interval, the experiments could be grouped according to the differences or similarities of the means. These results are shown below:
<table>
<thead>
<tr>
<th>Experiment</th>
<th>Season</th>
<th>Intolerant interactions (no./min)</th>
<th>Grouping</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scattered-A</td>
<td>Mid-late breeding</td>
<td>0.0471</td>
<td>a</td>
</tr>
<tr>
<td>Central-C</td>
<td>Mid-late breeding</td>
<td>0.020</td>
<td>ab</td>
</tr>
<tr>
<td>Central-B</td>
<td>Early breeding</td>
<td>0.016</td>
<td>bc</td>
</tr>
<tr>
<td>Central-A</td>
<td>Non-breeding</td>
<td>0.0250</td>
<td>c</td>
</tr>
<tr>
<td></td>
<td>(late winter)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scattered-B</td>
<td>Non-breeding</td>
<td>0.0112</td>
<td>c</td>
</tr>
<tr>
<td></td>
<td>(autumn)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The grouping of the experiments according to levels of intolerant behaviour is closely related to the breeding season rather than the experimental treatment (food regime). The two experiments occurring in the middle to late breeding season show very much higher levels of intolerance. The other three types of behavioural interaction show some variation between experiments (Table 3.3), but are not necessarily consistent. It is noticeable that the frequencies of all interactions are typically low for *R. fusipes* in all experiments.

The Watch (time) Effect within the experiments was due to the dramatic changes in the interaction frequencies in only two of the experiments: Scattered-A and Central-C. These experiments show statistically similar mean levels of intolerance and occurred at the same time in the breeding season. By comparison, the other three experiments maintained more even levels of interaction over the
different watches. This information is gained from scanning the frequency data over time for each experiment (see Appendix 3.1).

An attempt to interpret the Watch Effect could be viewed in two ways:

1. Interpretation of the events occurring during each atypical watch of experiments Scattered-A and Central-C.
2. Interpretation of some accumulating time effect by testing the fit of a linear or quadratic model to the data.

No significant linear or quadratic components were found for either experiment, indicating that there is no single relationship between intolerance behaviour and time, but an ANOVA revealed a strong Watch Effect ($F_{a1} = 5.295, P < 0.01$) for experiment Scattered-A, suggesting that there may have been some atypical Watches in that experiment. Although the Watch Effect in experiment Central-C was not statistically significant, it is illustrated with Scattered-A in Figure 3.4. As there were no radical changes in weather conditions during either experiment, which could account for the variation in intolerant behaviour, the interpretation of these graphs may depend upon insight into the changing social conditions within each experiment.

To summarise the analysis so far:

1. The frequency for all interactions are positively correlated. When one type of behaviour increases it is indicative of an increased rate of encounter of most types. Intolerant behaviour and amicable behaviour are not positively correlated
in this way.

2. Enclosures represent statistical replicates of each experiment (recall that experimental variables were food distribution, season and number of individuals).

3. There is a difference between experiments and they can be grouped according to breeding season rather than food regimes.

4. There is a significant change in the frequency of intolerant behaviour during the breeding season and the pattern is not a function of time alone.

3.3.5 Social Structure and Social Rank

Socially, the four individuals in each enclosure population were not equal participants. That is, they did not engage in equal numbers of types of social interactions. In 65% (13 out of 20) of the enclosures, there were significant chi-square values indicating non-uniform involvement in tolerant and intolerant behaviour by the individuals (Table 3.4). This result is unaffected by the sex of the dominant individual.

Among the four individuals in each enclosure, there was evidence of a linear dominance hierarchy. There were some instances, particularly in the non-breeding season experiments and in scattered food experiments in which non-dominant individuals exchanged rank or vacillated between two ranks regularly. This hierarchy was initially established subjectively from behavioural observations made during each enclosure Watch. At the risk of being anthropomorphic, dominance was essentially scored on the basis of an animal's apparent
'confidence' while it moved about its space and engaged in social interactions.

The conclusions from these subjective assessments of dominance were strengthened by a strong correlation using a more objective measure of rank based on winning ability of individuals \( r = 0.891 \), \( P < 0.01 \). Winning ability was calculated for each individual \( i \) as follows:

\[
\text{Winning ability } (A_i) = \frac{\text{Number of wins}}{\text{Number of losses}} (W_i)
\]

(recalling that wins were any form of supplantation of one individual by another and losses were any form of displacement or fleeing). Individuals were then ranked according to the value of \( A_i \) and the order compared with the subjectively-determined ranks using a rank correlation. The correlation coefficients were pooled after use of \( Z \) transformation and a test for homogeneity. This resulted in a pooled Spearman rank correlation already given \( r_s = 0.891 \), \( P < 0.01 \). That is, social rank was highly correlated with winning ability. It is important to point out, however, that the subjective analysis of social rank was not entirely independent of winning ability. The observations of wins, losses and draws, as well as non-social behaviour were inherently included in the subjective ranking of individuals applied throughout. Any disagreements between the two forms of assessment may be explained by the additional information gained from observing the individual's attitude and space-use behaviour independent of ability to win interactions. A number of these points are explored later in this Chapter.
Of the 20 enclosures, only five revealed male dominance and in each of these cases there were no parous females in the group. In addition to this, four of these five cases occurred in scattered food experiments with only one male becoming dominant in a central food experiment.

Winning ability (expressed as a proportion of interactions observed), social rank, sex, and breeding success have all been combined in a composite diagram of social relationships for each enclosure population (Figures 3.5a, b, c, d). The highest ranked individual is positioned in the bottom left corner of the matrix with ranks decreasing upward and to the right. An interaction matrix of four animals (4 x 4 matrix) results in only six unique cells (see Figure 3.5a). Only these six cells are represented in the subsequent diagrams. The ability to win in interactions with any other individual is indicated by shading, draws are indicated by stipple and losses by blank areas. The relative proportion of observed interactions which involved a given pair of individuals is indicated by the size of the circles. Only three of the five experiments are included as representatives of two food regimes (scattered and central), breeding and non-breeding seasons.

There are several points to be made about the relationships depicted in this way.

1. The distribution of interactions is not even among pairs of individuals and the dominant individual does not necessarily engage in more interactions than other animals.

2. The distribution of wins and losses is not even. The
dominant animals win most frequently and are able to regularly supplant most of the other individuals. This is particularly true of dominant females.

3. Social interactions tend to be more decisive in the breeding season than in the non-breeding season and the distribution of interactions is more even in the non-breeding season. That is, the circles are approximately the same size in the Scattered B experiment, for example, and show proportionately more stippled areas (more 'draws').

4. Where a female was known to breed (indicated by "B"), she was also the dominant animal. Parous females showed a very strong tendency to win over all other individuals.

5. No individual always won encounters. The relationships are dynamic. Dominance may develop or change, so that at different times, each individual may experience both wins and losses. A subordinate (non-dominant) may successfully defend against the advances of a dominant animal (particularly at their nest-box) and thus accumulate 'wins' against the more dominant intruder. This is indicated by the inclusion of win, loss and draw symbols in most cells of the interaction matrix.

6. Rank is not absolute. Individuals may share rank or
change them during the course of the experiment. These cases are indicated by square brackets.

3.3.6 The Relationship between Sex, Weight and Social Rank

Social rank is not a function of the relative weights of the individuals involved. Since dominance hierarchies were quickly established in each enclosure, the initial weights of the animals were ranked and tested against social rank. A Spearman rank correlation was calculated for each of the 20 enclosures. As \( N = 4 \) is too small to test significance, a 'z transformation' and a homogeneity test \( (X^2 = 15.00) \) was used to combine the coefficients and obtain a non-significant correlation \( r_s = 0.1586 \). Rank is not related to initial weight.

Rank is, however, related to sex. When ranks 1 to 4 are tested for their association with sex, the result is significant, \( X^2 = 11.32 \) (df = 3, \( P = 0.01 \)). This is a consequence of a positive female bias in rank 1 and fewer than expected in rank 4. The opposite is true of males.

3.3.7 The Relationship between Breeding Status and Social Rank

The relationship between breeding and social rank was absolute for females. Only dominant females were known to become pregnant and rear litters. Non-dominant females in the same enclosures were not seen to engage in sexual interactions with males or become pregnant. Monitoring for reproductive condition was continued for three weeks after the end of the experiment when animals were left in the enclosures, and for another two weeks when they were retrieved to the laboratory.
On the other hand, not all dominant females were parous; in only five of the 15 cases did the female in the top social rank actually give birth, and one other dominant female engaged in sexual activity but died before giving birth (Experiment Central-C, Enclosure "B"). She had four foetuses. These six cases, however, account for all instances of female dominance in experiments conducted in the middle of the breeding season. Two of these experiments, Central-C and Scattered-A were also found to showed outstanding levels of intolerance according to the analysis of variance reported earlier.

Male reproductive status could not be assessed. Relative testes size was not a good indication of social rank, nor was body weight. Females were promiscuous and solicited attention from either of the males during oestrus, although the higher ranked male often chased the lower ranked male away from an oestrous female.

3.3.8 The Relationship between Space-Use and Social Rank

An assessment of the use of space in enclosures involves consideration of several factors: the effect of the observer; the effect of, or relative use of available shelter; the effect of one animal on the spatial activity of another and the effect of restrictions imposed by an animal's own modification of its environment (e.g. development of runways). Each of these is considered below.

The observer effect is clearly shown in Figure 3.6. In each enclosure represented there, the total frequency with which animals were observed in each part of the grid is represented on the vertical axis. The spatial dimensions of the enclosure are represented on the horizontal plane. Frequencies are actual counts of the observations. If an animal was seen running from A to B at the time of sampling,
then an observation was recorded at every 2 metres along that path, or half-way, if the total distance was less than 2 metres. The result is a definite skewed pattern in the corners of the enclosure farthest from the observation hide. The reason for this effect is unclear, as the possible observer effect is compounded with the fact that the adjacent sides of the enclosure directly below the hide were made of solid metal, whereas the other two sides were made of open mesh at ground level. Animal activity along the sides of the enclosure with open mesh may be associated with motivation to escape.

The use of shelter, particularly of nest-boxes, is shown in Figures 3.7a, b, c and d for the same four enclosures as above. The exclusive use of home sites was investigated and revealed that in 10 of 16 enclosures analysed, there was non-random (selective) use of nest-boxes and burrows (for results of chi-square test, see Table 3.5). Included in these are five enclosures in which there were parous dominant females, two enclosures with dominant males and the remaining three were conducted during the breeding season.

There are several observations which are relevant here. From the diagram of use of nest-boxes, it is clear that not all fixed shelters were used. They were all visited or used to house caches of food cubes or even contained nests, but not necessarily used as home sites. In addition to nest-boxes, burrow systems were developed along the edges or under objects and generally used, for some time at least, as home sites. Chambers of these burrows were found to contain food and grass.

The nest-boxes were often modified by the residents. Complex tunnels and burrows were dug underneath them, and several entrances developed along the edges while the original entrance was blocked. Breeding females constructed elaborate nests inside modified
nest boxes and generally built mounds of dirt and debris around the
bricks (Plate 3.4). All holes were kept plugged except when the
animal entered or left the nest-box.

Nest-boxes often contained pairs or groups of animals. The
pairs were persistent and generally continued to occupy the same nest
for some time. Breeding females were usually found nesting alone up
to two weeks before parturition. The temporal pattern of nest box use
is not shown in Figure 3.7 and thus exclusive occupation is not
immediately apparent in these diagrams.

When enclosures were opened and animals were allowed free
passage into the neighbouring occupied enclosures, they were usually
found to visit the new area during the night, but returned to their
original area during the day. This is particularly true of the
scattered food experiments in both breeding and non-breeding seasons.
In contrast, there was some emigration to a new area by animals in
both of the central food experiments shown in Figure 3.7. In all but
one set of enclosures (Experiment Scattered-B, Enclosures C and D),
the number of movement or overnight visits to the neighbouring
enclosure coincided with an unequal involvement in social interactions
by individuals in the home enclosures as reported earlier.

3.3.9 Space-Use in the Enclosures

The use of space is restricted to runway systems established
during the first few days of the enclosure experiment. An overlay of
frequency of observations at each grid point on the mapped runway
system shows the adherence to pathways (Figures 3.8a, b, c and d).
There are, however, areas which contain runways but no observations
and thus can be attributed to the "observer effect" (Section 3.3.8).
The dominant animal also has an effect on the space-use patterns of other individuals. The dominant individual patrols the runways and shows the greatest activity while other individuals show depressed activity and restricted space-use. This was true no matter which sex was dominant and regardless of the food regime (compare Figures 3.8a, b, c and d).

The enclosures shown in Figures 3.8 (a to d) were all observed during the breeding season since activity during the non-breeding season was so low that no pattern could be readily discerned. Individuals spent most of the time huddled close to the perimeter during the non-breeding seasons and there was little apparent difference in individual space-use. Clear runway systems did, however, develop at that time, indicating that there was more activity than observed but that it occurred during periods when observations were not being made.

3.3.10 The Relationship between Intolerant Behaviour and Space-Use Complexity

There was a significant correlation between the levels of intolerant behaviour recorded within an enclosed population and the complexity of the runway system \( r = 0.897, P = 0.01 \). Complexity was measured by counting the number of runway intersections. As the levels of intolerance rose, the runway system became more complex. The relationship between runway complexity and levels of intolerance may be the result of avoidance behaviour or efforts to reduce the probability of interaction. This essentially increases the population's 'effective space': the population occupies more space by utilizing the interior of a patch rather than extending the dimensions of the patch (habitat). Attempts by the rats to expand their living
space was prevented by the walls of the enclosure, so any increased complexity of space-use by the rats has been interpreted here as indication of the 'intention to spread out' or disperse.

Runway systems became more complex and intolerance levels were highest when breeding females were present. In Figure 3.9 parous females were labelled A to E and three of these females (C, D and E) are associated with lower levels of tolerance than either A or B, but this can be explained. Parous female D died before giving birth and therefore contributed less to the levels of intolerance behaviour than would be expected. Female E gave birth to a litter several days after the end of the observation period of the experiment, as did Female C. The contribution of neither female is totally accounted for. As a result, there appears to be a gradient in that females observed closest to birth accumulate more intolerance behaviour. The latter are associated with more complex runway systems.

Complex runway systems also developed where males were socially dominant during breeding season (Figure 3.9, males a and b). In both instances, no females were known to become pregnant. Males c and d were both dominant during the non-breeding season and were from cohorts going into their first winter.

Any attempt to separate central food experiments from scattered food experiments on the basis of runway complexity is not justified. In both cases the number of runways reflect the frequency of intolerant interactions rather than food regime provided for the residents. The correlation illustrated here highlights the effect of the social environment on the pattern of movements in the spatial environment.
3.3.11 The Timing of Intolerant Behaviour of Parous Females

The frequency of intolerant interactions changed with time and apparently changed with reproductive condition (Figure 3.10). The five females that gave birth during the experiments are represented on the same graph and the birth date for each of their litters is set at "zero days". The peak of oestrus occurs 22 to 24 days prior to birth (Taylor, 1961; Taylor and Horner, 1972) which means that the peaks in intolerant behaviour shown in Figure 3.10, are in phase with both birth and oestrus. From direct behavioural observations and from the diagrams of wins, losses and draws (Figures 3.5, 3.6 and 3.7) the involvement in intolerant interactions most likely reflects self-initiated aggression and frequent wins on the part of the dominant female.

3.4 DISCUSSION

This study offers evidence of a dominance hierarchy among a group of bush rats. The apparent control, by the dominant animal, of the use of space and successful prevention of reproduction among subordinates, supports the notion that social behaviour may influence recruitment and reproduction of conspecifics. But the results of enclosure studies such as these cannot be interpreted in isolation and should be related to the social structure of natural populations (Chapter 2) to define the limitations of enclosures as experimental tools for studying natural phenomena. The limitations of enclosure experiments for studies on R. fuscipes are discussed below and some of the significant observations made under these circumstances are discussed. A more detailed integration of results from enclosures and
from field studies is contained in the concluding chapter (Chapter 5).

Limitations of Enclosure Studies

Enclosures limit the amount of accessible space: this is an inherent problem and is particularly important in the study of social spacing. In this case, however, it was assumed that limited space would result in a dominance hierarchy which would be translated into spacing behaviour in natural populations. Interactions which would result in wins and losses or escalated intolerance between individuals in enclosures, were seen to represent occasions when these animals would flee from each other or avoid contact in the wild. Thus the outcome of interactions were seen as the direct cause of animal spacing. An interpretation also applied by Kinsey (1971, 1976) in a study of spacing behaviour of Neotoma fuscipes.

Enclosures limit dispersal and provide little opportunity for passive avoidance by certain individuals. The importance of dispersal and the dramatic effects of restricted dispersal have been well documented (i.e. Lidicker, 1975, 1976, 1978, 1979; C.J. Krebs, 1966). In addition to the limitation of dispersal, there is a possibility that restriction within the enclosure induces aberrant behaviour by an unnatural and forced increase in the frequency of intraspecific encounters (FIE). In addition changes in physiology or condition may result from unequal distribution of food resources in confined areas (i.e. Stueck and Barrett, 1978), and change in animals health or physiology will be reflected in their social behaviour. For reasons provided below, these criticisms of the use of enclosures to study social behaviour are seen as inapplicable to this study.

First, the dispersal problems, as described by Lidicker (1975), are avoided by using short term experiments. If dispersal is
primarily an age-related or seasonal phenomenon, so that the juveniles or subadults of the population disperse at a predicted time each year, it would be an experimental problem only when the experiments incorporated juveniles or subadults, and occurred at the time of dispersal. Hence, age-related dispersal is only a problem when attempting to study population growth over one or more generations. When such dispersal is prevented, the social structure and age structure of the experimental population changes, thus affecting the interactions observed in the population. However, short-term social avoidance behaviour (i.e. dispersal which is not necessarily age-related) was hindered by lack of escape routes and lack of available retreats, other than nest boxes. These attempts to escape, indicated socially-induced dispersal and were monitored through changes in patterns of space-use. These changes were used to measure the effectiveness of dominance and antagonistic behaviour i.e. causing re-spacing or flight in subordinate bush rats. In the natural situation, the probable outcome of intolerant interactions would be to disperse but in the enclosures, the outcome is a complex network of runways and temporary escape routes.

Secondly, the possibility of inducing physiological changes through non-uniform resource allocation such as those demonstrated by Stueck and Barnett (1978) including an of subordinate mice to assimilate food efficiently when resources were clumped was considered a desirable outcome, not an obstacle to interpretation. Any outcome which pointed to an unequal partitioning of resources associated with social rank was considered desirable. This was partly the reason for introducing both central and scattered food regimes; so that such affects may be exaggerated as they might be in natural populations when food resources are clumped or evenly dispersed, depending on the
season. The results, however, indicate that there are very few
behavioural differences between enclosures with different food
distributions. Differences were more easily accounted for by the
season in which the experiment was conducted.

