Use of habitat by the black rat (*Rattus rattus*) at North Head, New South Wales: an observational and experimental study

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Abstract   This study investigated the habitats used by an introduced species of rodent, the black rat *Rattus rattus* (Linnaeus), at North Head in New South Wales, Australia. At a coarse scale, combined live-trapping and radio-tracking indicated that animals used forest proportionately more than open, heath or scrub macrohabitats that were available. To identify the components contributing to this pattern, microhabitat use was assessed by scoring vegetative and structural features around trap stations, and by using spool-and-line tracking. The results indicated that rats preferred microhabitats providing a deep cover of leaf litter and dense understorey with numerous vertical stems. As statistical analysis did not distinguish which of these components was more important in determining habitat use, we designed an experiment to test the importance of a single component: leaf litter. Cover of litter was enhanced experimentally at 75 trap stations and reduced at 75 others, and the response of rats monitored by live-trapping on two occasions. Although no clear response was found in the first run of the experiment, due to low numbers, rats strongly selected trap stations with enhanced leaf litter in the second run. These results indicate that litter cover affects use of habitat by the black rat. Access to food resources and avoidance of predators may contribute to the observed local patterns of abundance.

Key words: black rat, habitat use, introduced species, macrohabitats, microhabitats, *Rattus rattus*.

INTRODUCTION

A crucially important component of the environment for any organism is its habitat (Morse 1980). This can be viewed as the physical space that an organism uses to gain resources required for growth, survival and reproduction (Levins 1968; Partridge 1978). For some organisms residency may be possible in a single habitat type, whereas others require a mosaic of different habitats, especially if each provides specific and different resources (Law & Dickman 1998).

Animals may perceive and respond to habitat characteristics at a variety of scales (Morris 1987; Stapp 1997). The use of large-patch types (macrohabitat), the size of which is defined by the ecological attributes of an organism, may result in part from selection for small patches (microhabitat), and *vice versa* (Morris 1984). For example, it has long been recognised that birds use cues at the fine scale of nest selection which are different to those at the broad-scale selection of territories (Hilden 1965). Few researchers, however, have attempted to incorporate scaling in studies of habitat use by less-far-ranging organisms such as small mammals (Morris 1984, 1987; Stapp 1997).

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Detailed study of habitats and other resources used by animals often provides essential information for conservation and management. For native or endangered species, knowledge of habitat use is important for maintenance of viable populations (Chambers 1991; Dickman 1996). For introduced taxa, insight into habitat use enables us to understand and predict invasion of natural and modified environments, to identify possible overlaps in habitat use with native species and to mitigate any adverse effects of such species by the development of control programs.

In Australia, introduced animals such as the black rat (*Rattus rattus*) and house mouse (*Mus domesticus*) have prospered, occupying habitats that were previously underutilized, out-competing native animals for remaining natural habitats, or occupying a broad range of habitats as ecological generalists (Clark 1981, 1982; Dickman 1992; Dutton 1994; Newsome 1995). Such highly adaptable species are often well known from studies of captive or urban populations (Elton 1942; Chitty & Southern 1954; Singleton 1989; Newsome 1995), but remain overlooked in less disturbed areas (Amarasekare 1994). The focus of this study is the black rat, a nocturnal, partly arboreal rodent introduced to Australia with the landing of European settlers some 200 years ago (Watts & Aslin 1981). Since

its arrival, the black rat has spread through much of the continent. The species reaches greatest numbers near human habitation, and is common in many natural and disturbed habitats (Watts 1983). We investigate a population in heterogeneous bushland, and quantify habitat use at macro and micro scales. Although there is a dearth of studies on the black rat in the Australian environment, we predict that animals should make disproportionate use of certain macrohabitat and microhabitat components, such as vegetative cover (Watts & Aslin 1981). We test this against the null hypothesis that habitats are used equally by employing a combination of observational and experimental methods.

METHODS

Study site

The study was conducted at North Head in Sydney Harbour National Park (33°55′S, 151°10′E), New South Wales. North Head is situated on the northern headland of the entrance to Sydney Harbour, 10 km from the city of Sydney, and constitutes a mosaic of cleared and disturbed areas, together with less-modified natural environments.

A combination of sources, including vegetation surveys (Chambers 1991; National Parks and Wildlife Service 1992), aerial photographs, ground-truthed data and our own site visits was used to define four macrohabitat categories:

1. Open: areas of short grass lawn around roads and buildings, with isolated introduced and/or native trees or shrubs, located on a variety of soil types.

2. Heath: reaching 2 m, dominated by sclerophyllous vegetation such as *Banksia ericifolia, Allocasuarina distyla, Persoonia lanceolata* and *Epacris microphylla*. Soils supporting this macrohabitat are thin and stony and derived from low-relief Hawkesbury sandstone.

3. Scrub: growing from 2 to 8 m, encompassing a variety of heterogeneous vegetation types dominated by *Leptospermum laevigatum, Banksia serratifolia* and *Monotoca elliptica*, and occurring on aeolian sand deposits.

4. Forest: with an upper stratum exceeding 8 m, dominated by *Angophora costata* and *Eucalyptus botryoides* with a mesic, sclerophyllous understorey. This macrohabitat is found primarily on Hawkesbury sandstone hillsides and moist gullies sheltered from ocean exposure.

A fifth macrohabitat, *Gleichenia* swamp, was identified by Chambers (1991). This formation is dominated by *Gleichenia dicarpa* with a dense understorey of other fern and sedge species, and occurs with or without a canopy of *Melaleuca quinquenervia*. In 1997 only one small patch remained; the lack of replication of this

macrohabitat type precluded it from further use in the present study.

Realistically, vegetation communities occur as a gradation from one formation to another. Classification into distinct types or 'habitats' must, to some extent, be considered arbitrary (Beadle & Costin 1952). In the area covered by this study, the macrohabitats differed substantially in terms of vegetation strata (Chambers 1991) and species composition (National Parks and Wildlife Service 1992); variation within macrohabitat types was therefore considered small compared with the variation between them.

Macrohabitat use

Two methods were used to assess macrohabitat use: live-trapping and radio-tracking.

Live-trapping

Live-trapping was conducted from March to June 1997 within three different patches of each of the four macrohabitat types. Replicate rectangular grids, 0.12 ha in area, were established in each patch, and positioned toward the patch centre to minimise possible edge effects. Grids contained 24 trap stations spaced 10 m apart in two parallel lines. Habitat patches were separated by a minimum distance of 300 m, approximately twice the mean adult home range length of *R. rattus* (Innes & Skipworth 1983; Dowding & Murphy 1994). To investigate temporal consistency in patterns of habitat use, all habitat patches were trapped on two separate occasions in March and May for three consecutive nights each, with traps cleared and reset at sunrise.

One Elliott folding metal trap (33 × 10 × 10 cm) (Elliott Scientific, Melbourne) was placed at each trap station. Each contained a mixture of rolled oats, honey and peanut butter for bait, non-absorbent cotton wool for bedding, and was covered with a plastic bag for insulation. Captured rats were sexed, inspected for reproductive condition, weighed, ear-clipped for individual identification and released at the point of capture. Age classes were defined by body weight and reproductive condition (Tanton 1969). Non-reproductive animals (males < 120 g, females < 80 g) were regarded as juveniles. Potential or experienced breeders (males $\geq$ 120 g, females $\geq$ 80 g) were classified as adults (Downes *et al.* 1997). Males were judged to be in reproductive condition if the testes were scrotal, females if the teats were swollen or the vagina bruised or open.

The mean number of animals caught per grid was used to obtain an estimate of relative density for each macrohabitat type (Caughley 1977; Hallett *et al.* 1983). A Cochran's test was used to check for homogeneity of variances within the data set, and a

single-factor analysis of variance (ANOVA) was implemented, with sites used as replicates, to determine whether animals used macrohabitat types differently. A subsequent Student–Newman–Keuls' (SNK) test indicated which habitats were used more than others. Differences in proportions of age classes and sexes between macrohabitats were investigated by χ^2 analyses.

Radio-tracking

As patterns of relative abundance do not necessarily provide reliable assessment of habitat use (Van Horne 1981), radio-tracking was used to confirm trapping results.

Three adult male *R. rattus* were tracked from May 1997 until late June 1997. The battery-operated transmitters (LTS single-stage tags; Titley, Ballina, NSW), attached to a zip-tie plastic collar, weighed 2 g: less than the suggested maximum load increase of 5% of the animal's body weight (Brander & Cockran 1971; Cockran 1980). Battery life extended for 40 days, with collars being removed at the cessation of radio-tracking.

Table 1. Categories used to classify microhabitat components in a 1-m radius around each trap station during live-trapping for *Rattus rattus* at North Head

Microhabitat use	Category	Category description
Leaf litter depth (cm)	0	Leaf litter absent
	1	0.01–1.0
	2	> 1.0
Leaf litter, understorey, canopy cover (%)	0	Zero cover
	1	1–33
	2	34–66
	3	67–100
Understorey height	0	Understorey absent
	1	0.1–66 cm
	2	0.67–1.3 m
	3	1.31–2 m
Canopy height (m)	0	Canopy absent
	1	2.01–7
	2	7.01–12
	3	> 12
Number of vertical/ ground stems	0	Vertical stems absent
	1	1–10
	2	11–20
	3	> 20
Number of logs	0	logs absent
	1	1–2
	2	3–4
	3	> 4
Alive/dead trees	0	Trees absent
	1	1–4
	2	5–10
	3	> 10