The twenty enclosure experiments analysed in this study were
spread over two food regimes (centralised and scattered) and two
seasons (breeding and non-breeding). The number of individuals or the
number of unique interactions was increased when the rats in two
enclosures were given access to each other after becoming established
in isolation. Of the variables involved in this design, the food
distribution seemed least important in contributing to social
relationships and the use of space by individuals. Food cannot be
considered unimportant, however, since one possibly relevant feature
was not tested, that is, food shortage (Braithwaite and Lee, 1979;
Hansson, 1979). Food was always available in excess and thus
observations on intraspecific competition for a limited resource,
other than space per se, were not possible. In reality, space may
represent a reservoir of such limited resources (food, nest sites,
cover) which are permanently bound to the benefits of exclusive space
ownership. The absence of a test with other restricted resources does
not alter the relevance of these experiments, since it is the
mechanism of spacing behaviour which is being investigated.

Relationship Between Intolerance Behaviour and the Use of Space

The mechanism by which spacing was ultimately maintained was
through intolerant behaviour. But the frequency of such overt
behaviour was very low. Indeed, the frequency of any form of
behavioural interaction was low. Relationships were established
quickly, and assuming that individuals were able to recall outcomes of
encounters recognised each other, as Sadleir (1965) suggests for *Peromyscus*, overt aggression need not have occurred more frequently. In natural situations, this would be particularly valuable to female rats which maintain the same space for long periods (see Chapter 2).

Overt displays appear to serve two purposes; to establish immediate dominance or 'right-of-way' when animals meet on neutral ground, and to defend an area against intrusion or use by conspecifics. Observations of captive bush rats introduced into spatially 'neutral' enclosures supported these conclusions. At first, all animals were engaged in exploration and tended to avoid each other, or when encounters occurred, right-of-way was quickly established after a brief threat display or high-pitched squeak. At this early stage, individuals could be considered relatively equal entities in a neutral space, thus fitting well into a molecular approach to social behaviour (Pearson, 1960). Later, however, encounters involved overt displays and dominance was established. Interrelationships between individuals varied as shown by the uneven distribution of tolerant and intolerant interactions and the hierarchies shown by the win, loss and draw diagrams (Figures 3.5, 3.6 and 3.7). The dominance became more subtle and interactions were muted in the non-breeding populations. This contrasted with the breeding populations, in which overt displays and the defence of space were very prominent. The first female to enter oestrus, or at least actively solicit males, also defended all the available space. Her defence of space was facilitated by the existence of runways. On these the dominant female quickly surveyed the area, presumably detecting the odour of any other active individual (Calhoun, 1962; Stoddart, 1976; Price, 1977) and would quickly seek them out. For the subordinate individuals, runways served as pathways for retreats to
safety. As the dominant female approached parturition and intolerance levels rose, the system for retreats and avoidance became more complex (Figure 3.9), and the total use of space by subordinates became restricted (Figures 3.8a, b, c and d). Several authors have reported the importance of runways in other rodent populations (*Microtus californicus*, Pearson, 1960; Lidicker and Anderson, 1962; *Rattus norvegicus*, Calhoun, 1963; Barnett, 1975; *Mus musculus* and *Dipodomys* sp., Eisenberg, 1972; *Microtus ochrogaster*, Getz and Carter, 1980), but very few authors have realised the important role that runways may play in facilitating aspects of social interference and hence, social regulation.

**Relationship Between Social Dominance, Space-Use and Breeding**

The spacing behaviour of all animals in enclosures, tested in the breeding season, was affected by the activity of dominant animals. Commonly, a female was dominant and her intolerance was in phase with her oestrus cycle and pregnancy (Figure 3.10). Females which become pregnant and dominant were not necessarily the largest. Unlike the well-documented hamster (*Hesperocricetus auratus*) (Brenner et al., 1978) and some *Rattus* spp. (S.A. Barnett, Hocking and Dickson, 1979), body weight was not an accurate predictor of social status. Either sex, age, experience, health or reproductive condition can potentially influence, if not determine, the social status of an individual. Of these variables, reproductive condition may be the most important in determining the social dominance of individual bush rats. The results of the enclosure experiments suggest that there is a social advantage in being the first female to enter oestrus. Her intolerant behaviour would either drive all other females away in a natural population, or if they remained, delay them.
It is not entirely clear whether a socially dominant bush rat entered oestrus first or whether first oestrus ensures social dominance. It is, however, interesting to consider the possibility of a reproductive strategy which involves both an early oestrus, social dominance associated with the physiological state of oestrus and pregnancy, and a competitive advantage for critical resources associated with social dominance.

The possibility of such a strategy is supported by studies of the changes in behaviour that result from hormonal changes associated with oestrus and pregnancy. For example, a peak in testosterone levels in female rats during oestrus (Belanger et al., 1981) is associated with increased activity levels (W.P. Bellingham, personal communication). Such an increase in activity was shown by parous female bush rats in the enclosures. With the onset of oestrus and throughout pregnancy, the tendency to patrol the runways intensified. The coincidental and dramatic increase in intolerant behaviour of reproductive female rats cannot be explained by the flush of testosterone associated with oestrus although testosterone is generally responsible for increased aggression in males, but not females (Tollman and King, 1957; Pfeff, 1969; Payne and Swanson, 1971). Instead the rising levels of progesterone during pregnancy (Hashimoto et al., 1980) may be responsible for the inflated levels of social intolerance shown by parous females (Crowcroft, 1966; Scott, 1966). However, higher levels of progesterone and oestrogen have a synergistic effect facilitating female receptivity. Thus on the one hand, increases in hormone cause increased aggression and activity and consequently increased spacing behaviour, while on the other hand, they cause the same female to become more reproductively receptive towards males (Feder, 1978; Komisariuk, 1978). Thus, the first female
to enter oestrus gains both a reproductive and social advantage over other rats.

**Secondary Social Cues**

Animal spacing and social interactions may also be affected indirectly through olfactory cues associated with the physiological and hormonal changes of a pregnant rodent. Payne and Swanson (1972) showed that male hamsters become more docile and more tolerant of parous females while non-parous females use the same cues to increase their avoidance of the dominant female. In the enclosures, there was only indirect evidence that olfactory cues were responsible for the reduced space-use by subordinates. Both intolerant behaviour and olfactory messages resulting from the dominant female's increased patrolling activities may be responsible for the spatial avoidance by others. The smell of a receptive female may entice and passify males (Payne, 1979), while it causes other females to 'disperse'. This familiar effect might be appropriately and anthropomorphically labelled the 'Chanel No. 5 Effect'.

Similar observations have been made on other species of rats. Under semi-natural conditions, female *R. norvegicus* in oestrus were observed actively marking and defending territories by marking scent on the ground and on rocks (Calhoun, 1962). The response of males and other females to this scent and the ability to discriminate an oestrous female from any other, is dependent on previous sexual experience (reviewed by Keverne, 1978). Experience may partly explain the various levels of avoidance response shown by subordinate bush rats in the enclosures with parous females. Such response variability may be associated with the existence of the linear dominance hierarchy and we might further speculate that the dominance hierarchy is to some
extent dependent on sexual experience. Results from enclosures in the non-breeding season can be examined in this light. The animals in these enclosures showed a weak dominance hierarchy, considerably more tolerance than intolerance toward each other and no sexual activity. As these animals were primarily subadults, they may have been sexually naive as well as sexually immature. We could, therefore, predict that the repertoire of responses that would normally be associated with breeding animals, including attraction, avoidance and intolerance, would be absent. By the same token, reproductively experienced adult females which persist into their second winter, carry with them their experience of responses to other adult rats. This is perhaps the basis of the continued spacing by adult females witnessed in the natural populations over winter (see Chapter 2).

**Spacing Behaviour and its Relevance to Natural Populations**

That the social behaviour of females should emerge as a central theme in the spacing of bush rats, is not entirely unexpected. The important role of spacing behaviour by females in controlling population processes such as dispersal, recruitment and juvenile survival has been demonstrated of other rodents is well documented (e.g. Krebs and Myers, 1974; Wolff, 1980 and papers therein; Svendsen, 1974; Armitage, 1976; Krebs, 1978a; Redfield, Taitt and Krebs, 1978; Krebs, 1979; Mihok, 1979). However, the particular characteristics which result in dominance and space ownership by certain females is not clear. In the field, dominance relationships may only exist in crowded conditions or effectively crowded patches of the environment. In more sparse populations, dominance, or its translation into avoidance behaviour, may be less critical. At high density, the establishment of social rank and the 'physiological benefits'
associated with entering into oestrus becomes more important. The initiation of oestrus may be triggered by environmental cues such as a change in nutrition, or ingestion of phytoestrogens that have been shown to stimulate mammalian reproduction (Negus and Berger, 1977; Labov, 1977). A change in food quality may stimulate male reproductive behaviour and act synergistically with photoperiod to stimulate females (Pinter and Negus, 1965), thus accounting for the time delay in the spring breeding behaviour of females relative to males (see Chapter 2). Alternatively, females may require contact with strange males in order to begin the oestrous cycle. It was shown that virgin female Microtus ochrogaster required stimulation by strange males in order to become reproductive (Batzli et al., 1977; Carter et al., 1980). The typical spring pulse of immigration and wandering behaviour in male R. fuscipes may, then, serve as a stimulus to female reproduction in conjunction with other environmental cues.

The first females to be stimulated to become reproductive may have the advantage of becoming 'spatially' dominant. Their space may be a measure of the resources necessary for successful breeding. While all of the females may eventually become breeders in populations of bush rats in summer (see Chapter 2), there is presumably still some advantage in being first to breed and own space. The stimulus for this is not understood, the physiological basis is only speculative, but evidence of a behaviour mechanism for bush rat spacing is persuasive.

Spacing behaviour and dominance systems such as that witnessed here in R. fuscipes are dependent on typically low interaction rates and mutual avoidance in space. Animals forced into excessively crowded living conditions show a complete breakdown of this behaviour. An example of this is provided by the colony
experiments conducted on *R. fuscipes*, in which 12 animals (6 males and 6 females) were housed in a cage 1 x 1.3 m² with 4 adjoining nest-boxes (see S.A. Barnett *et al.*, 1979 for details of method). The bush rats displayed behaviour very unlike other wild-trapped congeners, including *R. rattus*, *R. norvegicus* and *R. villoisissimus* (S.A. Barnett, personal communication) and most like laboratory-reared albino *R. norvegicus*. This may attest to their extremely plastic social system and may help to explain aspects of seasonal clumping behaviour (see Chapter 2 and enclosure experiment Scattered-B, in on-breeding season) and the social organization of dense island populations (Robinson, 1976; Hobbs, 1971). Or it may stress the importance of space in the establishment of a normal social structure in this species.
PLATE 3.1: The outdoor enclosures.
PLATE 3.2: Runways in the outdoor enclosures. Runways were not always the most direct route between two points.
PLATE 3.3: Runways in the outdoor enclosures were detected in the first couple of days of each experiment by using infrared photography (a) and were so well developed a few days later that they appeared as clear pathways through the grass (b).
Plate 3.4: Nestbox of a breeding female in the outdoor enclosures. Entrances were stuffed with grass and debris and the ground around and underneath was excavated. The entrances were only open at night.
<table>
<thead>
<tr>
<th>NON-SOCIAL</th>
<th>SOCIAL</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Postures</strong></td>
<td>Intolerant</td>
</tr>
<tr>
<td>rolled up (a)</td>
<td>barging/hip throwing (f)</td>
</tr>
<tr>
<td>hunched/crouched</td>
<td>kicking-off (g)</td>
</tr>
<tr>
<td>one paw raised alert (b)</td>
<td>defensive sideways posture (h)</td>
</tr>
<tr>
<td>upright alert</td>
<td>upright threat of defence (h)</td>
</tr>
<tr>
<td><strong>Locomotion</strong></td>
<td>boxing/dual upright attack-retreat (i)</td>
</tr>
<tr>
<td>walking (tail-high or low) (c) (d)</td>
<td>rolling right (j)</td>
</tr>
<tr>
<td>running</td>
<td>chasing (k)</td>
</tr>
<tr>
<td>hopping</td>
<td>harassing at nest-box</td>
</tr>
<tr>
<td>leap (changing direction in mid air)</td>
<td>Tolerant</td>
</tr>
<tr>
<td>climbing</td>
<td>stretched-out approach (l)</td>
</tr>
<tr>
<td>digging</td>
<td>huddling (m)</td>
</tr>
<tr>
<td>exploring (slow walk, sniffing and tail high)</td>
<td>crawling under (n)</td>
</tr>
<tr>
<td>patrolling runways</td>
<td>walking over</td>
</tr>
<tr>
<td></td>
<td>nose-to-nose/vibrissae</td>
</tr>
<tr>
<td>Maintenance</td>
<td>contact (o)</td>
</tr>
<tr>
<td>self-grooming</td>
<td>allogrooming (p)</td>
</tr>
<tr>
<td>consumatory (foraging, feeding, drinking)</td>
<td>draping (q)</td>
</tr>
<tr>
<td>maintenance of nest</td>
<td>Investigatory and Sexual</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Either Social or Non-Social</th>
<th>Following</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vocalization</td>
<td>head-to-tail sniffing (r)</td>
</tr>
<tr>
<td>tooth chattering</td>
<td>mounting</td>
</tr>
<tr>
<td>squealing</td>
<td></td>
</tr>
<tr>
<td>squeaking</td>
<td>Aloof</td>
</tr>
<tr>
<td>Displacement</td>
<td>sitting together</td>
</tr>
<tr>
<td>face wiping (e)</td>
<td>foraging together</td>
</tr>
<tr>
<td>tail flicker</td>
<td>exploring together</td>
</tr>
</tbody>
</table>
Table 3.2: Description of some social and non-social behaviour of *R. rattus* seen regularly in the outdoor enclosures.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intolerant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Attack</td>
<td>Leap on the other rat, with or without biting</td>
<td>Barnett and Harries 1980</td>
</tr>
<tr>
<td>Barging</td>
<td>Synonym: apertact, and/or broadsiding, hip-throwing or offensive sideways posture. The animal stands on all four feet with body raised off the ground, back arched, flank presented to other animal and head turned towards it. May be accompanied by piloerection and squealing.</td>
<td>Barnett 1975, 1979, 1981</td>
</tr>
<tr>
<td>Defensive sideways posture</td>
<td>Very similar to 'barging' but head turned away. Often accompanied by head being held low and some squealing and piloerection. The animal may also raise the back leg to kick at the opponent.</td>
<td>Calhou 1963</td>
</tr>
<tr>
<td>Upright posture</td>
<td>Animal stands on hind feet with forepaws in the air. Sometimes forepaws rest on the other animal. This occurs in defensive rather than offensive display. Accompanied by piloerection and squealing. The animal being threatened is usually the one squealing. Usually accompanied by withdrawal of other animal.</td>
<td>Regg and Nelson 1977</td>
</tr>
<tr>
<td>Boxing</td>
<td>Both animal are reared up on paws, neck stretched out, head held high, balance with tail, body stiff. Feels may come into contact. Accompanied by squealing and squeaking and piloerection.</td>
<td>Barnett 1975</td>
</tr>
<tr>
<td>Rolling fight</td>
<td>Rolling and wrestling. Two rats pounce and tumble, one generally attempts to get on top of other, eyes partially open. Involves biting on back and face.</td>
<td>Calhou 1962; Ewer 1971</td>
</tr>
<tr>
<td>Chasing</td>
<td>Active pursuit. One animal bites at tail of other often followed by attack or rolling fight.</td>
<td>Ewer 1971</td>
</tr>
<tr>
<td>Harrass at nest box</td>
<td>One animal attempts to enter nest box, digs at it, runs around it or sits at entrance. Other animal squeals and attempts to push the intruder away, often stuffing entrance of nest box with nest material. Involves piloerection, squealing, biting, pushing. Can last several minutes. Both males and females do this, although females do it most often.</td>
<td>This study</td>
</tr>
<tr>
<td>Tolerant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stretched out approach</td>
<td>Body held low to ground and extended. Tail may be stiff and raised horizontally. Eyes and ears fixed on opponent.</td>
<td>Regg and Nelson 1977</td>
</tr>
<tr>
<td>Huddling</td>
<td>Animals sitting or crouching beside each other in contact. May involve one animal on top or partially over another.</td>
<td>Barnett 1975</td>
</tr>
<tr>
<td>Draping</td>
<td>One animal stretches over a group of other individuals huddled together. Most frequently occurs in non-breeding season. Actor is generally the dominant individual.</td>
<td>Jannett 1980</td>
</tr>
<tr>
<td>Crawling under, walking over</td>
<td>One animal approaches and clings over the other. Alternatively, one may crawl under the other. One animal may urinate on the other. There is no definite pattern of who crawls under or over associated with dominance rank.</td>
<td>Barnett 1975</td>
</tr>
</tbody>
</table>
Table 3.2 (continued)

<table>
<thead>
<tr>
<th>Note to nose</th>
<th>Synonym: nose-touching and face-to-face nuzzling. Vibrisae of two animals come in contact facing each other. Often preceded by stretched-out approach by both animals.</th>
<th>Callomon 1962 McCartney and Marks 1973 E.C. Grant 1963</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allogrooming</td>
<td>Gentle pawing and nipping of the fur of the other rat, especially around the neck. May become &quot;aggressive grooming&quot; when one animal presses the neck of the other flat to the ground - usually when males allogroom females.</td>
<td>In this case males were observed allogrooming females.</td>
</tr>
<tr>
<td>Investigatory and Sexual</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Following behind</td>
<td>One animal stretched out follows directly behind another, usually attempting to sniff at anal area. Generally results in upright defense posture and animal being followed often squeals. Occurs between and within each sex.</td>
<td></td>
</tr>
<tr>
<td>Head to tail sniff</td>
<td>Both individuals are engaged in anal genital sniffing. Hair may be erect, back arched. May involve some pushing with the head or attempts to raise the leg of the other animal.</td>
<td>Regg and Nelson 1977</td>
</tr>
<tr>
<td>Aloof</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sitting together, foraging, exploring</td>
<td>In all cases two animals are recorded as being within normal interaction distance of each other. Are aware of the other's presence but do not make any obvious actions to engage in active interaction.</td>
<td>This study</td>
</tr>
<tr>
<td>Displacement</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Face wiping</td>
<td>Animal wipes its face several times while in semi-upright posture. Action is jerky and fast.</td>
<td>Regg and Nelson 1977</td>
</tr>
<tr>
<td>Tail flicker</td>
<td>Body held stiffly and only slightly off the ground. Tail is flicked rapidly from side to side. Eyes face forward. Often in response to stranger or sudden move.</td>
<td></td>
</tr>
<tr>
<td>Vocalization</td>
<td>All are distinct sounds which may or may not be the response to presence or actions of another animal. They are described in detail elsewhere (see Barnett and Stewart 1975).</td>
<td>Barnett and Stewart 1975</td>
</tr>
<tr>
<td>Patrolling runways</td>
<td>A distinct action pattern performed, generally by the established dominant animal. The animal walks slowly with tail low and sniffs the ground.</td>
<td>This study</td>
</tr>
</tbody>
</table>
TABLE 3.3: Mean frequency of each type of interaction (No./min.) for each experiment. Enclosures are pooled as replicates. Only intolerant behaviour showed a significant effect due to treatment (experiment) and the experiments are thus ordered and grouped according to results of t-test on experiment means.