To determine a target animal's position, fixes were taken between sunset and midnight every hour using a Titley receiver, Sirtrack (Havelock North, New Zealand) hand-held antenna and a hand-held prismatic compass, indicating the bearing to the position of a rat. Hourly fixes were considered to be independent of one another, based on the assumption that individuals could move between any two points in their home range within this period (White & Garrott 1990; Rooney *et al.* 1998) and observations that rats occasionally traversed the home range within an hour. To minimize disruption, fixes were taken from four positions 10 m apart, on tracks or roads bordering the study site. The cumulative number of fixes was plotted against the increase in home range size to determine the minimum number of fixes per animal that would give a reliable estimate of home range (Kenward 1987). Plots reached an asymptotic value after 25 fixes, hence the use of 30 fixes per animal was viewed as adequate to estimate home ranges. Fixes were used to estimate not only home range sizes, but also overlaps with up to three different macrohabitat types. Bearings were converted to local coordinates using the program Locate (Nams 1990) and manipulated by the home range program Ranges V (Kenward & Hodder 1996) to define minimum convex polygons.

To determine the habitats used most frequently, home ranges were plotted onto a map of macrohabitats across North Head. The proportional area of macrohabitat type within the home range of each animal was estimated using a planimeter. Each animal's home range was then rotated randomly, 20 times, from an arbitrary fixed point which was taken to be the capture site, and the proportion of each macrohabitat type again calculated and averaged. This procedure provided an estimate of the macrohabitats potentially available to each individual (see Manly *et al.* 1993). With each animal as a replicate, a paired *t*-test was used to compare the proportion of each macrohabitat type used in the actual home range to the habitat potentially available in the 'averaged random' home range. This comparison indicated the habitats most used by rats, as estimated by radio-tracking, in relation to availability.

Microhabitat use

This was assessed by scoring microhabitats around the live-capture traps, and by spool-and-line tracking.

Microhabitat classification at trap sites

Eleven microhabitat components were scored in a 1-m radius around each trap station from the three replicate trapping grids in each macrohabitat type (after Barnett *et al.* 1978; Moro 1991; Wilson 1991; Maitz 1995). An area of 3.14 m² was deemed sufficient to detect a microhabitat response as similar-sized

areas have successfully indicated variations in microhabitat use in numerous species including *R. rattus* (Amarasekare 1994; Bray 1994). The microhabitat components were:

1. Leaf-litter depth: a minimum of five measurements was made within the trap radius to determine leaf-litter depth, and the average used to classify the site into one of three litter-depth categories (Table 1).

2. Leaf-litter cover: the percentage cover of leaf litter was estimated by eye, on two separate occasions, and averaged.

3. Understorey cover: the density of understorey was scored using a cover board (50 cm × 50 cm, divided into 25 squares of 10 cm × 10 cm), which was placed upright in four directions enclosing the trap. The percentage cover was calculated from the number of squares on the board not visible when viewed 1 m from the trap. The four estimates were combined to give a total average percentage cover.

4. Understorey height: the maximum height of all vegetation (to 2 m) was measured using a graded pole.

5. Canopy cover: the percentage cover of the canopy over the trap was assessed using the same method as for leaf litter cover.

6. Canopy height: the maximum height of the canopy was estimated by eye, once during each trapping session, to ensure reliability of estimates.

7. Number of vertical stems: all stems standing between 45° and 90° and less than or equal to 10 cm in diameter were counted.

8. Number of ground stems: stems less than or equal to 10 cm in diameter, lying on or parallel to the ground, were counted.

9. Number of logs: all logs greater than 10 cm in diameter, lying on or parallel to the ground, were counted.

10. Alive trees: all living trees greater than 10 cm in diameter, standing between 45° and 90° to the ground, were counted.

11. Dead trees: all dead trees greater than 10 cm in diameter, standing between 45° and 90° to the ground, were counted.

To facilitate analysis, each microhabitat component was divided into categories (Table 1).

To determine initially if there was a response by *R. rattus* to individual microhabitat components, captures of rats were tallied for each of the microhabitat categories and compared with the numbers expected if individuals were utilizing the microhabitats in proportion to their abundance at trap sites. Significance was tested by χ^2, and *a posteriori* comparisons made using the Bonferroni *Z*-statistic (Alldredge & Ratti 1992). Data for the two trapping sessions were examined separately, with only first-captured animals used in analyses. To determine if preferred microhabitat components (i.e. those yielding significant χ^2 results) were more abundant in a particular macrohabitat type,

a Cochran's test followed by a single-factor ANOVA was used. For this analysis, each habitat patch was used as a replicate with a single value for each microhabitat component averaged from tallies taken at the 24 trap stations per site. Student–Newman–Keuls' (SNK) tests were then used to determine differences in the abundance of microhabitat components between macrohabitat types.

Multivariate techniques were used next to elucidate responses of animals to combinations of the microhabitat components. Data from both trapping sessions were combined for the following analyses. First, nonmetric, multidimensional scaling (nMDS) and analysis of similarities (ANOSIM) were used to determine if animals in different macrohabitats used the same microhabitats based on the 11 components measured and, if so, which variables contributed most to this similarity. All variables scored were used to compare the characteristics of traps entered by rats with a similar number of randomly chosen trapping stations that had not caught animals. Raw data were log-transformed in order to balance variables with large numbers (e.g. counts of ground stems) to those with smaller numbers (e.g. counts of trees). All variables-by-sample matrices were converted to similarity matrices using the Bray–Curtis similarity coefficient. Matrices were ordinated by nMDS and tested for significance by a one-way ANOSIM (Clarke 1993). The contribution of each variable to between-group similarities was examined by SIMPER (Company?, Town?). All analyses were performed on Primer Version 4.0 (M. R. Carr & K. R. Clarke, Plymouth Marine Laboratory, UK).

In addition to the nMDS analysis, a multiple regression model was constructed to investigate which microhabitat features were the most important predictors of habitat use. Each site was used as a replicate. A single value for each microhabitat component per site was obtained by averaging scores from the 24 trap stations within a site. Ranked variables, such as canopy density, were converted to a binomial by calculating the median of the percentage category scored. Scatter plots were viewed to ensure normality of data; no transformations were considered necessary. A correlation matrix including all microhabitat variables was then calculated to eliminate any highly correlated variables from the regression model. The iterative procedure recommended by Kendall (1980) was implemented, with component variables deleted from the model if they could be reconstituted by linear combinations of remaining variables; reconstitution was considered acceptable if R^2 exceeded 0.90. Remaining components constituted the independent variables for the regression, while capture rate per site was used as the dependent variable. A stepwise, step-up procedure was used, with entry of dependent variables into the model accepted when $\alpha \leq 0.05$.

The use of two multivariate procedures was expected

to explore fully the possible associations between *R. rattus* and microhabitat components. The nMDS approach used data on presence (i.e. trap stations that captured *R. rattus*) and absence (randomly selected trap stations that failed to capture *R. rattus*), making only partial use of the entire data set. Its strength was expected to lie in grouping traps with similar microhabitat components regardless of macrohabitat type and indicating which components contributed most to any groupings. In contrast, the advantage of multiple regression analysis was expected to lie in using data from all trapping stations. However, averaging of component values within trapping sites had the potential to mask significant rat–component associations at the level of the trap station.

Spool-and-line tracking

Six captured animals were fitted with a spool of fine thread (200 m quilting cocoon bobbins of two-ply nylon thread; Coats Australia Pty Ltd, Sydney) weighing 2.35 g. These were attached to hair on the back of the rodent's neck using cyanoacrylate 'super glue'. Spools were held in position for 1 min, the free end of the thread tied to a fixed point, and animals then released at the point of capture. Spools unravel from the inside, so that as animals move through vegetation the thread unwinds without impeding movement (Miles *et al.* 1981; Broughton & Dickman 1991). Excluding the initial 10 m of line, which was considered to represent

a flight response, the microhabitat components described above were scored at 5 m intervals along the tracking line until termination. A maximum of 10 scores was used for each line; if the line extended for more than 60 m, the 10 scores were chosen randomly from those collected.

Scores were averaged for each microhabitat variable for individual animals. Comparisons of actual microhabitats used with microhabitats available were made by averaging 10 sets of microhabitat measurements, taken at 5-m intervals, from a random line beginning at the site where the spools were attached. Data were analyzed using a Student's paired *t*-test, with individual rats as replicates.

Additionally, spool lines can indicate arboreal activity. The total length of thread on and above the ground was also measured and recorded for each individual rodent.

Field experiment

From the tracking and trapping, we found that *R. rattus* preferentially used sites providing dense leaf-litter and understorey cover with numerous vertical stems. We conducted an experiment to identify the effects of leaf-litter cover on the trap-revealed behaviour of the black rat. Leaf litter has been implicated in influencing the local distribution and abundance of several species of small mammals (e.g. Kaufman & Kaufman 1990; Moro 1991; Haering & Fox 1995); however, its importance has rarely been considered explicitly. Additionally, *R. rattus* appeared to spend most time foraging on the ground rather than in shrubs or trees, and probably obtains a substantial proportion of its food there (Bray 1994; Cox 1997).