<table>
<thead>
<tr>
<th></th>
<th>Mid to late breeding</th>
<th>Mid to late breeding</th>
<th>Early to mid breeding</th>
<th>Non-breeding Late winter</th>
<th>Non-breeding Autumn-winter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Scattered A</td>
<td>Central C</td>
<td>Central B</td>
<td>Central A</td>
<td>Scattered B</td>
</tr>
<tr>
<td>Intolerant</td>
<td>0.0971</td>
<td>0.0720</td>
<td>0.0361</td>
<td>0.0200</td>
<td>0.0112</td>
</tr>
<tr>
<td>Amicable</td>
<td>0.0106</td>
<td>0.0583</td>
<td>0.0282</td>
<td>0.0452</td>
<td>0.0492</td>
</tr>
<tr>
<td>Investigatory</td>
<td>0.0164</td>
<td>0.0164</td>
<td>0.0255</td>
<td>0.0289</td>
<td>0.0188</td>
</tr>
<tr>
<td>Aloof</td>
<td>0.0156</td>
<td>0.0246</td>
<td>0.0121</td>
<td>0.0177</td>
<td>0.0074</td>
</tr>
</tbody>
</table>
TABLE 3.4: Results of a $\chi^2$ test for the non-equal distribution of the number of observed agonistic and non-agonistic interactions among individual rats in each enclosure experiment.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Season</th>
<th>Enclosure</th>
<th>Sex of dominant individual</th>
<th>$\chi^2$ (df = 3)</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central food A</td>
<td>Breeding</td>
<td>A</td>
<td>F</td>
<td>2.01</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>(Oct-Nov)</td>
<td>B</td>
<td>F</td>
<td>6.27</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>F</td>
<td>15.17</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>F</td>
<td>28.83</td>
<td></td>
</tr>
<tr>
<td>Central food B</td>
<td>Breeding</td>
<td>A</td>
<td>F</td>
<td>11.59</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>(Nov-Dec)</td>
<td>B</td>
<td>F</td>
<td>5.17</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>F</td>
<td>4.52</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>F</td>
<td>16.80</td>
<td></td>
</tr>
<tr>
<td>Central food C</td>
<td>Breeding</td>
<td>A</td>
<td>F</td>
<td>41.49</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>(Feb-Mar)</td>
<td>B</td>
<td>F</td>
<td>9.70</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>F</td>
<td>2.31</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>F</td>
<td>3.25</td>
<td></td>
</tr>
<tr>
<td>Scattered food A</td>
<td>Breeding</td>
<td>A</td>
<td>M</td>
<td>13.08</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>(Feb-Mar)</td>
<td>B</td>
<td>M</td>
<td>15.96</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>M</td>
<td>92.93</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>M</td>
<td>107.28</td>
<td>***</td>
</tr>
<tr>
<td>Scattered food B</td>
<td>Non-breeding</td>
<td>A</td>
<td>M</td>
<td>14.56</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>(Apr-Jun)</td>
<td>B</td>
<td>M + F</td>
<td>2.24</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>F</td>
<td>13.42</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>M</td>
<td>12.97</td>
<td>**</td>
</tr>
</tbody>
</table>

(*P < 0.05;  **P < 0.01;  ***P < 0.001)
TABLE 3.5: Results of $\chi^2$ test for association between individual bush rats and nesting sites. One asterisk is used where the test is invalid because of large numbers of zeros in the matrix. In these enclosures animals generally made regular use of one common nest site. Double asterisk indicates an exclusive use of different nest sites by pairs of animals rather than individuals. The number of degrees of freedom is adjusted where an animal has died or escaped.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Enclosure</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p(one-tailed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central A, non-breeding</td>
<td>A</td>
<td>22.59</td>
<td>12</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>season, late winter</td>
<td>B</td>
<td>25.02</td>
<td>12</td>
<td>&lt;0.025</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>9.59</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>11.68</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Central C, breeding</td>
<td>A</td>
<td>49.29</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>season, late summer</td>
<td>B</td>
<td>6.98</td>
<td>8</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>32.28</td>
<td>12</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>16.61</td>
<td>8</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Scattered A, breeding</td>
<td>A</td>
<td>28.30</td>
<td>12</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>season, late summer</td>
<td>B</td>
<td>97.65</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>138.48</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>111.55</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Scattered B, non-breeding</td>
<td>A</td>
<td>*</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>season, autumn to winter</td>
<td>B</td>
<td>*</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>38.44**</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>*</td>
<td>12</td>
<td></td>
</tr>
</tbody>
</table>
FIGURE 3.1: Experimental design used in the enclosure experiments on spacing behaviour in *R. fusipes*. Two food regimes were tested on groups of rats ($N_1 = 2$ males and 2 females) in breeding season and non-breeding season. Two enclosures were allowed to intermix after establishing themselves separately ($N_2 = 2 \times N_1$). Spatial arrangements of nest-boxes and amount of space were kept constant throughout and the amount of food was never restricted.
FIGURE 3.2: Plan of enclosures showing the arrangements of nest-boxes to each other and to food and water in (a) the central food regime and (b) the scattered food regime. During any one experiment, all four enclosures were run as concurrent replicates of the same food regime.

- central food and water
- scattered food; water at each nest box
- nest box
- hole between enclosures
Figure 3.3: Simplified illustrations of some of social and non-social behaviour of *R. fuscipes*.

The letters used here correspond to those in Table 3.1.
Figure 3.4: Change in frequency of four types of social interactions with time ("Watch Effect").

- Heavy solid line = Intolerant behaviour
- Long dashed line = Amicable behaviour
- Thin solid line = Investigatory behaviour
- Short dashed line = Aloof behaviour
Figure 3.5: Summary of the dominance hierarchy established between four individuals and the proportion of the interactions observed between each pair of individuals that resulted in wins (solid area), losses (clear area), and draws (dotted area). The outcomes reference those individuals along the ordinate when paired against those along the abscissa. A line connecting two individuals indicates that they shared or interchanged their social ranks. The size of the circles represents the relative proportion of the total interactions which involved a given pair of individuals. "B→" indicates breeding ♀.

a) the six unique cells in the matrix of interactions used in these figures.
b) Experiment Central-C; Enclosures A to D
c) Experiment Scattered-A; Enclosures A to D
d) Experiment Scattered-B; Enclosures A to D
(c)
Figure 3.6: Three dimensional diagrams of four enclosures illustrating the effect of the observer (whose position is indicated by an arrow) on the activity of confined bush rats. The number of times any individual was observed in each of the grid locations of each enclosure is shown in the third dimension (scale given for each enclosure).

a) Experiment Central-C; Enclosure C
b) Experiment Central-A; Enclosure A
c) Experiment Scattered-A; Enclosure A
d) Experiment Scattered-A; Enclosure C
Figure 3.7: The use of each of the four nest-boxes and other burrows by bush rats in each enclosure experiment. Each quadrant represents a nest-box while burrows are shown by clusters of symbols around the perimeter of the nest-boxes. The movement of animals from Enclosure A to Enclosure B after the holes were unplugged is indicated by the arrow. Likewise for animals from Enclosures B, C, or D moving into their adjacent enclosure. An asterisk indicates statistically non-random use of nest-boxes by all animals combined. "B +" indicates that breeding occurred at that nest-box. Squares indicate males and circles females. Solid symbols indicate higher social rank and open symbols indicate lower social rank.

a) Experiment Central-A
b) Experiment Central-C
c) Experiment Scattered-A
d) Experiment Scattered-B
FIGURE 3.8: Space-use by individuals of different social rank in the same enclosure. A grid was used to determine the frequency with which individuals visited different areas within each enclosure. Accumulated observations on all animals is shown in "A" along with the runway system that developed. Observations on animals of each social rank are shown in "B", "C", "D", and "E" on each page.

The four enclosures illustrated are:

a) Experiment Central-C; Enclosure A  
b) Experiment Central-C; Enclosure C  
c) Experiment Scattered-A; Enclosure A  
d) Experiment Scattered-A; Enclosure C
Experiment Central-C; Enclosure A
No. of Observations

\[
\begin{array}{c}
\text{20} \\
\text{10} \\
\text{0}
\end{array}
\]

(b)

Experiment Central-C; Enclosure C
(c)

Experiment Scattered-A; Enclosure A
No. of Observations

20
10
0

A

B

C

D

E

(d)

Experiment Scattered-A; Enclosure C
FIGURE 3.9: The relationship between the frequency of intolerant interactions and complexity of the runway system. See text for further explanation of symbols.
FIGURE 3.10: The relationship between frequency of intolerant interactions and the stage of pregnancy of the breeding females. C1, C2, and C3 represent different Central food enclosures and S1 and S2 represent different Scattered food enclosures (see text).
AN EXPERIMENTAL STUDY OF THE RELATIONSHIP BETWEEN SPACING BEHAVIOUR AND SOCIAL INTERACTIONS IN INDOOR ENCLOSURES.

4.1 INTRODUCTION

Observations on enclosed populations of *Rattus fuscipes* have revealed that when the opportunity to disperse is denied, the animals become organized in a social dominance hierarchy that is reinforced through agonistic behaviour, is affected by sex and breeding condition of the individuals involved (Chapter 3). In natural populations, where rats are free to disperse as they choose, there is evidence that individuals tend to space themselves to form predictable dispersion patterns according to age, sex and season (Chapter 2). It is therefore possible that the spacing patterns measured in these natural populations result from the same type of social interactions that maintain dominance hierarchies in confined populations. The relationship between social interactions and patterns of space use is explored further in this chapter.

Several new questions were raised by the methods used and observations made in the semi-natural enclosures. In particular, there were unsatisfied queries about the possible effects of changes in the quantity of food available, in the density of animals and in the effects of seasonal changes in temperature. In the outdoor enclosures, bush rats experienced natural temperatures. As a result, the clumping behaviour observed in the non-breeding season (winter) may be an adaptation to low temperatures rather than being the result of a change in breeding conditions of the individuals (see also Wolff
and Lidicker, 1960). In the same experiments the 'actual' density of the animals remained constant throughout, although the mixing of two enclosures changed the 'effective' density and, as a result, the potential frequency of encounters. This led to questions involving the effects of changing 'actual' density. Likewise the problems involving food availability remain unsolved. While the distribution of food was altered, the amount of food available could not be controlled since grass throughout the enclosures could be used as feed at any time. In addition, questions were raised regarding the development and use of runway systems through the grass. One might enquire whether runways were simply the paths of least physical resistance between two objects (i.e. the grass in the enclosures may have caused some resistance to movement) or whether runways would exist where movement was uninhibited. If runways exist when the surface can be traversed easily in any direction, then the role of runways as avenues created for easy movement is doubtful. There is much speculation regarding the purpose of runways, but their existence is accepted as a general phenomenon in studies of space use by animals (Pearson, 1960; Lidicker & Anderson, 1962; Hediger, 1967 and papers therein; Mykytowycz, 1974; Staples and Terman, 1977).

The purpose of the study presented in this Chapter was threefold. First, it was intended to experimentally assess the development, use and effect of runways in a very simple environment. Secondly, the experiments performed in outdoor enclosures were to be repeated and special attention paid to the consequences of manipulating food supply and animal density were manipulated, and temperature was maintained at a constant level. The third purpose was to design a method by which these study aims could be achieved; thus, ways of building and monitoring indoor enclosures were devised. The
results offered preliminary indications of the value of this approach.

4.2 EXPERIMENTAL DESIGN AND METHODS

The experimental design was very similar to that used in the outdoor enclosures. There were four enclosures and two food regimes (central and scattered food). As in the outdoor enclosures, animals in adjacent indoor enclosures (called “pools” herein) could gain access to the other pool through holes in their common wall. These holes were closed during most of the experiment. Each pair of pools had the same food regime so that two replicates of both central food and of scattered food experiments could be run simultaneously. The four pools were labelled A, B, C and D respectively. A total of six replicates of each food distribution (total of 12 pools were observed) were completed and each experiment lasted for one month, or until a parous female gave birth to her first litter.

In addition to short-term experiments, four pools (2 central food and 2 scattered food) were allowed to run for approximately one year (from 26 March 1979 to 14 March 1980). Continuous records of breeding and health (wounding etc.) were kept and monthly weights of individuals were obtained for each population.

The bush rats used in both long and short-term experiments were wild-trapped at various localities within the ACT at a minimum of one week before the start of each experiment. They were treated for ectoparasites using Malawash and held in separate cages under reversed lighting conditions. The light/dark phases were adjusted monthly in accordance with natural day length. Individuals were ear-tagged using Haupner fingerling tags and their fur was dyed using a code for
individual identification. Each experiment began with two males and two females, except in one of the long-term experiments, where a pool with central food began with an accidental mixture of three males and one female.

Behaviour was observed under red light for three hours every second day for the first 21 days of both the short and long-term experiments and irregularly after that in the long-term experiments. Observation periods consisted of 15-minute rotations between pairs of enclosures during which time individual behaviour, social interaction and movement were continuously recorded. Movements were drawn on maps of each pool and interactions were scored according to type and outcome (see Chapter 3). A total of 45-minute observations were thus made on each population during each session.

In addition to direct observation of behaviour, remote sampling was done using an overhead camera and wide angle lens (21 mm) set to take a picture once every hour. The camera and flash unit were driven by a timer set for two hours before and two hours after the dark period each day. As only one pair of pools could be monitored in this way during each experiment, there were only six photographed pool populations.

Each pool consisted of a rectangular wood frame supporting metal walls, 1 m high. Pilot experiments were performed in circular units made from frames of children’s swimming pools. The shape was changed in order to mimic that of the outdoor enclosures while the original design gave rise to the name “pools”. Each pool occupied an area of 8.64 m² (2.6 m x 3.6 m) and was separated from an adjoining unit by a single wall. The floor was specially designed to be absorbent and relocatable. It therefore consisted of tiles (60 cm x 60 cm) each of which could be moved and replaced. A total of 24 tiles
in each pool were made of sheets of 26 guage galvanised metal covered with fine wire mesh which protected a sheet of absorbent paper placed between the two layers. Tiles were held in place on the floor by grooved plastic runners. A photograph of two pools with centralised food and the standard distribution of four nest-boxes is shown in Plate 4.1. Nest-boxes were simple metal boxes (approximately 20 cm x 10 cm x 10 cm) partly covered by a lid of transparent red perspex. As a result, animals could be seen inside nest-boxes without physical disturbance or exposure of light. Each nest-box was initially provided with 20 g of coloured cotton wool, a different colour in each. By doing this, any hoarding or movement of nest material by the rats could be easily recorded. Additional bedding was either scattered in the pool or placed in a wire basket near a centralised water source depending on the food regime. The water was provided in water bottled on a centrally situated retort stand (central food experiments) or in metal holders attached to each nest-box (scattered food experiments). Food was either thrown randomly over the floor or placed in a central food tray. The water was mixed with minute amounts of fluorescein powder which enabled detection of aged and fresh rat urine on the floor of the pool when it was exposed to ultraviolet light. A hand-held UV unit was used to periodically map the patterns of urine deposits in each pool. On the 17th or 18th day of the experiment, the patterns were disrupted by shifting the floor tiles within each pool. Movements and social interactions were carefully noted before and immediately after the 'switch'.

Three days after moving the tiles and observing the rats’ response to the rearranged floor, the food in each pool was left unreplenished for the next three days. On the fourth day normal allotments of food were renewed. The nature and number of food hoards
were monitored during those four days of food shortage. Throughout the rest of the experiment food and water were provided in excess.

4.3 RESULTS

Throughout this section the results have been illustrated by typical experiments. That is, unless otherwise stated, the results shown are considered to be typical under the stated experimental conditions.

4.3.1 Short-term Experiments

4.3.1.1. Factors Affecting the Frequency of Social Interaction

Each of the 12 indoor populations of bush rats (i.e. a group of four animals consisting of two males and two females) observed during short-term experiments developed clear dominance hierarchies and ten of these involved some breeding. Eleven of the 12 populations (5 with central food and 6 with scattered food) were dominated by a female while one population with central food resource had a dominant male.

The dominance hierarchies developed rapidly in the first few days of each experiment. They were not static after that time and there were generally some minor changes in the relative status of some individuals, particularly the non-dominants. In comparison to the rate of interaction observed in the outdoor enclosures, the rate in the pools was high. For example, the mean frequency of encounters per minute was 0.40 and 0.47 in one set of central and scattered food pools respectively, whereas the rates were 0.14 (Central-C) and 0.13 (Scattered-A) in two matching outdoor enclosures. This difference in
the rate of interaction is not directly proportional to the relative
difference in the size of the enclosure or density of animals. The
indoor enclosures were 8% of the size of the outdoor enclosures, but
housed the same number of individuals.

It was difficult to determine what a typical sequence was in
the establishment of social dominance hierarchies. The rate at which
hierarchies developed, the initial rates of encounters and general
patterns of space use varied enormously between groups of rats,
regardless of the food regime. The best example of contrasting
results was shown by a replicate pair of pools set up and observed
concurrently during winter. Both had a central food source and were
photographically monitored once every hour. In one group (Pool A)
there was a great deal of negative interaction from the onset.

Animals tended to avoid each other, squeal on contact or threaten each
other. Consequently, the general pattern of space use was dispersed.
The adjacent pool (Pool B) was the opposite. Individuals showed a
great deal of amicable behaviour and were generally observed clumped
together. The 286 photos taken of these pools confirm this. The
group size was significantly smaller in Pool A than Pool B ($X^2 = 80.33$
P < .001, df = 3). The frequency with which groups of different sizes
were observed is summarized below. Expected values are underlined.

<table>
<thead>
<tr>
<th>GROUP SIZE (No. of individuals)</th>
<th>Mean Group Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Pool A</td>
<td>367</td>
</tr>
<tr>
<td>339.62</td>
<td>91.13</td>
</tr>
<tr>
<td>Pool B</td>
<td>233</td>
</tr>
<tr>
<td>260.38</td>
<td>69.87</td>
</tr>
</tbody>
</table>
The dominance hierarchies in these pools also differed. Pool A had a female dominant rat and Pool B was the only pool experiment of the twelve in this study which had a dominant male. Dominance was assessed subjectively in each pool and included observations on individual behaviour and tendency to win or lose encounters. The hierarchies thus established were compared with the likelihood of individuals to be out of a nest box when the photos were taken. The results are given below.

<table>
<thead>
<tr>
<th>Social Rank</th>
<th>Pool A</th>
<th>Sex</th>
<th>% Photos Present</th>
<th>Pool B</th>
<th>Sex</th>
<th>% Photos Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>F</td>
<td>61.4</td>
<td></td>
<td>M</td>
<td>93.1</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>M</td>
<td>68.3</td>
<td></td>
<td>F</td>
<td>95.9</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>F</td>
<td>62.1</td>
<td></td>
<td>F</td>
<td>91.0</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>M</td>
<td>54.5</td>
<td></td>
<td>M</td>
<td>86.2</td>
<td></td>
</tr>
</tbody>
</table>

The trend of these data show that the lowest ranked individual is the least active, followed by the third ranked individual in both cases. The top two individuals do not follow this trend in either pool. In the female-dominated Pool A, all of the animals were consistently less active than those in the more amicable and male-dominated Pool B. This tendency to avoid each other and disperse was confirmed also by the nesting habits of the two groups. In Pool A all four animals were never found to nest together. During the 31 days of the experiment, only 5% of the observations involved three animals per nest-box, about 50% involved two animals
and the remainder involved only one individual. In contrast, the animals in Pool B were always found together, although they were inconsistent about the use of any particular nest-box.

When the animals were active the degree of intolerance shown by the dominant female did not necessarily affect the degree of clumping or amicable behaviour shown by the subordinate (correlation coefficient $r = .042$). There was no increase in amicable associations among subordinates. Nor was there a decrease in the amount of amicable behaviour expressed. Figure 4.1 provides a summary of these results for pools in which females were known to become dominant.

### 4.3.1.2. Social Interactions and the Patterns of Space Use

In all twelve experiments bush rats were observed to regularly mark areas of the pool with fresh urine. Immediately after dark, rats moved around the pool urinating at specific sites. This was not the exclusive activity of the dominant animal, as all rats behaved in this way to some degree. The latrines did not conform to any apparent pattern, although they most frequently occurred in corners or places where animal traffic was particularly high. It is hard, in this case, to determine which of the factors, high visitation rate or urine deposits, was the cause or effect. Figure 4.2 shows the pattern of urine marking revealed by UV light. Not only do latrines become apparent but patterns of dribbled urine are shown to coincide with regular patterns of movements. They were considered to be indications of runways developed in a simple environment and were recorded as such.

The pattern of movements of individuals on Days 1, 6, 18 and 21 are shown for two pools with central food and two with scattered food regimes (Figures 4.3a, b and 4.4a, b). On the first day, animals
tended to wander about the entire pool. The lines indicating the
rats’ movements were irregular and widely spread, although a great
deal of time is spent on the edges of these pools. By Day 6 a regular
pattern of space use was established. The animals moved in a
predictable manner and lines depicting animal movements were smooth
(i.e. not erratic or meandering) and clustered. The urine pattern
shown by fluorescense spots on the floor tiles, coincided with the
rats’ movement patterns. On Day 17 or 18, the floor tiles were
relocated and the movements which followed were correspondingly
erratic. The rats spent much of their time in alert postures,
tail-flicking or wandering about sniffing the ground. The result was
an irregular movement pattern similar to that seen on the first day.
On Day 21 the animals had resumed a regular pattern of space use.

In order to quantify this dramatic increase in displacement
behaviour, the frequency of tail-flicking observed before and
immediately after the rearrangement of the floor tiles were compared.
Twelve pools, 6 central food and 6 scattered food, were included in a
t-test which was used to compare the number of observed tail-flicks
per 15-minute period before and after the ‘switch’. The mean
frequency of tail-flicking before was 0.128/min (SD = 0.014 N = 12)
and after, 1.05/min (SD = 0.668 N = 12). The t-test showed a highly
significant increase in the frequency of this behaviour (t = 5.185 df
= 11, P < .001).

An attempt to numerically assess this change in pattern of
space used failed. A drawn grid of 344 units (24 x 16) was placed
over a map of each pool on the days mentioned above (Days 1, 6, 18 and
21). The number of squares transected by lines representing movements
during 15-minute observation periods were counted. The numbers of
transected squares shown below did not reveal the different movement
patterns which were visually so obvious. A comparison of the values on Day 6 and Day 18 are only slightly significant at the 5% level (X² = 8.23 df = 3 P < .05). Other columns and rows of the same table also show significant significant chi-square values thus invalidating the test.

<table>
<thead>
<tr>
<th></th>
<th>Exploring</th>
<th>Established</th>
<th>Disrupted</th>
<th>Re-established</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>new space</td>
<td>pattern</td>
<td>pattern</td>
<td>pattern</td>
</tr>
<tr>
<td>Central food</td>
<td>Pool A 153</td>
<td>216</td>
<td>174</td>
<td>277</td>
</tr>
<tr>
<td>Scattered</td>
<td>Pool B 178</td>
<td>173</td>
<td>205</td>
<td>123</td>
</tr>
<tr>
<td>food</td>
<td>Pool C 250</td>
<td>179</td>
<td>152</td>
<td>127</td>
</tr>
<tr>
<td></td>
<td>Pool D 208</td>
<td>219</td>
<td>209</td>
<td>116</td>
</tr>
</tbody>
</table>

There was no consistent difference between the number or positions of runways in the two food regimes. The pattern of faeces on the floor was, however, more evenly dispersed in the scattered food than central food experiments. This corresponded to the tendency of rats to eat the food wherever it was found and to defaecate at that site.

In addition to altering the pattern of space use by individuals, the relocation of the floor tiles also affected interaction rates between animals. The rates of interaction varied with time (Figure 4.5). In the two scattered food experiments illustrated here, the timing of the peaks of interactions relative to the breeding state of the dominant female was not the same. There were however, similarly low levels of interaction at the beginning of
both experiments and on the day when the floor tiles were moved. The interaction rate in an unfamiliar environment among unfamiliar animals was similar to that in a familiar environment with familiar animals and a relocated runway system. Within a couple of days the interaction rate had began to rise again, coincidental with the re-establishment of movement patterns.

4.3.1.3. Dominance, Body Weight and Breeding in Short-Term Experiments

Results from one pair of central food experiments and one pair of scattered food experiments were used here as examples of the types of association generally observed between social dominance, body weight and reproductive status of individuals in each pool population. The results are given in Table 4.1.

Initial weight of animals was not a good indicator of social status. Sex is a better indicator as females are generally dominant. In the single case where a male is dominant, the two females were "a cut of adult weight (110 g) at the onset of the experiment. Among males, however, the heavier animals were generally the higher ranked of the two and were often seen to sit near the dominant female in the pool. Change in weight was also a good indicator of social rank and it was generally the case that the dominant animal improved in body weight more than any other. This trend was confirmed by a re-analysis of unpublished experiments performed by S.A. Barnett in small colony cages (for description of experimental design see Barnett, Dickson and Hocking, 1979). Six trials involving 12 (6 male and 6 female) bush rats giving a total of 72, showed the same trend. In this case dominance was measured by the consistency with which an individual was
active on the cage floor. Dominant animals consistently showed the best weight gain.

With one exception only the highest ranking female gave birth during the short-term pool experiments. In Pool D, (see Table 4.1) the subordinate female successfully mated during the 3-day absence of the dominant female. Twenty-two days later, and sometime after the end of the experiment, the subordinate gave birth to a litter. The subordinate did not engage in sexual behaviour in the presence of the dominant female.

4.4 The Effect of Food Shortage

The restricted food trials were only three days long. This was insufficient time to observe differences in the rates or nature of interactions between individuals. There was however, a difference in the rate of hoarding. Food shortage alone did not stimulate an increase in the number of caches observed. But the re-introduction of food on the fourth day of the trial resulted in a rapid development of new caches. The mean number of caches before food restriction was 1.5 (SE = 0.33) and the mean number of caches after reintroduction of food was 4.13 (SE = 0.95). The results after eight restricted food trials are given below.
4.3.1.5 Behaviour Associated with Pregnancy and Rearing of Young

The development of hoards could not be entirely attributed to the effects of food shortage, since the amount of hoarded material also showed a dramatic increase during the latter phase of pregnancy. Plate 4.2 shows an example of a nest which was prepared with bedding material hoarded from all of the other nest-boxes, and surrounded with food. The breeding female was generally seen to protect the nest and the hoard from any interruption from other animals during the hours of darkness. In the central food experiments, dominant breeding females were seen to interrupt other animals as they fed or drank. But these events may have been the result of their intolerance of the presence of any rat in the pool and not their intention to interrupt their feeding. Likewise, in each of the six scattered food experiments, the water bottles associated with the nest-box of a dominant female
remained full when others were empty. She protected it from use by others while excluding them from her vicinity.

During the latter stages of pregnancy the intensity of intolerant interactions increased and as a result of the fighting and chasing, the objects in the pool were often scattered and turned over (see Plate 4.2). By this stage, the maternal nest became very large and bulky and had only one small circular entrance. Just before giving birth the mother urinated over the piles of nesting material and food and then apparently urinated on her young for the first few days after they were born, as they were often found wet with urine.

The young first emerged from the nest at about 15 days. In contrast, young are first trapped in the field at about 28 days of age (Chapter 2). For the first two weeks after emerging from the nest (Days 15 to 29), the young followed the adults very closely (Plates 4.3 and 4.1). The juveniles in the pools did not discriminate between their mother and other adults and appeared to follow any adult. They were often seen huddled with other adults or sometimes sucking at the mouth of these animals, a behaviour also described by Ewer (1971) for R. rattus. The dominant male was particularly tolerant of the young and was often found in a nest-box brooding a group of juveniles, or huddled with them in the corners of the pool. Whereas the mother would usually rush out of her nest when disturbed by my activity while inspecting nest-boxes, the brooding male would sit very quietly and could be prodded or handled without any response.

4.3.2 Long-Term Experiments

4.3.2.1 Breeding Potential

The long-term experiments lasted for 348 days. During this time each pool population had a maximum breeding potential of 15
litters per female. This assumes a gestation period of about 23 days and independence of young between 15 and 28 days. Of the 210 litters possible in all four pools, only 13 were realised. Figures 4.6a, b and 4.7a, b summarise the breeding performance of each population for the 12 months period.

Litters were born at any time of the year in this indoor environment but few litters were successfully reared. The degree of success was particular to each pool and was not related to the food regime. Five of the 13 litters survived a short period before being killed, five litters were killed immediately after birth and one litter was born in the last few days of the experiment. It was reared successfully in a separate cage.

4.3.2.2 Breeding Performance in Each Pool

The breeding performance in each pool can be summarised briefly.

Central food. Pool A: five litters were born; one founder female bred and two of her daughters also gave birth. Only one litter of the founder female was successful and the daughters bred only after the mother died. Only one of the daughters successfully reared a litter. The other litter was killed. The sister of the breeding female cooperated in rearing the young and was found to have swollen nipples at the same time as the successful mother. It was not clear whether or not surrogate mothers actually lactated.

Central food. Pool B: two litters were born to one of the founding females which survived most of the experiment. No other females were known to become pregnant.

Scattered food. Pool C: two litters were born to only one of the
founding females and she also survived the experiment. No other females were parous.

cattered food. Pool D: four litters were born. Both of the founding females gave birth to a litter but the dominant female took over the litter of the subordinate mother. She successfully reared it along with her own. There was cooperation for three days before the dominant female began to violently exclude the other mother from the nest. After that, only the dominant female continued to breed and she also survived the experiment. None of her daughters became pregnant during that time.

4.3.2.3 Intolerance Levels

Associated with breeding and different stages of the colony growth were changes in levels of intolerance. The pools were scored on a regular basis for the severity and frequency of intolerant interactions observed in a 15 minute watch. The scale of intolerance was set from 0 to 5 and was based on the approximate amount of time out of each observation period that some individuals in a given pool were engaged in intolerant behaviour. Intolerance was either very rare (score 0) or it was observed for at least 20% (score 1), 30% (score 2), 50% (score 3), 75% (score 4) or 90% (score 5) of the time.

These changes are shown in the same Figures (4.6a, b and 4.7a, b). In Pool A the levels of intolerance were associated with the time of breeding. At the beginning the levels were high and there was an immediate establishment of a dominance hierarchy. When the dominant female died, one of her daughters became the dominant individual and also acted very intolerant. She was the first of the siblings to breed, although her litter was unsuccessful. In contrast,
the males rarely fought or threatened each other in this pool or in any other.

In Pool B the initial levels of intolerance were low and may have reflected the composition of the founding group. In this case there were three founding males and one female. When the litter grew to become subadults, and as a consequence, the group structure became more complex, the levels of intolerance also rose. In Pool C both founding females were in oestrus at the beginning of the experiment. They both solicited males and were amicable to each other. The levels of intolerance rose after that and only one female gave birth although a second female developed swollen nipples at the same time but did not give birth. Previously two sibling females of Pool A showed the same behaviour; one gave birth and the other developed enlarged mammarys. Intolerance levels peaked when the young were subadults. After the first litter, breeding behaviour ceased and the animals appeared very unhealthy and became relatively inactive.

At the onset of Pool D, the dominant female was very intolerant and quickly established her social dominance. The second female however, managed to build a nest and gave birth to a litter. The dominant female destroyed this nest when she prepared her own and then took over the litter after her own was born. As in other pools, the dominant female was intolerant of all animals, except young when they began to wander about the pool. She excluded both subadults and adults however, whenever she prepared a new nest.

4.3.2.4 Fatherhood

Fatherhood was assumed using two criteria: 1) the degree of attention paid to the oestrus female and her acceptance of him, and 2) the degree to which his testes were descended. This latter
characteristic was variable among males and subordinate males often had clearly under-developed scrota.

Only one male in Pool A had fully descended testes at the start. The other male was of subadult weight and did not show descended testes until Day 30. Two of the males in Pool B had descended testes while the third did not develop until approximately Day 90. Only one of these males, however, gave constant attention to the female and interrupted any social interaction with her. In Pool C the dominant female accepted the occasional attention of only one male. She fought, chased and bit the other male, although both males displayed descended testes. The situation was very similar in Pool D. One male was favoured by the dominant female. The father of the subordinate female's litter, however, could not be determined with equal certainty. There were difficulties in ascertaining fatherhood where the subadults had fully developed scrota (e.g. as in Pool A). Their possible contribution to the litters cannot, therefore, be excluded. Incest could not be overruled.

4.3.2.5 Weight Profiles

The weights of the founding rats and their offspring are shown in Figures 4.8 and 4.9. The young in Pool A gained weight very rapidly and maintained adult proportions shortly after three of the founding individuals died. Among the dead was the dominant female. A spread in the relative weights of the siblings appeared at about 2.5 months when they reached a weight of about 110 g. However, in Pool B, in which the breeding female persisted, the young weighed only 80 g at 2.5 months. At this time the body weights of the siblings began to diverge (Figures 4.8 and 4.9). This was also true for Pool C where the young at 2.5 months had begun to show a spread in weights ranging
between 80 and 100 g. In Pool D where the dominant female survived and was extremely tolerant throughout the duration of the experiment, the young weighed less. At 2.5 months they weighed between 60 and 85 g and showed some individual differences. The young in Pool A, where most of the adults died early, appeared to do particularly well when compared to the litters in other pools where the founding adults persisted.

4.4 DISCUSSION

An Experimental Approach to the Study of Social Spacing

Small indoor enclosures called pools were used to verify and explore some of the observations that were made in the larger outdoor enclosures described in Chapter 3. These smaller enclosures provided controlled environments in which experiments similar to those performed outside could be repeated while giving closer attention to those aspects of bush rat behaviour that might help in understanding social spacing in this species. This behaviour included the development and use of runways by bush rats, the establishment of social dominance hierarchies and the relationship between social status and the use of space and resources by each individual. In particular, the pools were designed to enable the rearrangement of objects in the rats' environment as well as a rearrangement of the runways they developed. In this way it was possible to disrupt the strict pattern of space use by the rats, exemplified by their runways, and observe any associated changes in the patterns of social interaction among the residents. Short and long-term experiments
using these pools provided comparative information of the effects of high density, and confinement on the survival and breeding success of adults and on the growth and survival of young bush rats. The results of these experiments were interpreted in the light of certain limitations inherent in the use of enclosures to study natural behaviour of animals.

Limitations of the Study

The limitations of enclosure studies stem from the prevention of escape and the necessity to share all resources (including space) which may be unnatural circumstances for bush rats. In general, enclosures are apt to induce aberrant social behaviour, and this is therefore an important consideration in the interpretation of the behaviour observed under these conditions. Ever (1971) criticizes some of the fundamental work on the behaviour of wild rats confined to enclosures (Barnett, 1958) on the grounds that it is difficult to distinguish natural from enclosure-induced behaviour.

Populations biologist are aware of the problems of dealing with enclosure-induced behaviour and the difficulties of interpreting demographic data from enclosed populations (e.g. Lidicker 1975, 1979). However, it was only because of the negative effects of enclosures that some population biologists were able to identify the importance of such phenomena as dispersal in regulating local numbers of animals. It became clear that only enclosure populations showed boom-and-bust population cycles (e.g. Myers and Krebs, 1971, Krebs, 1978a) thus indicating that confinement had affected the natural behaviour of the individuals and had effectively blocked emigration. Other important side-effects of confinement include the development of strict social hierarchies which become exaggerated in enclosed populations.
(Calhoun, 1952), and the tendency for small crowded enclosures to result in certain social conditions that lead to the cessation of all reproduction among residents e.g. Crowcroft and Rowe, 1954; Terman, 1965).

The present study is affected by at least one other limitation; the lack of strict experimental controls. It was not possible to eliminate variation in all but one variable to identify the precise variable inducing a behavioural response, and then to set up a precise control. For example, although increased hoarding was associated with a change in food supply (Section 4.3.1.4), the reproductive state of individuals was changing during these observations and may have influenced the results. Breeding females generally hoarded vast quantities of nesting material and as Wallace (1979) and Ewer (1968) argue, the motivation for hoarding behaviour in rats can be any one of a number of complex stimuli among which are the physiological state of the animal, the portability of the objects, as well as the shortage of food. The problems associated with interpreting some of the findings in these enclosure experiments limit the value of some of the manipulations and are therefore taken into consideration throughout the following discussion.

Use of Space and Development of Runways

The observations of bush rats in small pool enclosures confirmed the findings of the larger outdoor enclosures and of the field studies on natural populations that bush rats do not use space randomly, nor evenly. Bush rats confine most of their activity to runways and nest-boxes. That is, animals adhered to pathways for movement between shelter and food and during social encounters. The runways that developed in the pools were not as noticeable as the worn
pathways found in the outdoor enclosures, but their effect on the
behaviour of the animals was equally profound. As in the outdoor
enclosures, runways became apparent after the first four or five days
of the experiment and they were quickly re-established after they were
purposefully disrupted.