A similar trapping procedure to that conducted during macrohabitat analyses was implemented. All experimental trapping stations were established in forest macrohabitats as these contained the densest populations of *R. rattus*. Leaf litter was manipulated in a 1-m radius surrounding 150 trap sites. An area of 3.14 m² was considered appropriate as this was the same area as used in microhabitat analyses. Leaf litter was increased to cover > 67% of the 1 m radius around 75 randomly chosen trapping stations and reduced to < 34% at the remaining stations. All other microhabitat components were left unchanged. A single Elliott trap was placed in the centre of each experimental trapping station, and all were opened simultaneously on three consecutive nights during July 1997. The experiment was refined and repeated in August of the following year. Treatments were reversed between trap nights so that the 75 trap stations where leaf litter cover was increased initially to > 67% had litter cover reduced to < 34% on the following night and reversed again on the third night of trapping.
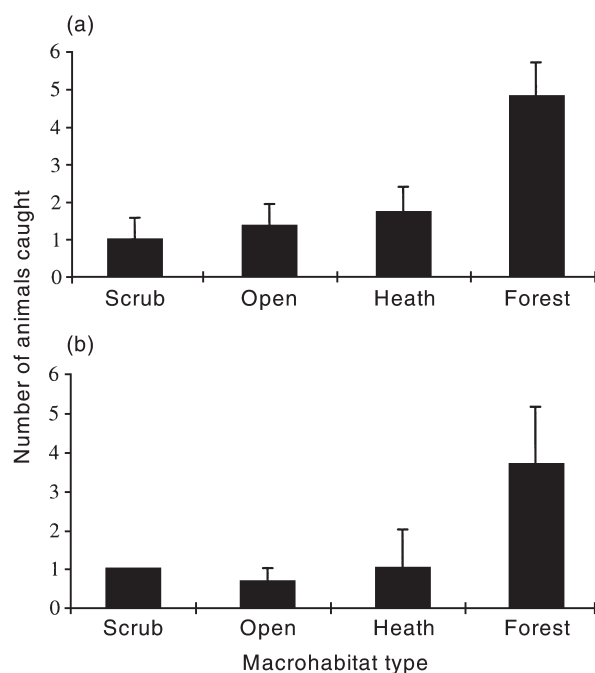
Fig. 1. Mean (+ SE) number of *Rattus rattus* caught per three grids in four macrohabitat types at North Head for (a) the first trapping session in March 1997 and (b) the second trapping session in May 1997.

A χ^2 test was used to determine whether animals responded to variations in litter cover. To maintain independence, only first-captured animals were used in all analyses.

RESULTS

Macrohabitat use

Live-trapping

From March to June 39 rats were caught a total of 55 times, 26 individuals in the first trapping session and a further 13 in the second. No animal was trapped at more than one site, indicating independence of trapping sites. *Rattus rattus* were caught in all macrohabitat types (Figs 1a, b). Abundances were different between macrohabitat types for the first ($F = 6.84$, $P < 0.05$) but not the second trapping session ($F = 2.71$, NS). An SNK test on the first session results showed that the abundance of *R. rattus* in forest sites was greater than in heath, open or scrub macrohabitats, none of which were significantly different from each other.

There was no difference in the proportion of juveniles to adults or males to females in either trapping session (χ^2 values ranged from 0.14 to 0.67, $P > 0.05$). On a habitat basis, age and sex comparisons could be made reliably only for rodents trapped in the forest as captures in other habitats were sparse; no differences were found in the proportions of juveniles to adults and males to females (χ^2 values ranged from 0.0 to 3.0, $P > 0.05$).

Radio-tracking

The home ranges of the three radio-tracked *R. rattus* were 0.76 ha, 0.34 ha and 0.40 ha. These individuals incorporated more forest ($t = 3.93$, d.f. $= 2$, $P = 0.048$), less open ($t = -4.65$, d.f. $= 2$, $P = 0.043$) and less 'other' habitat, comprising heath and scrub ($t = -8.41$, d.f. $= 2$, $P = 0.014$) into their home ranges based on the proportional availability of these habitats. The animal with the largest home range appeared to traverse the smallest amount of forest. To determine if this association was consistent with the three individuals tracked, home range area was correlated with proportion of forest within each range and shown to vary inversely ($r = -0.996$, $P = 0.05$). The evident preference for forest revealed by radio-tracking is consistent with the live-trapping results, despite the small sample size of radio-tracked animals that was available.

Microhabitat use

Trap sites

The numbers of captures of *R. rattus* differed from those expected for four of the 11 microhabitat components in both trapping periods (Table 2): leaf-litter cover, understorey cover, number of vertical stems and canopy height. Captures with respect to the number of logs at trap stations varied only during the first trapping session.