The development of runways was monitored through the use of
fluorescose in the drinking water. Rats urinated as they ran along
their pathway or as they sat hunched in corners and using this
technique permitted areas of greatest use to be identified when
exposed to ultraviolet light. This made it possible to map paths and
rest spots and to experimentally rearrange these later in the study.
The initial reaction of rats to the rearranged runway system was an
increase in exploratory behaviour and a more random movement around
the pool. Erratic movements were accompanied by a drop in the rate of
social encounters between residents. Thus bush rats appeared to
respond to their rearranged environment in a manner similar to animals
introduced to a new environment (Figure 4.5) suggesting that runways
must contain cues regarding the familiarity of an animal’s environment
(Hykytowycz, 1974). There was also an increase in displacement
behaviour (Barnett, 1975, p244) such as alert postures and
tail-flicking (Section 4.3.1.2) suggesting that runways may give
resident animals the confidence to move freely within a familiar space
and the reassurance that certain resources including shelter and food
will be found by following one or the other of these pathways:

The use of runways appears to be a natural behaviour for
bush rats. Their use may have been exaggerated but was not induced by
confinement in enclosures, as supported by evidence of the use of
runways by bush rats under natural conditions at Kioło (Section
2.3.3.4). In the outdoor enclosures runways occurred in both the
breeding and non-breeding seasons and in the presence of either scattered or central food and it seemed that runways were not solely the consequence of continuous movement back and forth between resources such as food and shelter. Nor did runways appear to be the 'line of least resistance' to movement through dense vegetation as was clearly illustrated by the development of a runway system in the pools where the substrate was smooth and uncluttered. Runways appear to serve several purposes. They mark the boundaries of an animal’s familiar space, permit ready access to critical resources, provide escape routes from predators and provide a means for collecting information about conspecifics in the same area.

The social component of runway systems was best illustrated in the outdoor enclosures where their use by resident rats was controlled by the dominant animal and the runway system itself became more complex as the rate of antagonistic interaction initiated by the dominant animal increased. Since they could not disperse, subordinate animals could only respond in one of two ways. Either they would try to use the runway when the dominant rat was not active, resulting in some temporal partitioning of the enclosure among themselves (as shown for some rodents in the wild, Connolly, 1975) or they would try to use some alternative pattern of space use so that they could avoid physical contact or the odour of the dominant animal.

It is possible that the nature of the runway systems seen in the pools and outdoor enclosures reflected 'conditioned responses' of individual rats that had had previous experiences in this regard. Since all experimental animals were wild-trapped, they would have had experience in use of runways and responding to the runways of others in their natural environment. The importance of such social experience on olfactory-guided behaviour was demonstrated by Richards
and Stevens (1974) who showed that socially naive mice in isolation were less discriminating in how they marked their space and responded to space already scent-marked by others. The possibility that runways exist as a consequence of conditioned social behaviour, may be tested by observing a group of young and socially naive rats in enclosures without the influence of wild-trapped adults.

Use of Space and the Effect of Social Dominance

In the natural situation runways may result in a reduction in the number of social interactions because they may transmit social cues which replace the need for encounters. Runways may offer a trespasser olfactory cues regarding space ownership and the message that other rats should avoid occupied territory. In the pools dominance hierarchies were established and maintained through overt antagonism and were reflected in unequal partitioning of space among residents. The dominant animal moved freely about the entire pool while others fled from her (only once did a male become dominant) or huddled along the perimeter. The dominant animal was intolerant of the other rats and they made frequent attempts to escape by trying to dig under the walls of the pool, trying to jump out or trying to chew out the plugs in the wall between pools. As the dominant female became more intense in her efforts of expel the others, they became more restricted in their activities. In more colonial species such as R. norvegicus or R. similis, overt aggression such as that observed for R. rattus is minimal and dominance is often maintained through stylized fighting behaviour (Barnett and Stewart, 1975; Begg and Nelson, 1977; Barnett and Harpley, 1981) or various forms of amicable behaviour (discussed by Flannelly and Lore, 1975). Rattus fuscipes is not colonial and except for autumn and winter, it is not
likely to be found living in groups (see Chapter 2). It is therefore unlikely to have well developed stylized social behaviour patterns. Instead, females in breeding season maintain their relationships through spacing behaviour essentially achieved through mutual avoidance. The occasional reinforcement of spatial dominance through overt agonistic behaviour may encourage the existence of a typical avoidance response by all rats in order to avoid costly physical interactions (Devi, 1979).

Social Behaviour and the Effect of the Dominance Hierarchy

It is hard to understand the particular features of the environment over which females are fighting to maintain strict and exclusive control. While food and shelter were not in short supply in the pools, it is likely that social dominance secures priority of access to food, shelter and mates in natural situations. This situation has probably evolved over a long period of time and it is possible that the fight for social dominance no longer requires a proximal stimulus other than the presence of another individual or potential competitor. Wynne-Edwards (1962) states that this relationship between dominance and access to resources had led to selection for individuals who fight directly for social dominance rather than fight directly for food or other resources. However, Baenninger (1970) argues for the opposite point of view and he demonstrated that spontaneous social hierarchies are quite unrelated to water or food hierarchies in the Norway rat. Instead, he suggests that there are three separate hierarchies related to food, water or social status and that social dominance confers no priority access regarding food or water to the socially dominant animal. There are two reasons for rejecting these suggestions of Baenninger (1970)
including the means by which he assessed dominance. His measure of social dominance was based on the wins and losses tallied during dyadic encounter. Food and water-related dominance were based on the relative amount of each resource consumed by individuals. Dyadic encounters lasting only a few moments in a neutral arena would not be a useful measure of social dominance in R. fuscipes. Dyadic encounters are useful tools for determining whether the mutual response of two strangers is amicable, antagonistic, avoidance or neutral, but such encounters are not useful in determining relative social rank of the animals. Dominance hierarchies may take days to establish among a group of R. fuscipes and once the highest rank is established all others may continue to change indefinitely. Part of the changeability is due to the overwhelming effects of the onset of oestrus on the spacing behaviour of female bush rats.

The second argument for opposing Baenninger's (1970) suggestions is that it was unlikely that dominance would develop in conjunction with spacing behaviour if the process did not involve rivalry for valuable resources critical to survival or breeding. As a result of owning space an animal may be the first to breed or may be the only one to breed. In the pools the first to breed has several advantages among which is the survival of her litter. In these experiments the first litters weaned were also the only litters which survived the duration of the long-term experiments.

Successful breeding was clearly a function of social dominance in these small enclosures. Only one female successfully bred and reared her own young to weaning. Other females which became pregnant but were not socially dominant either failed to give birth or lost their litter shortly after birth. Their young either died or were taken over by the dominant female. These subordinate females
were the focus of a great deal of hostility and were often harassed in
their nest-boxes, chased or bitten by the dominant female. As a
consequence their health generally deteriorated and they made no
further attempts to breed while confined to the pool. This
relationship between social dominance and breeding among members of
confined social groups has been revealed for *Mus musculus* (Delong,
1978; Crowcroft and Rowe, 1957), *Peromyscus maniculatus* (Terman, 1965,
1975), *Microtus ochrogaster* (Thomas and Birney, 1979) and *Rattus
norvegicus* (Calhoun, 1952), suggesting that social inhibition of
reproduction may be a natural phenomenon in some rodents. We would
expect intrasexual competition for reproductive status to be high
where some members of a population can regulate the breeding success
of other members (Emlen and Oring, 1977) and the possibility of such
an effect would prevent grouping of animals during breeding and would
encourage females to space themselves as much as possible. In the
wild, the dispersion of female bush rats is probably a compromise
between maintaining proximity to resources and maintaining distance
between conspecifics.

The exclusive breeding rights of the dominant female in the
pools included the apparent right to take over any other litters born
in the same pool. On two occasions litters were born to subordinate
females and were conceived either before the experiment began or
before the dominance hierarchy was completely established. On both
occasions the litters were stolen by the dominant female. Since the
dominant animal usually travelled about the pool urinating on objects
including nesting material and food, any alien litters would, as a
consequence, carry her smell as well. This may make it very difficult
for her to distinguish her own young from the young of others in the
few days after birth when olfactory cues are essential for recognition.
between mother and young (Stoddart, 1976). The stealing of litters is probably accidental rather than 'intentional' and as such is an aberrant behaviour associated with confined social groups of rats.

Animals other than the dominant female were quite tolerant of the new litters and were often found sharing the duties of minding the young in the nest or huddling with the young once they emerged from the nest. On three occasions subordinate females shared in nest duties for the litter of the dominant female and on two occasions the nest was attended by the highest ranked male. A description by Horner (1969) of the 'child-minding' behaviour shown by male bush rats on several occasions suggests that some individuals other than the mother will not only tolerate juveniles but become involved with their care. Observations on male behaviour at the nest invite speculation regarding the value of paternal behaviour in the wild. Such behaviour may be advantageous since it is possible that as a wandering sire in the springtime, the young any male encounters by mid-summer may be his own. Although parental care of young has been observed in other species such as Microtus ochrogaster (Thomas and Birney, 1979).

Social Signals Transmitted by Urine-marked Runways

The social rank of an individual rat, its success, the manner in which it uses the space available and its ability to gain ready access to food and shelter are priorities which are established and reinforced through overt antagonism and olfactory cues. Runways may serve as focal points in the transmission of olfactory information. The adherence of rats to runways marked with urine on the flat and barren floors of the pools and the confusion that ensued after the floor tiles and the runway system were rearranged (Section ), suggest that the pathways rats construct carry information for
residents about their environment both social and physical. Urine used to mark runways and familiar areas may contain messages regarding space ownership significant to other animals encountering the pathway. As a consequence, runways may serve to reduce the number of actual encounters between rats as they make efforts to avoid marked territory in the wild. This notion is supported by work on Norway rats (Price, 1977) which indicated that they tended to avoid areas marked with fresh urine and spend more time investigating unmarked areas or areas marked with aged urine.

Just as the age of the urine on a runway may indicate the frequency with which the area is patrolled by its owner, so might the quality of the urine indicate certain characteristics about the animal that deposited it. Since the more dominant animals of many mammal species is generally the one to do most of the scent marking (Johnson, 1973; Howe, 1977) the information conveyed through marking will generally pertain only to the individual with the highest social rank. For example, the urine may contain messages about that animal’s breeding condition (Price, 1975) or about its social rank (Krames et al., 1969). By deliberately marking trails, objects, young animals and sometimes other adults with urine, rats are advertising characteristics of themselves or their intentions (Eibl-Eibesfeldt, 1953; Calhoun, 1962; Telle, 1966; Schultz and Tapp, 1973; Barnett and Cowan, 1976; Stoddart, 1976, 1978).

Olfactory clues present in the urine of some individuals can induce physiological changes in others and can lead to inhibited reproduction as was tested for some micotropic rodents (see Batzli, Getz and Hurley, 1977; Getz and Carter, 1980; Terman, 1980; Cowley and Wise, 1972). For example, a substance in the urine of pregnant mice was found to inhibit the growth and maturation of young mice (Cowley
and Wise, 1972), and a substance in male house urine causes
synchronization of oestrus in females (Marsden and Bronson, 1964).
Virgin female Microtus ochrogaster become reproductively activated
when exposed to male urine (Getz and Carter, 1980). While none of
these effects have been tested on R. fuscipes, it is possible that
such social feedback through olfactory cues may exist.

In the pools, pregnant females were the most active and
regularly patrolled their space. If urine marking in this species is
hormonally controlled, as it is in R. norvegicus (Price, 1975), then
it is possible that the parous females are depositing not only
frequent messages regarding space ownership and social dominance, but
also saturating the area with reproductive inhibiting substances.
This is supported by the observation that only the highest rank female
in each enclosure reproduced successfully. The inhibitory effect of
one female on another was particularly well demonstrated by Pool D,
shown in Table 4.1. When the dominant female escaped and was absent
for three days, the subordinate female immediately mated. Whether it
was overt behaviour which prevented mating when the dominant female
was present, or olfactory inhibition, or a combination of both, is not
known.

Cowley and Wise (1972) report the effects of urine from a
pregnant female in suppressing the growth of young mice. Although it
is difficult to determine whether this or other factors, in particular
intolerance behaviour, were more important in the growth of confined
R. fuscipes, a similar result was found in the present study. The
young bush rats grew faster in pools where the dominant and breeding
female had died. In the pools where the dominant female survived for
a longer time to breed the young bush rats showed suppressed growth
rates (Figures 4.8 and 4.9).
In addition to having deleterious effects urine may also contain cues which are critical to homing behaviour in juvenile rats (Galef and Heiber, 1976). Young rats are able to discriminate home odours from other odours as early as 12 days of age (Gregory and Pfaff, 1971) and weanlings prefer to explore areas which contain the urine deposited by conspecific adults (Galef and Heiber, 1976). Urine of adults may help to guide the young back home or to direct them to their first meals of solid food in the natural environment (Galef and Heiber, 1976).

Potential of this Experimental Approach

In spite of its shortcomings, this attempt to study the social behaviour of bush rats in small enclosures has led to observations which partly elucidate how and why female bush rats maintain the strict spacing found in natural populations and, more importantly, has helped to establish useful techniques for future studies of animal spacing behaviour.

The use of new techniques such as the addition of fluorscence to the drinking water to dye the urine in which was visible under ultra-violet light, but was not detectable by the rats, gave information on the formation of runways. The establishment, maintenance and strict use of these runways by rats was one of the most significant observations in this part of the study on spacing behaviour. The provision of coloured cotton wool provided a means for confirming the tendency of females to hoard enormous quantities of nesting material before parturition and for confirming the social dominance of certain individuals as advertised by their indiscrimate gain of all portable property such as nesting material (Section 4.3.1.4). The design of the enclosures (pools) also provided a means
for studying the use of space in this species. By using relocatable
floor tiles in each pool, the set patterns of space use dependent upon
environmental cues could be disrupted without altering any other
components of the social or physical environment.

The design of the pools and in particular, the
interchangeable floor tiles, may prove useful in further experiments
which attempt to separate the effect of primary social cues such as
overt antagonistic behaviour and physical contact, from the effect of
secondary cues transmitted through olfaction on the behaviour and
reproduction of groups of bush rats. The results of such studies may
be crucial to our understanding of why animals use marked paths and
the effect of paths on social behaviour of individuals.
PLATE 4.1: Indoor enclosures ("Pools") arranged with a central food and water source. The floor of each Pool consisted of 24 tiles each of which could be relocated.
PLATE 4.2: Indoor Pools showing a nest of a breeding female built of cotton wool collected from all other nest boxes. The intolerant behaviour of the dominant female often resulted in nest boxes being scattered around the Pool.
PLATE 4.3: Indoor Pool with juvenile following its mother.
Body weights of individuals in a set of short term Pool experiments with a comparison of their rank with respect to weight improvement and their social rank assessed independently. Reproductive performance is also indicated for the females in each pool. "B" represents birth of a litter.

<table>
<thead>
<tr>
<th>I.D.</th>
<th>Initial</th>
<th>Final</th>
<th>ΔWt (g)</th>
<th>Rank ΔWt</th>
<th>Social Rank</th>
<th>Reproductive status</th>
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<tr>
<td>M1</td>
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<td>81</td>
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<tr>
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<td>137</td>
<td>-13</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>F1</td>
<td>103</td>
<td>121</td>
<td>+18</td>
<td>1</td>
<td>1</td>
<td>B (Day 31)</td>
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<td>118</td>
<td>+15</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
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<td>135</td>
<td>+13</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
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<td>+29</td>
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<td></td>
</tr>
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<td>+27</td>
<td>2</td>
<td>2</td>
<td>B (Day 34)</td>
</tr>
<tr>
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<td>113</td>
<td>+5</td>
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</tr>
<tr>
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<td>+9</td>
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<td>+5</td>
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<tr>
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<td>125</td>
<td>-1</td>
<td>3</td>
<td></td>
<td>B (Day 36)</td>
</tr>
</tbody>
</table>

* escaped from Day 12 to Day 15.
** litter born after end of experiment.

F denotes female; M denotes male.
Figure 4.1: The relationship between the intolerant behaviour of the dominant female and the frequency of the amicable interaction between non-dominant rats.
FIGURE 4.2: Pattern of urine marking revealed by UV light after the addition of Fluorescein to the drinking water. Shaded areas represent wet spots that were regularly marked with urine and shaded rectangles represent the nest-boxes and the food tray.
Figure 4.3: Pattern of movements of individuals on Days 1, 6, 18 and 21 of short-term pool experiment. The pattern on day 18 represents the response of animals immediately after floor tiles were relocated.

a) Central food: Pool A
b) Central food: Pool B
Figure 4.4: Pattern of movements of individuals on Days 1, 6, 18 and 21 of short-term pool experiment. The pattern on Day 18 represents the response of animals immediately after floor tiles were relocated.

a) Scattered food: Pool C
b) Scattered food: Pool D
FIGURE 4.5: Variation in the rate of interaction between individuals during the pool experiment including their response after relocation of the floor tiles.
Figure 4.6: Breeding performance of individuals in long-term pool experiments. Subjective assessment of the levels of intolerance are represented on a relative scale of 1 to 5, where 5 is the highest level of intolerance. For details see text.

Square symbol = male  
Round symbol = female  
a) Central food : Pool A  
b) Central food : Pool B
Figure 4.7: Breeding performance of individuals in long-term pool experiments. Subjective assessment of the levels of intolerance are represented on a relative scale of 1 to 5, where 5 is the highest level of intolerance. For details see text.
An asterisk indicates that the young were fostered and reared by another female.
Square symbol = male
Round symbol = female
a) Scattered food : Pool C
b) Scattered food : Pool D
Figure 4.8: Weight profiles of animals and their offspring in long-term experiment.

- Stars = litter born
- Open symbols = male
- Closed symbols = female

Identification of individuals corresponds to the scheme used in Figure 4.6.

a) Central food: Pool A
b) Central food: Pool B
(b)
Figure 4.9: Weight profiles of animals and their offspring in long-term experiment.
Stars = litter born
Open symbols = male
Closed symbols = female
Identification of individuals corresponds to the scheme used in Figure 4.7.
a) Scattered food: Pool C
b) Scattered food: Pool D
CHAPTER 5

THE ROLE OF SOCIAL BEHAVIOUR AND SPACING IN POPULATIONS OF THE
BUSH RAT (R. FUSCIPES) - A SYNTHESIS

In the foregoing chapters I have examined the possibility that there exists a social component in the spacing of mammals which provides a link between the environment and mammal abundance. The southern bush rat, Rattus fuscipes, was seen as a suitable candidate for such a study. Like other Rattus species, however, the bush rat retains a capacity for prolific reproduction under suitable conditions, and while populations oscillate annually, in this species they never reach plague proportions, which occasionally occur in some other Australian Rattus (McDougall, 1944, 1946; Newsome and Corbett, 1975; Carstairs 1974, 1976; Redhead, 1979; Lee, Baverstock and Watts, 1980; Watts and Aulin, 1981). Clearly something is restraining population growth.