Use of the Bonferroni Z-statistic indicated that, despite apparently high capture rates of rats at traps with dense leaf litter, the observed number of animals in the 67–100% cover category was within the expected range for both sessions ($P > 0.05$). The difference detected by χ^2 was probably due to the lack of captures in areas with sparse leaf litter cover. Captures where trap stations lacked an understorey (i.e. category 0) consistently fell outside the Bonferroni range ($P < 0.05$). Fewer animals were caught at trap stations with between zero and 10 vertical stems in the first session, and zero vertical stems for the second ($P < 0.05$). The Bonferroni test showed

**Table 2.** Analyses of microhabitat components used by *Rattus rattus* at North Head

Microhabitat component	First trapping session		Second trapping session	
	χ^2	Z	χ^2	Z
Leaf litter cover	7.78*	NS	10.87*	NS
Understorey cover	22.17**	> Category 0	17.14**	> Category 0
Number of vertical stems	7.9*	> Category 1	13.26*	> Category 0
Canopy height	8.38*	NS	10.4*	< Category 3
Number of logs	11.41**	> Category 1	1.16	
Leaf litter depth	0.01		2.24	
Understorey height	3.09		7.54	
Canopy cover	4.65		4.56	
Number of trees alive	4.49		2.09	
Number of trees dead	0.65		0.63	
Number of ground stems	2.34		7.02	

χ^2, result of chi-squared test; Z, Bonferroni Z-statistic, indicating which category fell outside the Bonferroni range; **$P < 0.01$; *$P < 0.05$; NS, no significant difference.

that canopy-height categories fell within the expected range for trapping session one, while more animals were trapped at stations with canopies 7.1–12 m tall during the second. The fewer than expected captures in the first trapping session, at trap stations with 1–2 logs, were outside the Bonferroni range ($P < 0.05$).

Availability analyses illustrated that these five microhabitat components differed significantly in abundance between macrohabitats (d.f. = 8, F-values ranged from 5.42 to 64.5, with P-values from 0.025 to < 0.001). The SNK tests showed that forest sites provided denser leaf litter and understorey, more numerous vertical stems and a taller canopy than either heath or scrub sites, and that open macrohabitats lacked these components altogether. The SNK tests indicated further that there were fewer logs in open sites, but failed to distinguish between the remaining three macrohabitat types.

The nMDS plot showed that the combination of microhabitat components surrounding traps that caught animals was different to the combination at traps that did not (Fig. 2). The ordination produced a moderately high stress value of 0.27, indicating that the plot is not an exact two-dimensional representation of the rank order of the similarity matrix. However, ANOSIM confirmed that successful trap stations were markedly different to unsuccessful ones (Global $R = 0.355$, $P < 0.001$). The main components contributing to the average dissimilarity between the two groups were understorey cover (average contribution to dissimilarity = 17.2%), leaf-litter cover (15.1%), number of vertical stems (14.8%) and the number of ground stems (14.6%).
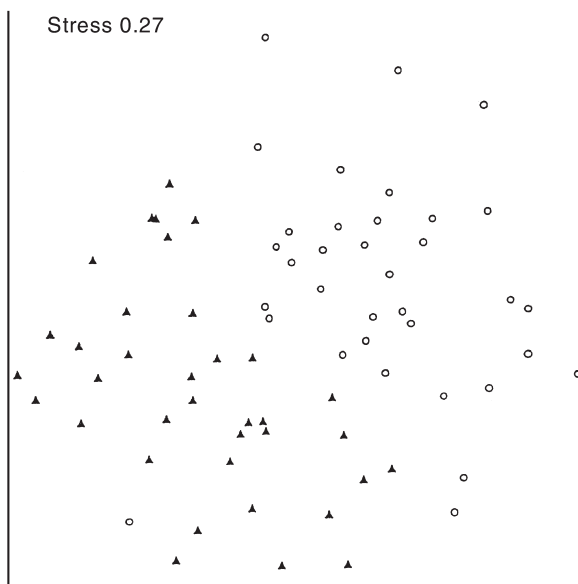
Fig. 2. Two-dimensional nMDS plot of trap stations which caught *Rattus rattus* compared with an equal number of trap stations which did not (▲ capture; ○, no capture). Comparisons were based on the 11 microhabitat components scored in a 1-m radius around each trap station.

Two components, numbers of ground stems and vertical stems, were deleted prior to multiple regression analyses on the grounds that they were highly correlated with, and could be reconstituted by, combinations of remaining variables. Entry of each independent variable separately into the regression analysis yielded low t-values of 0.19–2.68 with associated P-values of 0.075–0.861. The failure of the model to identify individually significant variables was probably due partly to the large number of independent variables and the consequent lack of degrees of freedom, but primarily to standard errors that ranged from 37.4% to 662% of each variable's b-values. However, inspection of the original correlation matrix suggested that three variables were more important than others: leaf-litter cover, $r = 0.60$ ($P < 0.05$), canopy height, $r = 0.79$ ($P < 0.01$) and leaf litter depth, $r = 0.90$ ($P < 0.001$). Correlations for other variables were not significant, ranging from –0.30–0.36 ($P > 0.05$).

Spool-and-line tracking

Six adult rats (three males and three females), captured in forest, provided spool lines. These animals used areas containing denser leaf litter ($t = 3.69$, $P = 0.014$), more understorey cover ($t = 5.29$, $P = 0.003$) and more vertical stems ($t = 4.2$, $P = 0.009$) than expected. Other microhabitats were used in proportion to availability (t-values ranged from –1.18–1.74, $P > 0.05$). These results support those obtained from trapping. Further analysis of spool lines showed that rats were most active on the ground (92% of the spool lines), ranging from 74.4% to 100% for the six individuals. All lines showed that animals readily traversed logs and fallen branches, while entangled threads indicated that most rodents paused to consume food at least once while spooled.

Field experiment

In the first run of the experiment, four adult males and five adult females were caught 19 times. Baseline trapping revealed that no animal was trapped at the same station prior to, or during, experimental trapping. There was a tendency for more animals (67% of total captures) than expected to be caught in traps where leaf litter had been experimentally added and fewer (33% of total captures) than expected in traps where litter was reduced (Fig. 3). However, due presumably to the small number of individuals recorded, this trend was not significant ($\chi^2 = 1$, d.f. = 1, $P > 0.05$).

In the second run of the experiment, 10 females and 15 males were caught 40 times. A χ^2 test for homogeneity indicated that the data could be pooled for the three nights ($\chi^2 = 1.25$, d.f. = 1, $P > 0.05$). One-tailed testing for the combined data showed that more

R. rattus were caught at sites with increased ($\chi^2 = 6.76$, d.f. = 1, $P < 0.01$) rather than reduced leaf litter (Fig. 3).

DISCUSSION

The black rat exhibited clear patterns of habitat use in the North Head study area, despite the relatively low abundance of animals. On a macrohabitat scale *R. rattus* preferred forest habitat to others that were available. This preference was statistically significant only for the first trapping session; the inability to detect differences in habitat use for the second session was probably due to the high variances in capture rates within macrohabitats, and the small but variable sample sizes in each macrohabitat type. Radio-tracking confirmed the preference of rats for forest, and also supported earlier observations that forest is selected when a mosaic of macrohabitats is available (Bray 1994).

Forest may provide rats with several benefits. First, because *R. rattus* nest predominantly in trees in natural environments (Innes & Skipworth 1983; Dowding & Murphy 1994), forest habitats should provide most nest sites. Similar associations have been demonstrated for many bird and small mammal species (e.g. Morse 1980; Wardell-Johnson 1986; Dickman 1991). Second, forest may provide a ready or more reliable access to food and water resources. *Rattus rattus* is omnivorous and, in a parallel study (Cox 1997), has been demonstrated to take a small amount of flower material that is available only in forest macrohabitats. Elsewhere in the Sydney region, black rats are ubiquitous visitors at artificial bird nests in forest (Matthews *et al.* 1999), and can be presumed to take eggs or nestlings from this source (Watts & Braithwaite 1978). Norman (1970) found that, without supplementary water, black rats fail to maintain body weight. Access to free water may limit the distribution of *R. rattus* in Australia (Watts 1983) and may be the cause for preferential habitat use on a localized scale. However, at North Head rats were not confined to the forest, suggesting that sufficient water was available in all macrohabitats. A third explanation is the strong association between the distribution of *R. rattus* at North Head and specific microhabitat components. Morris (1984) suggested that species using several macrohabitats may be opportunistic in habitat use, but within these large patches, individuals may preferentially use some areas, or microhabitats, more than others. In accordance with Morris (1984, 1987), specific microhabitats appeared to act as cues in determining macrohabitat use of the black rat. It was therefore essential to recognize both scales of habitat to interpret the local pattern of distribution of this species in the study area.

The black rat preferentially used microhabitats providing a dense understorey, numerous vertical stems and dense leaf-litter cover which together create a structurally complex and dense local environment. There was some evidence that rats responded to a single microhabitat component, leaf litter, at least in the second run of the experiment. The lack of a clear result in the first run of the field experiment may reflect small sample size or a seasonal habitat shift, with rats making less use of litter in winter when this experiment was carried out than in summer and autumn when initial patterns were observed. Seasonal shifts in habitat use have been demonstrated in other species of small mammals (e.g. Southern 1979; Statham 1982), as well as in black rats (King & Moller 1997).