The bush rat is found in patches of woodland and forest which meet certain structural criteria in tall heathlands and in vegetation along water courses (see Chapter 2 for details). Earlier studies have shown that within these areas of suitable habitat R. fuscipes maintains seasonal home ranges which at certain times show little or no overlap. These predictable features of bush rat spacing and habitat use logically lead to a hypothesis concerning intraspecific competition for space and resources and the possibility that spacing behaviour may influence population density through affects on dispersal, recruitment and survival.

The purpose of this Chapter is to (a) assess whether the techniques used in this study helped to elucidate details regarding
the relationship between the spacing of bush rats is a consequence of social behaviour which is related to environmental factors such as resource distribution and abundance. (b) Assess whether certain aspects of the social behaviour of bush rats could influence population density; (c) assess whether the experimental results are consistent with field observations and (d) critically evaluate these findings and any logically derived hypotheses regarding the bush rat populations.

Evidence of the relationship between social behaviour, social spacing and the availability and distribution of resources was sought in both natural and enclosed populations. In natural populations the spacing of R. fuscipes was expected to become most critical and evident at times of resource shortage (winter) and/or high resource demand (breeding season). A trapping and tracking regime was established to determine whether this was so. Animal spacing was shown to be a seasonal phenomenon and sex-related. Furthermore, spacing increased during breeding and decreased during winter (Chapter 2). In the enclosed populations, any social mechanism which had evolved to maintain the spacing of individuals observed in the field study was expected to become exaggerated, for in this situation, opportunity for spacing was limited. Complications found in many enclosure studies (see Chapter 3) were avoided by using short-term experiments. Short-term studies enabled observations of the development of spacing behaviour among a group of rats, and long-term studies were used later only to confirm the possibility that breeding may be socially inhibited.

The life history of the bush rat in its simplest form can be pictured as a straight line along a time axis from birth to death for each cohort of individuals. This line conceptually includes three
biological processes, namely, maintenance, growth and reproduction (see Gadgil and Bossert, 1970. Each 'line' is subject to a number of environmental forces (physical, social and physiological) which determines its length (i.e. longevity), its position in real space (i.e. animal distribution) and affects the probability that individuals within a cohort will encounter each other at the appropriate time for successful breeding. Figure 5.1 illustrates this model. Those factors which were tested or incidentally investigated in the course of this study are illustrated by closed boxes.

There are many factors which were not tested. Some of these, such as predation, may be important in limiting the numbers of individuals (Pearson, 1964, 1971; Newsome et al., 1976; Pitelka, 1973). While the effects of predation were neither tested nor observed in this study, the introduced fox is known to consume large numbers of *R. fuscipes* elsewhere (Green and Osborne, 1981). According to Freeland (1972) the high juvenile mortality typically found in populations of *R. fuscipes* can be accounted for by predation. It could be argued that the low number of juveniles surviving predation in summer and autumn would result in a depressed number of potential breeders in the following spring, and as a consequence, bush rat populations are extrinsically limited by predation. Keith (1974) points out that, while predation may increase the amplitude of oscillations, increase the intervals between peaks and cause regional synchrony in prey numbers, predation does not initiate any of these processes. It is unlikely that the regular demographic patterns of *R. fuscipes* could be accounted for by predation alone.

The food of the bush rat is another partially limiting factor. Both the distribution and abundance of food can affect population growth. While two aspects of food distributions were
observed and tested on experimental populations, the relative abundance of food was not adequately assessed in the current study. The influence of food shortages should not be overlooked (see Flowerdew, 1976a, 1978; Press, 1979; Hansen and Batzli, 1978; White 1978; Braithwaite and Lee, 1979; Hansson, 1979) as seasonal food shortages or changes in food quality might be responsible for the timing as well as the total effort put into breeding. The duration of the breeding season and the number of animals that successfully reproduced were dramatically altered by the addition of food to food-limited populations of Peromyscus maniculatus and Microtus townsendii (Taitt, 1981; Taitt and Krebs, 1981). Warneke (1971) suggested that winter food shortages affect winter survival of R. fuscipes and that a spring flush in insect abundance triggers breeding. There was insufficient evidence to suggest food shortage at the main study area (KioLoa) during winter (Chapter 2) and there was even some evidence to suggest the opposite. For example, it was found that in the autumn and winter, when food is most likely to be limited, the bush rats 'ate well'. They cached and ate large numbers of the highly nutritious although potentially toxic cycad seeds, as well as fungi, plant leaves and stems (Woodside and Watts, in prep.). The rats seemed to be unaffected by the toxic plants (Woodside and Monahan, in prep.) and resident rats appeared to maintain body weight throughout the winter. However, even in situations where the quantity of food is not limited, the quality of certain foods can affect both survival and reproduction (Batzli and Pitelka, 1971; Cole and Batzli, 1979). This can be further complicated by the possibility of differential food selection between sexes and age groups (see Clark, 1980 regarding Rattus rattus). Without a more detailed analysis of the diet of the bush rats and a thorough investigation of the quality
and quantity of available foodstuff, it is not possible to state whether or not these complications are relevant.

Winter is the most likely season when food resources can be expected to become strained and limited. It was hypothesized that larger body size could be of some social advantage for bush rats overwintering where the quality and quantity of food is low, and competition for resources is high. The three study areas described in Chapter 2 provided some interesting comparisons with regard to the survivorship of large and small animals. In both of the temperate zone study areas (Kioloa and Lees Creek), where winter was more harsh and plant growth seasonally inhibited, there was no advantage in being either small or large in body size although it might be argued that physiological stresses in temperate climates favour lower winter weights (Iverson and Turner, 1974; Stewart, 1979). In the mild winter setting of Mt. Glorious, however, larger animals showed significantly better survival that small animals and this was particularly true of females. The population at Mt. Glorious also showed the highest proportion of females surviving to breed in their second year. Adult females that already possessed a home range and have thus secured resources for overwintering may have some advantage over the subadults. Intraspecific competition may cause smaller females (or perhaps socially inexperienced subadults) to disperse from the area resulting in an overestimate of the ability of larger animals to survive winter. Beacham (1980b) found a similar pattern for Microtus townsendii. The high apparent survivorship of larger adults could be explained by the dispersal of smaller individuals. The importance of body weight as a variable in determining the fate of individuals in a population has been confirmed for several species of microtine rodents (Myers and Krebs, 1971; Krebs et al., 1976; Beacham 1979; Krebs,
1979). For example, Beacham 1980b was able to obtain actual measurements of dispersing voles in his study. The size of dispersing bush rats was not known in any of the study areas described in this text.

The influence of interactions between individuals sharing resources in a limited environment were more thoroughly investigated in this study than were the limiting factors per se. It was found, for example, that the habitats suitable for R. fuscipes were patchily distributed and that habitat discontinuities resulted in clumped distributions of animals. It became apparent that observations within each habitat patch would be necessary for the understanding of competitive animal interactions (Chapter 2 and Dickman and Woodside, 1982). Habitat patchiness influences many features of a population including its ability to survive when numbers are few (den Boer, 1971) and the degree to which a number of species will compete for available resources (Levin, 1974, 1977; Slatkin, 1974; Fenchel, 1975). Dickman and Woodside (1982) and this study indicate that while R. fuscipes does not appear to compete with the other species regularly caught in the same study area, there is a strong intraspecific competition for patchy distribution resources. Evidence for this can be found in both the field study (Chapter 2) and enclosure studies (Chapters 3 and 4) and is expanded upon throughout this discussion. Both Lonmnicki (1980) and Gill (1974) have argued that habitat patchiness, together with differences in individual competitive ability, influence population density. The unequal distribution of resources between competitors could affect both survival and breeding. The results of the outdoor enclosures and indoor pools in this study confirm the negative effects of intraspecific competition for space ownership on breeding and suggest some possible effects of competition on the health and
survival of competitors (Chapter 4). Subordinate individuals in both the outdoor and indoor enclosures showed less weight gain than the dominant animal. Many of the deaths observed in the long-term indoor enclosures involved physical injury and deterioration of general health. The dominant animal usually maintained good condition although they did not always live the longest. Social dominance, space ownership and breeding performances were mutually correlated in each of the enclosure experiments analysed. In this regard, social dominance in the enclosures might be seen as a direct reflection of how competition may influence population density in the natural environment.

Evidence for the existence of intraspecific competition among bush rats logically leads to three questions: (a) for what particular resource are they competing within each habitat patch? (b) how do they go about competing (i.e. what is the nature of the interaction)? and (c) what constitutes a winner or a dominant individual? These questions will be dealt with separately.

In *R. fusipes* the 'contest' for resources changes in character and intensity with each season. In both the field and enclosure studies it was the females which showed spatial dominance or attachment to home ranges and while the females compete for space, males compete for mates. This observation is a typical finding for many small mammals (C.J. Krebs, 1978). Spacing behaviour ensures that the female has a nest site and adequate food resources for the growth and development of her young. In the enclosures and pools the defence of nest sites and the savage harrassment of any other rats occupying nest-boxes within the space patrolled by a dominant female attest to the importance of having good nest sites within their home range. Perhaps nest sites are normally at a premium during the breeding
season. Even more rare may be the occurrence of good nest sites and adequate resources for rearing young all within one defendable patch of habitat which also meets the necessary criteria on structurally complex vegetation. This idea was exemplified at Kiolea where the population of bush rats became more and more dispersed as patches of appropriate habitat dwindled. At the same time both breeding and immigration declined but when part of the habitat improved, the population began to recover (see Chapter 2).

Competition between individuals for space (spacing behaviour) appears to occur primarily during the breeding season. Competitive intolerance between adult males and between adult females in breeding season emerged as an important phenomenon at all levels of this study. Female bush rats appear to employ three of the four possible strategies for maximizing their reproductive fitness. First, they may compete directly for the ownership of spatially distributed resources. That is, the best ‘fighter’ or most ‘aggressive’ individual wins the space. In the enclosure, the breeding female was the one to show a tendency to win more social encounters with others, and to influence their use of space. Secondly, breeding females can interfere with the reproductive performance of others. In the enclosures dominant females were seen to interrupt interactions between other individuals, to kill the litters of others and to steal litters (for discussion, see Chapter 3). Thirdly, dominance can be established by ‘beating others to the punch’. Rather than just fighting to own space in which to breed, female bush rats can also become spatially dominant as a result of being first to breed. This strategy was clearly demonstrated in the enclosure and the pool experiments where in all but two cases, the first female into oestrus was socially dominant and was the only successful breeder. In the
other two cases a subordinate female gave birth first and either killed her litter or had the litter stolen and reared by the dominant individual. Competitive dominance established by any of the three strategies proposed so far was positively associated with breeding success and the ownership of everything in the enclosed space. In the enclosures, the females which became subordinate and non-breeding would probably represent those individuals that would disperse in the natural situation. The existence of alternative patches of appropriate habitat would therefore be crucial to survival and the breeding success of these vagrant females.

The fourth strategy for maximizing reproductive fitness is to 'plan for the future'; to begin to combat for resources while still young and immature in order to ensure access at a later stage.

The idea that competition for space may occur in immature animals is supported by unpublished work by J.L. Barnett (personal communication) who found that stress levels as indicated by cortico-steroid levels in the serum was very high in male subadults in autumn, and coincided with their increased likelihood of winning dyadic encounters with adult males. C.R. Dickman (personal communication) has shown that a daughter bush rat will occupy the maternal home range when it becomes available. This may indicate the existence of competition between sibling females and perhaps competition between the mother and her daughters for space ownership in the autumn and winter. The 'clumping behaviour' measured in all three study areas (Chapter 2) may represent a less 'congenial' coexistence of rats than previously suggested so that mothers and daughters sharing winter burrows may be competing for resources rather than cooperating. Interactions between age classes and within age
classes requires further attention to elucidate the nature of adult-offspring relationships in different seasons.

The third strategy appears to be one of the most interesting to be revealed during this study. It would appear that by being the first female to enter oestrus in the spring ensures some priority in access to resources and hence a breeding advantage. The aggressiveness of a parous female ensures ownership of a resource space and females without sufficient resources cannot breed. Thus, space ownership associated with early oestrus may constitute a competitive interference mechanism which limits the number of breeding females in a limited habitat (see Gill, 1978). A female which is first to enter oestrus in spring when stimulated by environmental changes (see discussion, Chapter 3) or by an increased interaction rate with new males as a result of an increase in male movements (Chapter 2), would therefore possess some selective advantage.

Temperature, light, nutrition and social environment all influence reproductive success and these conditions are changeable during the early spring and variable between years. It would be advantageous to breed early in some and later in others.

The possibility of being either too early or too late to breed successfully would result in a high level of variability in the timing of female readiness to breed in a natural environment. This may be particularly true in spatially or temporally heterogenous habitats such as those occupied by R. fuscipes (Chapter 2), where some patches may be better than others at different times (Stenseth, 1978). The coexistence of different breeding strategies simultaneously may be more relevant in the highly changeable and patchy environment at Kiokea than in the more temporally stable environments at Lees Creek and Mt Glorious (see Chapter 2). To confirm these ideas it would be
necessary to survey for the readiness with which females can enter oestrus to see if there is more variability in response at Kiolea than at the other study areas.

If being first to own space and first to breed was advantageous, then litters born early in the season would be expected to show higher probability of survival than those born later. The idea that spacing behaviour could affect the survival of animals born at different phases of population growth was tested by Beacham (1980a). His results supported this proposition for Microtus townsendii. A re-analysis of the survival data from the Kiolea study area (Table 5.1) shows that females born early do not necessarily survive better ($X^2 = 2.91$ ns) although sample sizes are small. This is disappointing, since it would be expected that females born earlier in the year may have benefitted by being able to compete for space earlier than those born later. The idea is strengthened, however, by the fact that the only female young to breed the following year were those born early in the breeding season. Male bush rats, on the other hand, survived better if born later in the breeding season ($X^2 = 3.44$, $p = 0.05$). It could be that males born later in the summer survived better because of the absence of adult males which had already experienced high mortality by that time. During the summer the adult males become stressed (A.K. Lee, personal communication) and are repeatedly expelled from patches of essential resources by females. Males born earlier may experience more competition from litter mates and stressed adult males. Unfortunately, aspects of male-male competition were not revealed in this study. Indeed, there was very little evidence to suggest that male bush rats would compete for anything but mates as adults in spring. Consistent with this observation is the fact that during the early spring, males begin to
show greater body weights than females. Larger size may serve some advantage, both in competition for mates and for protection against female aggression (Gipps et al., 1981).

What constitutes a dominant individual? Can social dominance be predicted? Dominance hierarchies established among a group of rats would normally be expected to be associated with some physical feature such as body size (S.A. Barnett et al., 1979), but this was not the case in this study. In the breeding season dominance was not related directly to weight but to sex and to relative weight gain measured over the course of the experiment. Weight improvement was probably the consequence of social rank; not the determinant of rank. Social rank and weight gain were positively correlated and as a consequence, the dominant female usually gained the most weight (Chapters 3 and 4).

It is difficult to determine from observations alone whether a socially dominant female is the one which breeds first or whether the first female to enter breeding condition becomes socially dominant. The evidence presented here, and parts of the foregoing discussion would suggest that the latter would be more likely: that the first female to enter oestrus has some social advantage. The evidence comes from several sources. First, females became dominant when they appeared to enter breeding condition. The social dominance hierarchies were either unclear or male-dominated until such time as a female entered oestrus (signalled by the attention of males and her soliciting behaviour). She then became socially dominant by her own 'behavioural assertion' and not because of superior body size (Chapters 3 and 4). Secondly, intolerance behaviour which was associated with space ownership and social dominance, increased dramatically with pregnancy (Chapters 3 and 4). Thirdly, there is a
body of literature which would support the argument that changes in physiological state are directly related to changes in activity and levels of intolerance (e.g. Tollman and King, 1956; Payne and Swanson, 1971).

It appears therefore, that breeding condition predisposes an individual to become socially dominant although it would be presumptuous to assume this to be the answer to the dilemma of predicting social dominance in all situations. Furthermore, social dominance was found to be a changeable circumstance in bush rats as dominance hierarchies evolved over time and the relative social ranks of individuals often changes abruptly (Chapter 3). This would suggest that dominance is a function of phenotypic characteristics of the individual which are influenced by environmental and physiological events rather than being a function of fixed genetic characteristics (excluding, of course, sex).

Krebs (1978) suggested that stable populations have phenotypically-controlled spacing behaviour while cyclic populations have genetically controlled spacing behaviour. This study supports the first part of this suggestion. At the population level, social spacing and social behaviour in *R. fuscipes* was found to be highly flexible. Changes in spacing behaviour reflected changes in the extrinsic environment (seasonal changes, habitat availability; Chapter 2), changes in the social environment (population structure, density, health; Chapters 2, 3 and 4) and changes in the individuals (reproductive physiology; Chapters 3 and 4).

Once established, social dominance requires a great deal of energy expenditure to maintain. Since space ownership is seen as an expensive proposition, Brown (1964) proposed that behaviour such as overt aggression involved with spacing could only evolve where
resources essential to reproduction are defendable. If a species exploits resources, none of which are defendable, then that species will evolve neither agonistic behaviour nor courtship (Geist, 1976).

The way in which dominant bush rats maintain their rank and secure their space was clear from the enclosure and pool studies. Dominants were simply and viciously intolerant of the presence of other adults. Instead of using the entire surface of the enclosure, they used runways which they marked with urine and patrolled regularly. As a result, the use of space by subordinates, unable to leave the enclosures, was severely limited and they were compelled to use the same runways (Chapter 3). In the natural environment any fresh messages left on a runway might be sufficient to cause spatial avoidance by an intruder. A fresh mark might signal ‘section closed’ (Leyhausen, 1971). Thereafter, intolerance behaviour such as biting and chasing seen in enclosures would probably not be evoked in nature, as social encounters would be rare. The importance of odour as a signal which contributes to animal spacing and the effect of odour on the behaviour of an individual encountering it, has been shown for many mammals (see Ropartz, 1968; Eisenberg and Kleinman, 1972; Mykytowycz, 1974; Richmond and Stehn, 1976 and C.F. Barnett and Cowan, 1976). Olfaction signals would remove the necessity for direct encounters. Both the enclosure and pool experiments illustrated the importance of runways in conveying olfactory messages. These messages may be signals of spatial familiarity, space ownership, presence of intruders, proximity to home, reproductive state of individuals or social dominance. By ‘sign-posting’ such information the need for direct, and energetically expensive, confrontation, is removed. The low levels of wounding found in the natural populations (Chapter 2) may confirm this idea. By offering animals an opportunity to escape
in the enclosures, these ideas regarding spacing by olfactory cues, rather than intolerant social interaction, could be tested. The fact that the behavioural repertoire of female *R. fuscipes* is lacking in variety of stylised fighting behaviour suggests that it is rarely needed. Breeding females may only rarely come in contact. Wandering males in the spring are more apt to encounter each other and may be more likely to sort out immediate 'right of way' through short behavioural displays. This may require the more elaborate threat displays reported for male bush rats. May (1974) showed that male *R. fuscipes* more readily engaged in overt intolerant behaviour during dyadic encounters than did females. Females tended to avoid each other. Such results reflect a sex-related spacing behaviour, a predominant theme in this study.

Sex-related spacing behaviour has been found in many rodent studies and male and female spacing has been shown to affect different aspects of population growth. For example, Boonstra (1978) showed that the survivorship of young *Microtus townsendii* was related to male density. The effect of male aggression on the growth and survival of young has been shown for other species (Sadleir, 1965; Healey, 1967; Flowerdew, 1974). Bujalska (1971) suggested that female spacing in a population of *Clethrionomys glareolus* affected recruitment and survival of young. Redfield, Taitt and Krebs (1978) discuss the independent nature of male and female spacing behaviour of *Microtus townsendii* and show that partial removal of one sex has no effect on the spacing of the other. Females probably restrict recruitment and affect juvenile survival in *R. fuscipes*. Female spacing behaviour, therefore, controls the 'permeability' of the population with respect to recruitment. This same phenomenon is probably active in
populations of *R. fuscipes*. Female spacing, particularly in spring, restricts the number of possible residents and consequently restricts the maximum number of breeders. The absolute maximum number of breeding females is, of course, determined by the amount of suitable habitat (and food) available. Female spacing therefore serves to relate the breeding population to the environment.

Watson and Moss (1970) presented four criteria that should be satisfied if spacing behaviour is to be shown to influence population density. These criteria are listed below and were used to guide much of this work; that is, these criteria helped to form a framework in which meaningful experiments could be devised and applied to both field populations and to enclosed populations (see also Krebs, 1978a).

**TABLE 5.2**

Conditions which show that spacing behaviour, via socially-induced mortality (or socially induced depression of recruitment), limits a breeding population.

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(a) **A substantial part of the population does not breed**, either because animals die; or because they attempt to breed but they and/or their young all die; or because they are inhibited from breeding even though they survive, and may breed in later years.

(b) **Such non-breeders are physiologically capable of breeding if the more dominant or territorial (i.e. non-breeding) animals are removed.**

(c) **The breeding animals are not completely using up some resource, such as food, space or nest sites. If they are, the resource itself is limiting.**

(d) **Social behaviour can compensate for variation in other factors.** For example, if mortality increased as a result of bad weather then mortality (or depressed recruitment) due to social behaviour will decrease. Taken from Watson and Moss (1970) p 170.

(e) **If conditions (a) to (d) are met, and numbers change following changes in food, then food and behaviour are both limiting population size.**
Throughout the following discussion effort has been made to highlight evidence which supports the criteria listed above. However, some qualifications of these criteria is necessary before applying them to low density populations of bush rats. First, evidence, in the form of actual captures to show that there are non-breeding females in a population is not seen as a 'necessary' condition since it is possible that all non-breeders may have died or dispersed making their capture impossible and all remaining resident animals may be successful breeders. Trying to find non-breeding animals, particularly in low density populations or in seasons when animals may not be dispersing, may lead to false conclusions about this criterion. Direct evidence for the existence of non-breeding females, especially those that had been 'pushed out' of good areas into any suitable habitat, may come from trying to catch them in the act of dispersing or by luring them into unoccupied habitat (e.g. Krebs, Redfield and Taitt, 1978). Their presence will also be shown if more of the females that remain behind can be encouraged to breed by providing food supplements (Taitt, 1981; Taitt and Krebs, 1981). However, it may be sufficient to show through direct observations of behaviour that the ownership of space by some residents can limit recruitment, or survival, or reproductive fitness of those which do not own space.

Secondly, spacing behaviour may influence population processes not only by limiting the density of 'breeding population', but by also limiting the number of individuals using critical resources regardless of their breeding status. This means that social spacing should be evident at times of resource shortage as well as during the breeding season. Therefore a condition which in this study is considered necessary to show that social spacing influences population density is that social spacing should have some seasonal
component which reflects both the timing of breeding and changes in
the availability of distribution of resources. This is only a slight
modification of condition (e) stated above and suggests that we may
look for evidence that spacing behaviour changes with seasonal changes
in resource availability, but that we need not look for seasonal
correlations with animal abundance. Since changes in abundance may be
out of phase (experience and daytime) with environmental changes, it
may be difficult to detect a correlation between them. In addition,
social spacing is not seen as a density-induced phenomenon but a
phenomenon which occurs at all densities.

Finally, the use of the word 'limits' in the statement by
Watson and Moss (1970) suggests that social spacing is seen here as a
single limiting factor in population density. These authors are
careful to point out that there may be other limiting factors
involved, but for clarity social spacing will be defined here as a
complex of responses to a 'limiting environment', which in itself is a
complex of limiting factors. Social behaviour by definition is the
medium through which environmental change or environmental limits are
communicated among conspecifics.

The data obtained in this study shows that *R. fuscipes*
satisfies some of the criteria of Watson & Moss (1970). For example,
the enclosures and pools studies provided evidence for the existence
of non-breeding females and that these females are capable of
breeding. But this evidence is restricted to studies of confined
groups of bush rats and there was little evidence of these in the
field.

In the field there is no apparent surplus of
non-reproductive females, nor is there any indication of increased
transience among females in the breeding season. It is therefore
impossible to satisfy this condition by stating that non-reproductive females move out of the main study area after attempts to establish some breeding space fail. This is further complicated by the evidence that suggests that *R. fuscipes* establishes home ranges during autumn long before the females enter breeding condition and, that they maintain that spacing throughout the following spring and summer when they breed. Subadults may overlapped with adults for part of this period, and probably take over home ranges left vacant through death of adults during winter. Because this spacing behaviour is out of phase with breeding, then the cause and effect association between spacing behaviour and existence of surplus females that are non-reproductive is not possible. In the enclosures, however, social dominance was attained by one female and with that she secured the exclusive right to breed. No other females in the same enclosure successfully reared young to weaning and this evidence is offered in partial satisfaction to condition (b).

The third criterion (c) involved excess critical resources. In the enclosures shelter and food were provided in excess but breeding was still limited to one female. In the natural environment, resources may indeed be limiting and may ultimately limit the breeding potential of the population. However, spacing behaviour is seen as a mediator in this process, thus causing vagrant individuals to look elsewhere for potential breeding space. Some of these animals are undoubtedly successful when they encounter a newly-available patch of appropriate habitat.

The fourth criteria (d) suggests that spacing behaviour should be flexible and should compensate for variation in other factors. At all levels of study, bush rat spacing behaviour was seen as being highly flexible with changes according to habitat
characteristics, season, population structure and physiological state of the individuals. For example, home range sizes differ between study areas and this probably reflects the size and quality of the resource patches available (see Figure 2.1a, b, and c). Social spacing and dominance are also dynamic features of the bush rat and are accompanied by a wide array of social signals including overt intolerance behaviour, olfactory cues left on runway systems, and subtle social interactions such as draping during clumping behaviour.

The fifth criterion (e) is most relevant to this study. All evidence presented on *R. fuscipes* in enclosures and the natural environment suggest a strong association between resource availability (especially distribution) and social spacing. No evidence has been provided to show that population size (or density) is limited by both of these factors, but evidence has been provided to suggest that this is possible and that certain population processes are affected by social behaviour (e.g. reproduction of subordinate females is suppressed). It was shown that individuals compete to own space which in natural environments may contain necessary resources for survival and reproduction. Spacing behaviour changes seasonally and probably reflects changes in the availability of resources as well as changes due to life history events.

In summary the spacing behaviour of *Rattus fuscipes* has been explored at three levels of study: in natural populations, in semi-natural enclosures, and in artificial environments in indoor enclosures. Each level of study provides information on different aspects of spacing behaviour all of which can be integrated into a model of the relationship between three factors: the competition for space, the density of animals and the survival value of social interactions (Figure 5.2). The curves shown are entirely speculative
and are offered as a summary of the type of evidence found at each level of this research. Area 1 of the graph might be thought of as representing a poor or marginal habitat, like that seen at Kioloa. Very small patches of good habitat were scattered throughout the area providing refuges for a small number of animals. Wolff (1980) and den Boer (1980) discuss the importance of habitat patchiness in the persistence of sparse populations each patch serves as an isolated refuge for potential breeders. The rate of social interactions in the refuges as a result of the low carrying capacity of the environment and the value of social interaction are high, especially in the breeding season. There would therefore be a premium on mobility for some portion of the population (i.e. male bush rats) while the limited availability of habitat would put a premium on spacing behaviour and competitiveness for another portion of the population (i.e. female bush rats). Area II of the graph represents a range of 'healthier' environments with higher carrying capacity and represents the 'costs-benefits' approach of animal spacing and social interactions taken by Taylor and Taylor (1978). The animals are clumped in patches where resources are abundant and more rats are then drawn to areas where other rats exist because presence of others reflects the availability of adequate resources. As a consequence, the value of being sociable would be high but as numbers continue to increase or as the size of the patch decreases, resources would be strained and an increase in competitive feedback through spacing behaviour would reduce the number of individuals that occupy a given habitat patch. In the outdoor enclosures and indoor pools, the density of individuals was high and the total space available was low. Such density may normally signal depleted resources and the associated increased rate of encounters with other animals may serve as a stimulus to the
extreme intolerance behaviours that were observed. In natural populations of *R. fuscipes*, the increase in animal density in autumn may be the proximal stimulus to the spacing behaviour which is so conspicuous.

Area III of Fig. 5.2 represents an extreme case of resource partitioning and individual competition in which there would be some negative effects on individual survival, growth or sexual maturation of poor competitors (social subordinates) that cannot escape to find a new space in which to live. Some of these effects were demonstrated in the pool experiments but none of these have been confirmed in the field since spacing behaviour prevents such high density of breeding animals from occurring. Area IV of the graph represents a more extreme density situation where bush rats are crowded in a very small space, such as that provided in the colony cage experiments performed by S.A. Barnett and referred to in Chapters 3 and 4. These are unnatural circumstances and such overcrowding would result in a complete breakdown of spacing behaviour, chaotic social cues and confused competitive interactions. Spacing behaviour would no longer function through olfactory cues, occasionally reinforced by overt antagonism, and the group may even appear 'amicable' under these stressful conditions. Most of the behaviour observed would probably be aberrant. The study of animals in small spaces can be a serious problem to behaviourists (Vestal and Helleck, 1977) and is particularly relevant to studies in behavioural ecology. The application of findings from contrived and manipulated environments must be carefully and selectively applied to the natural situations. Thus, it is important to seek consistencies in behaviour patterns at all levels of study, and the consistencies in the results from the pools and outdoor enclosures as well as three field populations
provide a substantial basis for the generalisations made regarding the spacing behaviour of *R. fuscipes*.

This work supports the contention that social behaviour and in particular, spacing behaviour plays an important role in the population biology of *R. fuscipes*. Spacing behaviour is dynamic, seasonal and sex-related and the expression of this behaviour is related to the social status and breeding condition of each individual. In enclosures space ownership and social dominance appeared to ensure the use of space and access to the resources within that space. If this is so in natural populations, then spacing by resident females as early as late-autumn, may secure exclusive breeding ranges for the following spring. This behaviour may lead to the expulsion or dispersal of any 'homeless' females. Thus the spacing of bush rats which initially reflects the distribution and availability of critical resources (food, shelter) may ultimately limit the number of breeding females.
The survivorship and breeding of *R. fuscipes* born at three different times of the year. Results are combined for three years at the Kioloa study area.

<table>
<thead>
<tr>
<th></th>
<th>Number of Individuals</th>
<th>Through Winter</th>
<th>Through Breeding Season</th>
<th>And Breeding</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early Summer</td>
<td>21</td>
<td>67</td>
<td>38</td>
<td>28</td>
</tr>
<tr>
<td>Mid Summer</td>
<td>9</td>
<td>56</td>
<td>33</td>
<td>0</td>
</tr>
<tr>
<td>Winter</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early Summer</td>
<td>27</td>
<td>48</td>
<td>11</td>
<td>11*</td>
</tr>
<tr>
<td>Mid Summer</td>
<td>12</td>
<td>58</td>
<td>50</td>
<td>50*</td>
</tr>
<tr>
<td>Winter</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*All males with descended testes were assumed to breed.*
Figure 5.1: Speculative representation of factors affecting population parameters of *R. fuscipes*. Both the extrinsic and intrinsic factors involved in this study are enclosed in boxes and the other factors are those whose importance has been previously mentioned in literature and those which should be investigated in the future.
Figure 5.2: Speculative relationship between social interactions, bush rat density and spacing behaviour (i.e. competition for space) at each level of observation discussed in the text. The delineation and significance of Areas I-IV are also explained in the text.
APPENDIX 2.1a Computer programme used in analysis of floristic similarity.

C*******************************************************************************
C
C FLORISTIC SIMILARITY INDEX ANALYSIS FOR
C FOR DEEDE WOODSIDE'S DATA
C*******************************************************************************
C
C UNITS:
C 6 PROGRAM OUTPUT
C 10 PROGRAM INPUT

PARAMETER LOCMAX = 67, SPCMAX = 125
PARAMETER LOCXMAX = LOCMAX*LOCMAX
INTEGER ABUND(LOCMAX,SPCMAX), AABUND(LOCMAX,SPCMAX)
INTEGER RES(LOCMAX,LOCMAX)
INTEGER LABEL(13), INTVAL(13), SPEC
REAL ES(LOCMAX,LOCMAX)
DATA LABEL /1HO, 1H1, 1H2, 1H3, 1H4, 1H5, 1H6, 1H7, 1H8, 1H9,
1H10, 1H11, 1H12, 1H13 /
DATA INTVAL/0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 0, 0, 0/

C
C *** INITIALISE ABUNDANCE ARRAY
DO 4 LOC = 1, LOCMAX
DO 3 SPEC = 1, SPCMAX
ABUND(LOC, SPEC) = 0
3 CONTINUE
4 CONTINUE
C
C *** READ IN THE DATA
DO 15 SPEC = 1, SPCMAX
READ(10, 150, END = 25) (AABUND(LOC, SPEC), LOC = 1, LOCMAX)
100 FORMAT(6X,67A1)
DO 9 LOC = 1, LOCMAX
DO 5 LAB = 1, 13
IF (AABUND(LOC, SPEC) .EQ. LABEL(LAB)) GO TO 7
5 CONTINUE
WRITE(6, 150) (AABUND(I, SPEC), I = 1, LOCMAX)
150 FORMAT(15 *** ERROR IN INPUT ***'/6X,67A1)
STOP INFERR
7 ABUND(LOC, SPEC) = INTVAL(LAB)
9 CONTINUE
15 CONTINUE
25 CONTINUE
MAXSPEC = SPEC
C
C
C *** INITIALISE THE COMPARISON ARRAY TO -9999
DO 29 I = 1, LOCMAX
DO 27 J = 1, LOCMAX
ES(I,J) = -9999.
27 CONTINUE
29 CONTINUE

C
C *** CALCULATE THE SUMS OF X AND Y
DO 55 I = 1, LOCMAX
DO 45 J = 1, LOCMAX
XSUM = 0.
YSUM = 0.
DO 55 K = 1, MAXSPEC
XSUM = XSUM + ABUND(I,K)
YSUM = YSUM + ABUND(I,J)
55 CONTINUE

C
C *** CALCULATE THE COMPARISON INDEX
IF (XSUM.NE.0) ES(I,J) = YSUM/XSUM
45 CONTINUE
55 CONTINUE

C
C *** FIND OUT THE NUMBER OF LOCATIONS
DO 57 I = LOCMAX, 1, -1
IF (ES(I,1).NE.-9999.) GO TO 59
57 CONTINUE
STOP MOLOC
59
MAXLOC = I.
KMAX = INT((MAXLOC+24)/25.)

C
C
C *** RANK THE DISTANCES
DO 135 I = 1, LOCMAX
DO 125 J = 1, LOCMAX
RES(I,J) = INT(10*ES(I,J))
135 CONTINUE
145 CONTINUE

C
C *** OUTPUT THE LOCATION MATRIX
WRITE(6,350)
350 FORMAT('1')
INDEX = 0
DO 667 K = 1, KMAX
DO 665 I = 1, MAXLOC
LOC = INDEX + I
IF (LOC.GT.MAXLOC) GO TO 666
INDMIN = INDEX + 1
INDMAX = MIN(I,25) + INDEX
WRITE(6,205) LOC, ES(LOC,J), J = INDMIN, INDMAX
205 FORMAT('I3,13,2X,25F5.2')
665 CONTINUE
666 CONTINUE
APPENDIX 2.1a continued

360 WRITE(6,360) (J,J = INDMIN, INMAX)
   FORMAT(6X,25I5)
   INDEX = INDEX-25

667 CONTINUE

C

C ***

C OUTPUT THE RANKED LOCATION SIMILARITY MATRIX

INDEX = 0
DO 67 K = 1,KMAX
   DO 65 I = 1,MAXLOC
      LOC = INDEX + I
      IF (LOC.GT.MAXLOC) GO TO 66
      INXMN = INDEX+1
      INXMAX = MIN(I,25) + INDEX
      WRITE(6,200) LOC,(RES(LOC,J),J = INDMIN,INMAX)
500 FORMAT(1X,13,2X,25I5)
65 CONTINUE
66 CONTINUE

C ***

C CALCULATE THE MEAN AND STANDARD DEVIATION

SMEAN = 0.
STDDEV = 0.
SUM = 0.
SUMSQ = 0.
N = 0
DO 77 I = 2,MAXLOC
   INDEX = I-1
   K = INDEX
   DO 75 J = 1,K
      SUM = SUM + ES(I,J)
      SUMSQ = SUMSQ + (ES(I,J))**2
500 INDEX = INDEX+1
75 CONTINUE
77 CONTINUE
IF (N.LE.1) GO TO 85
SMEAN = SUM/FLCAT(N)
STDDEV = SQRT((N*SUMSQ-SUM*SUM)/FLCAT(N*(N-1)))
85 WRITE(6,400) SMEAN, STDDEV
400 FORMAT(/' MEAN : ',F5.2/' STANDARD DEVIATION : ',F5.2)
STOP
END
APPENDIX 2.1b Computer programme used in analysis of social associations based on nearest neighbours.