Trap-revealed associations between *R. rattus,* canopy height and logs may indicate a relationship between the rat and these microhabitats or possibly be an artifact of macro- rather than microhabitat use (Bray 1994; Maitz 1995). Forest sites have a relatively uniform, tall canopy and an abundance of logs. Greater rodent densities in the forest could have driven the significant trap-revealed results; additionally, spool lines were analyzed only in forest areas, making it difficult to detect any preferential use of these microhabitat components generally across all macrohabitats.

The influence of specific microhabitats in determining macrohabitat selection is not uncommon in small mammals. Dueser & Shugart (1978) found that the rodents *Peromyscus leucopus*, *Ochrotomys nuttalli* and *Tamias striatus* inhabit particular forest types due to the availability of preferred microhabitats. Further fine-scale habitat analyses by Barnett *et al.* (1978), Braithwaite & Gullan (1978), Fox & McKay (1981) and Moro (1991) have associated the distribution of several species of Australian small mammals with microhabitat features such as vegetation cover or strata, ground cover and logs. These and similar studies with incidental trapping of *R. rattus* have indicated a broad affinity of this species with structurally complex vegetation. More specifically, Amarasekare (1994) and Bray (1994) found a higher abundance of
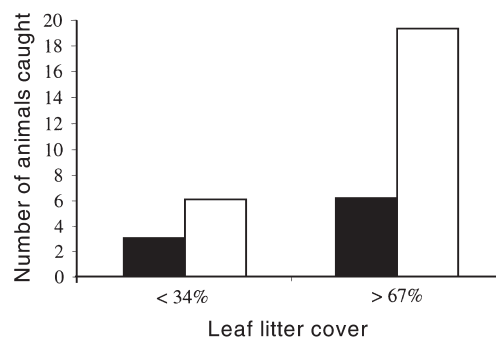
Fig. 3. The numbers of individual *Rattus rattus* caught at trap stations with depleted or increased leaf litter cover. In the first experiment (■) manipulation of litter cover was constant over three nights of trapping; in the second experiment (□) litter cover treatment was reversed on each of three nights of trapping.

R. rattus in microhabitats providing a dense cover of vegetation, with rapid declines in numbers as understorey became increasingly sparse and impoverished.

The mechanisms creating microhabitat patterns remain largely unknown, but may be attributed to one or a combination of factors. Dense microhabitats may provide abundant and/or accessible sources of preferred foods. Dietary analyses of *R. rattus* at North Head (Bray 1994; Cox 1997) indicate that this species consumes a large amount of root, fungal and flower material. This, combined with the direct observations and spool-and-line results, suggests that animals forage mostly at ground-level. A number of other studies have linked microhabitat use of rodents with food resources. For example, Amarasekare (1994) suggested that the use of dense microhabitats by *R. rattus* on Mauna Kea Island was related to the availability of naio berries and grass seeds, the dominant foods consumed by this population.

Animals could also be constrained to using dense, complex microhabitats due to avoidance of predators or competition from other species. Habitats providing dense cover offer refuge from potential predators such as *Felis catus* and *Vulpes vulpes* at North Head. Bray (1994) found a high percentage of rat in a scat analysis of introduced carnivores at the present study site, leading her to propose that low densities of *R. rattus* in open habitats were associated with predator avoidance. In accordance with Bray (1994), the predation risk imposed by cats and foxes at North Head may restrict the black rat to areas providing dense cover. Similarly, interspecific competition could exclude *R. rattus* from open habitats. However, it is unlikely that any mammalian species that coexist with black rats at North Head (*Pseudocheirus peregrinus*, *Trichosurus vulpecula*, *Perameles nasuta*, and *Mus domesticus*) would competitively exclude *R. rattus* from this macrohabitat type.

On a broader scale, competition may play a role in the distribution of this species in natural environments in Australia. The structurally complex habitats identified in the present study are used by *Rattus*, *Antechinus* and *Melomys* (e.g. Warneke 1971; Wood 1971; Barnett *et al.* 1978; Braithwaite & Gullan 1978; Gullan & Robinson 1980; Fox & Fox 1981; Wilson 1991). This would indicate a strong possibility of overlap in habitat use where these species occur with *R. rattus* in natural environments. Several studies have indicated that densities of the black rat are low in the presence of native *Rattus* species, even in habitats that appear to provide the study species with its preferred macro- and microhabitat components. Dickman (1983) recorded very low densities of *R. rattus* where *Rattus fuscipes* was in abundance in several forest regions with complex ground and understorey strata, but recorded many *R. rattus* at two forest sites where *R. fuscipes* was unexpectedly absent. Similar results have been presented by Braithwaite & Gullan (1978) in Victoria and

Barnett *et al.* (1978) in north-eastern New South Wales. This suggests that native *Rattus* species, such as *R. fuscipes*, a forest specialist or *Rattus lutreolus*, a dense, moist microhabitat specialist, are likely to persist at the expense of *R. rattus* where they occur together in natural environments.

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