C******************************************************************************
C NEAREST NEIGHBOUR ANALYSIS, CALCULATIONS OF CENTRES OF ACTIVITY, DISTANCES MOVED AND RANKS OF NEIGHBOURHOOD FROM TRAPPING DATA ON SMALL MAMMALS (D. WOODSIDE)
C******************************************************************************

UNITS:
  6 PROGRAM OUTPUT
  10 PROGRAM INPUT
  11 PROGRAM OUTPUT - FILE OF DISTANCES AND RANKS

SEAS IS EQUIVALENT TO SESS AND IS MAX NUMBER OF SESSIONS OF SEASONS TO BE CONSIDERED.
IDMAX IS MAX NUMBER OF INDIVIDUALS IN ANY SEASON OR SESSION.
FOR EACH NEW DATA SET CHANGE DATA READ STATEMENT
AND FORMAT(NUMBER 100). CHANGE THE CONVERSION FACTOR FOR METERS IF NECESSARY (LINES 52/53, 112/113)
AND ADD THE DISTANCE BETWEEN CATURE POINTS TO THE CALCULATION OF AADM (SEE LINE 128).
PARAMETER SEAS=16, IDMAX = 70, IDMAX2 = IDMAX*IDMAX
PARAMETER NPAGE=17
REAL XCOORD(IDMAX), YCOORD(IDMAX), P, N9
INTEGER TSP, TSEX, TID, TAGE, TRANK, TSEAS,
  ARRAY(IDMAX, INFARR(IDMAX), OUTARR(5, 3)
  INTEGER IDINFO(IDMAX, 3), SEX, AGE, SESS, NID(IDMAX)
  INTEGER DSTAT(IDMAX, IDMAX), RANK(IDMAX2)
  INTEGER RRANK(IDMAX2), RDISP(IDMAX, IDMAX)
  DIMENSION V20(4), V30(6), V40(5)
DATA V20(1), V20(3), V20(4)/
  '(/TX, ', '(I4, 3X, '), ')/
DATA V30(1), V30(3), V30(4), V30(5), V30(6)/
  '5X, ', '(', I1, 1X, ', ', I1, 1X, ', '))/
DATA V40(1), V40(2), V40(4), V40(5)/
  '1X4, ', '2X, ', '(I4, 3X, '), ')/
LOGICAL EOF

C
C ***
C READ FIRST RECORD
EOF = .FALSE.
WRITE(6, 50)
50 FORMAT(/)
READ(10, 100, END = 175) TSP, TSEX, TID, ITX, IY, TAGE, TSEAS
100 FORMAT(I1, I1, I1, I1, I4, 20X, 2(I13), I1, I1, 3IX, 12)
C
C ***
C TO CONVERT LOCATION INFO TO METERS
TX = ITX*1
TY = IY*1
SESS = TSEAS
C
C *** PROCESS EACH SEASON OR SESSION
DO 155 ISESS = 1, SEAS
WRITE(6, 1000) ISESS
1000 FORMAT('1 INDIV:CENTRE OF ACTIVITY:STD DEV OF X AND Y',
? 'COORD: AVERAGE DISTANCE MOVED: SAMPLE SIZE ', '(SEASON = ', I2,
? ',/', '5X, 'INDIV', '6X, 'XMEAN', '5X, 'XSTDDEV', '5X, 'XSTEP', '5X,
? 'YMEAN', '5X, 'YSTDDEV', '5X, 'YSTEP', '5X, '4AIIK', '1CX, 'X', '
/, '1X, 1CO('*'))
C
C *** initialise variables for this session
DO 11 I = 1, IDMAX
DO 13 J = 1, 3
IDINFO(I, J) = 0
11 CONTINUE
INDEX = 0
DO 13 J = 1, IDMAX
DIST(I, J) = 0
RDIST(I, J) = 0
RANK(I + INDEX) = 0
RRANK(I + INDEX) = 0
13 CONTINUE
INDEX = INDEX + IDMAX
XCOORD(I) = 0.
YCOORD(I) = 0.
15 CONTINUE
ID = TID
SEX = TSEX
AGE = TAGE
X = TX
Y = TY
C
C *** process each individual
DO 55 IID = 1, IDMAX
C
C *** initialise variables for this individual
XID = 0.
YID = 0.
XID2 = 0
YID2 = 0
I = IID
NID(I) = 0
XMEAN = 0.
YMEAN = 0.
S = 0
C
C *** calculate the centre of activity for this individual
25 IF (TID.NE.ID) GO TO 45
XID = XID + TX
YID = YID + TY
XID2 = XID2 + TX**2
YID2 = YID2 + TY**2
NID(I) = NID(I) + 1
READ(10, 100, END = 35) TSP, TSEX, TID, ITX, ITY, TAGE, TSEAS
TX = ITX*1
TY = ITY*1
F=0
IF(TID.EQ.ID)P=SQRT((X-TX)**2+(Y-TY)**2)
S=S+P
X=TX
Y=TY
GO TO 25
45

35
EOF = .TRUE.
45
IF (NID(I).NE.O) XMEAN = XID/FLOAT(NID(I))
IF (NID(I).NE.O) YMEAN = YID/FLOAT(NID(I))
XSTDDEV = 0
XSTDER = 0
YSTDEV = 0
YSTDER = 0
IF(NID(I).GT.1)XSTDDEV = SQRT((NID(I)*XID2-XID*XID)/
( NID(I)*(NID(I)-1)))
XSTDER = XSTDEV/SQRT(NID(I))
? IF(NID(I).GT.1)YSTDDEV = SQRT((NID(I)*YID2-YID*YID)/
( NID(I)*(NID(I)-1)))
YSTDER = YSTDEV/SQRT(NID(I))
N9 = 0
IF(NID(I).GT.1)N9 = (S/NID(I))+5

C

C ***
PRINT OUT CENTRE OF ACTIVITY INFOXATION FOR THIS INDIVIDUAL
WRITE(6,200) ID, SEX, AGE, XMEAN, XSTDDEV, XSTDER, YMEAN,
? YSTDDEV, YSTDER, N9, NID(I)

200
FORMAT(1X,14,'(\',11,1X,11,\',')',2(5X,F6.1,4X,F7.2,5X,F6.2),
4X,F6.2,5X,14)

C

C ***
UPDATE ARRAYS FOR THIS SEASON OR SESSION
XCOORD(IID) = XMEAN
YCOORD(IID) = YMEAN
IDINFO(IID,1) = ID
IDINFO(IID,2) = SEX
IDINFO(IID,3) = AGE
ID = TID
SEX = TSEX
AGE = TAGE
IF (EOF) GO TO 57
IF (TSEAS.NE.RESS) GO TO 57
CONTINUE
55
DO 59 I = 1, MAXID
IF (IDINFO(I,1).NE.O) GO TO 61
59
CONTINUE
61
MAXID = I
MAXID2 = MAXID*MAXID

C ***
CALCULATE THE EUCLIDIAN DISTANCE BETWEEN CENTRES
OF ACTIVITY FOR EACH PAIR OF INDIVIDUALS
DO 75 I = 1, MAXID
DO 65 J = 1, MAXID
DIST(I,J) = INT(SQRT((XCOORD(I)-XCOORD(J))**2 +
(YCOORD(I)-YCOORD(J))**2))
65
CONTINUE
75
CONTINUE
WRITE OUT THE MATRIX FOR EUCLIDIAN DISTANCES

*** VARIABLE FORMAT USED, MAX OF 15 ANIMALS ACROSS PAGE
WRITE(6,1001)
1001 FORMAT('1 DISTANCE BETWEEN INDIVIDUALS/" 'X,3C('*'))
NIX=MAXID/NPAGE + 1
LXIN=O
LMAX=O
DO 60 NIXX=NIX
   LXIN=LMAX+1
   LMAX=MINO((NIXX*NPAGE),MAXID)
   NTIMES=LMAX-LXIN+1
   ENCODE(300,ATIMES) NTIMES
300 FORMAT(I2)
   V20(2)=ATIMES
   V30(2)=ATIMES
   V40(3)=ATIMES
   WRITE(6,V20) (IDINFO(I,1),I=LXIN,LMAX)
   WRITE(6,V30) ((IDINFO(I,J),J=2,3),I=LXIN,LMAX)
DO 79 79 I=1,MAXID
   WRITE(6,V40) IDINFO(I,1),(DIST(I,J),J=LXIN,LMAX)
79 CONTINUE
60 CONTINUE
INDEX = 0
C
C *** SET UP A ONE DIMENSIONAL ARRAY TO SORT THE DISTANCES
DO 95 95 I = 1,MAXID
DO 85 J = 1,MAXID
   RANK(INDEX+J) = DIST(I,J)
85 CONTINUE
INDEX = INDEX+MAXID
95 CONTINUE
C
C *** CALL THE SORT SUBROUTINE TO SORT THE ARRAY
CALL SORTS(RANK,RANK,MAXID2)
C
C *** SET UP THE ARRAY OF RANKS
IRANK = 1
TRANK = RANK(1)
DO 115 K = 1,MAXID2
   IF (RANK(K).NE.TRANK) GO TO 105
   RRANK(K) = IRANK
105 IRANK = IRANK+1
   TRANK = RANK(K)
   RRANK(K) = IRANK
115 CONTINUE
C
C *** RANK THE DISTANCES
DO 145 I = 1,MAXID
   DO 135 J = 1,MAXID
      DO 125 K = 1,MAXID2
         IF (DIST(I,J).EQ.RANK(K)) RDIST(I,J) = RRANK(K)
125 CONTINUE
135 CONTINUE
145 CONTINUE
C
C
C *** OUTPUT 5 NEAREST NEIGHBOURS FOR EACH INDIVIDUAL
WRITE(6,2000)
2000 FORMAT('15 NEAREST NEIGHBOURS FOR EACH INDIVIDUAL'
  ' ************************************************')
  DC 225 I=1,MAXID
  DO 205 J=1,MAXID
  ARRAY(J) = DIST(I,J)
  INFARR(J) = J
205 CONTINUE
  CALL SORTS(ARRAY,INFARR,MAXID)
  DC 210 K=1,5
  ITNUM = INFARR(K+1)
  CUTARR(K,1) = IDINFO(ITNUM,1)
  CUTARR(K,2) = IDINFO(ITNUM,2)
  CUTARR(K,3) = IDINFO(ITNUM,3)
210 CONTINUE
  WRITE(6,215) IDINFO(I,1),((CUTARR(J,K),K=1,3),
  ARRAY(J-1),J=1,5)
215 FORMAT(16,I10,1X,5(I4,1X,'(',I1,1X,I1,),'1X,13,1X))
225 CONTINUE

C
C *** WRITE OUT THE MATRIX OF RANKS
C
VARIABLE FORMAT USED, MAX OF 15 ANIMALS ACROSS PAGE
WRITE(6,1003)
1003 FORMAT('1 RANKED NEAR-NEIGHBOUR DISTANCES /' '1X,33('')')
NIX=MAXID/NPAGE + 1
LMIN=0
LMAX=0
DO 146 NIXON=1,NIX
  LMIN=LMAX+1
  LMAX=MIN((NIXON*NPAGE),MAXID)
  NTIMES=LMAX - LMIN + 1
  ENCODE(300,ATIMES) NTIMES
  V20(2)=ATIMES
  V30(2)=ATIMES
  V40(3)=ATIMES
  WRITE(6,V20) (IDINFO(I,1),I=LMIN,LMAX)
  WRITE(6,V30) ((IDINFO(I,J),J=2,3),I=LMIN,LMAX)
  DO 149 I=1,MAXID
    WRITE(6,V40) IDINFO(I,1),RDIST(I,J),J=LMIN,LMAX
149 CONTINUE
148 CONTINUE
C*** WRITE FILE OF DISTANCES BTW SETS OF INDIV AND THE
C*** DISTANCE RANK (INCL. NO. OF OCCURRENCES OF EACH INDIV).
C
IMAX=MAXID-1
DO 153 I=1,IMAX
  JMIN=I+1
  DO 151 J=JMIN,MAXID
    WRITE(11,1500) SESS,(IDINFO(I,K),K=1,3),NID(I),
    (IDINFO(J,L),L=1,3),NID(J),RDIST(I,J)
1500 FORMAT(12,2(I1,I4,'(',I1,1I1,'',I1,1I1,),'1X,I2),2(I1,I4))
151 CONTINUE
153 CONTINUE
SESS = TSEAS
IF (EOF) GO TO 165
155 CONTINUE
C *** FINISH UP
165 STOP
175 STOP NOREC
END
Appendix 2.2: The contribution of constancy and periodicity to the predictability of seasonal rainfall during the periods 1957-1980 and 1975-1980 at Kiolus. Results of the G-test and the significance of contributions of each component of predictability are given, where appropriate.

<table>
<thead>
<tr>
<th>Months</th>
<th>Predictability $P = C + M$</th>
<th>Constancy $(C)$</th>
<th>Contingency $(M)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1957-1980</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SUMMER</td>
<td>DJF</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.3357$</td>
<td>$C = 0.2872$</td>
<td>$M = 0.0466$</td>
</tr>
<tr>
<td></td>
<td>$GP_{(30)} = 110.43$</td>
<td>$GC_{(10)} = 95.05$</td>
<td>$GM_{(20)} = 15.41$</td>
</tr>
<tr>
<td></td>
<td>$p &lt;&lt; .001$</td>
<td>$p &lt;&lt; .001$</td>
<td></td>
</tr>
<tr>
<td>AUTUMN</td>
<td>NAM</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.5286$</td>
<td>$C = 0.2593$</td>
<td>$M = 0.0694$</td>
</tr>
<tr>
<td></td>
<td>$GP_{(50)} = 111.90$</td>
<td>$GC_{(10)} = 88.28$</td>
<td>$GM_{(20)} = 23.62$</td>
</tr>
<tr>
<td></td>
<td>$p &lt;&lt; .001$</td>
<td>$p &lt;&lt; .001$</td>
<td></td>
</tr>
<tr>
<td>WINTER</td>
<td>JJA</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.3021$</td>
<td>$C = 0.2271$</td>
<td>$M = 0.0750$</td>
</tr>
<tr>
<td></td>
<td>$GP_{(30)} = 104.31$</td>
<td>$GC_{(10)} = 78.41$</td>
<td>$GM_{(20)} = 25.90$</td>
</tr>
<tr>
<td></td>
<td>$p &lt;&lt; .001$</td>
<td>$p &lt;&lt; .001$</td>
<td></td>
</tr>
<tr>
<td>SPRING</td>
<td>SON</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.3563$</td>
<td>$C = 0.2935$</td>
<td>$M = 0.628$</td>
</tr>
<tr>
<td></td>
<td>$GP_{(50)} = 88.84$</td>
<td>$GC_{(10)} = 73.19$</td>
<td>$GM_{(20)} = 15.65$</td>
</tr>
<tr>
<td></td>
<td>$p &lt;&lt; .001$</td>
<td>$p &lt;&lt; .001$</td>
<td></td>
</tr>
<tr>
<td>1975-1980</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SUMMER</td>
<td>DJF</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.3358$</td>
<td>$C = 0.2065$</td>
<td>$M = 0.1293$</td>
</tr>
<tr>
<td></td>
<td>$GP_{(21)} = 23.74$</td>
<td>$GC_{(7)} = 14.60$</td>
<td>$GM_{(14)} = 9.14$</td>
</tr>
<tr>
<td></td>
<td>ns</td>
<td>$p &lt;&lt; .05$</td>
<td></td>
</tr>
<tr>
<td>AUTUMN</td>
<td>MAM</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.3831$</td>
<td>$C = 0.1852$</td>
<td>$M = 0.1980$</td>
</tr>
<tr>
<td></td>
<td>$GP_{(21)} = 30.27$</td>
<td>$GC_{(7)} = 14.63$</td>
<td>$GM_{(14)} = 15.64$</td>
</tr>
<tr>
<td></td>
<td>$p &lt;&lt; .01$</td>
<td>$p &lt;&lt; .05$</td>
<td></td>
</tr>
<tr>
<td>WINTER</td>
<td>JJA</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.4182$</td>
<td>$C = 0.1501$</td>
<td>$M = 0.2682$</td>
</tr>
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APPENDIX 2.3: Likelihood of associations between different sex and age classes for the first five nearest neighbours (first to fifth). Plus and minus symbols represent the direction and degree of deviation from the expected values. Significance is given for chi-square test.

a) Kioloa

b) Lees Creek

c) Mt Glorious
### Levels of Neighbourhood

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\[ X^2 = 33.04^{**} \]

\[ X^2 = 22.13^{*} \]

\( A = \text{adult} \) \( I = \text{immature} \)
## Levels of Neighbourhood

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| **Winter** |       |        |       |        |       |
| Male       |       |        |       |        |       |
| A  | -   | ++   | 0    | -      | ++   |
| I  | ++  | -    | 0    | -      | ++   |
| Female    |       |        |       |        |       |
| A  | -   | 0    | -    | 0      | -    |
| I  | 0   | -    | +    | 0      | -    |

\[x^2 = 28.58**\]

| **Spring** |       |        |       |        |       |
| Male       |       |        |       |        |       |
| A  | 0   | 0    | -    | 0      | -    |
| I  | 0   | 0    | -    | +      | ++   |
| Female    |       |        |       |        |       |
| A  | 0   | 0    | +    | 0      | 0    |
| I  | 0   | 0    | +    | 0      | +    |

\[x^2 = 47.44**\] \[x^2 = 64.98***\] \[x^2 = 114.68***\] \[x^2 = 101.87***\] \[x^2 = 84.60***\]

| **Summer** |       |        |       |        |       |
| Male       |       |        |       |        |       |
| A  | 0   | 0    | 0    | 0      | 0    |
| I  | 0   | 0    | 0    | 0      | 0    |
| Female    |       |        |       |        |       |
| A  | 0   | 0    | 0    | 0      | 0    |
| I  | 0   | 0    | 0    | 0      | 0    |

\(A = \text{adult} \quad I = \text{immature}\)
APPENDIX 2.3b continued

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### APPENDIX 2.3c  MT GLORIOUS

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\[ x^2 = 20.01^{*} \quad x^2 = 25.54^{**} \quad x^2 = 29.42^{***} \]

*A = adult  I = immature*
APPENDIX 2.4 A comparison of the reliability of the seasonal centres of activity for male and female bush rats at three study areas using Mann-Whitney U test. The mean standard error of the X and Y coord is given with its standard deviation in brackets.

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<td>M</td>
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Ux = 99

Uy = 67

Ux = 20  (P<0.025)

Uy = 26  (P<0.005)

Ux = 7   (P<0.02)

Uy = 0   (P=0)
APPENDIX 2.5

FOODS EATEN BY RATTUS FUSCIPES. \( \%V = \% \) volume; \( F = \) frequency of occurrence

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Appendix 3.1: Frequency (No/min) of intolerant interactions of the first seven watches spanning the first eighteen days of each experiment. The higher values are underlined.

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<td>0.0269</td>
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<td>0.0200</td>
<td>0.0459</td>
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<td>0.0217</td>
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<td>0.0118</td>
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