Acta Theriologica 40 (4): 425–438, 1995.
PL ISSN 0001–7051

Small mammal microhabitat use in lowland rain forest of north-east Madagascar

Peter J. STEPHENSON*

Stephenson P. J. 1995. Small mammal microhabitat use in lowland rain forest of north-east Madagascar. Acta Theriologica 40: 425–438.

This study describes a systematic small mammal trapping programme in the lowland rain forest of Anandrivola, north-east Madagascar. Trapping in both primary and secondary forest revealed the presence of nine small mammal species. Twenty-six habitat variables measured around each trap site were used to determine microhabitat preferences in the three most common small mammal species. The tenrec *Microgale talazaci* Major, 1896 was widespread but favoured microhabitats with relatively dense herbaceous growth. The endemic rodent *Eliurus webbi* Ellerman, 1949 was most often found deep within primary forest, in microhabitats characterized by low herb densities and abundant lianes. The introduced rat *Rattus rattus* (Linnaeus, 1758) was trapped only in secondary forest, in microhabitats close to the forest edge with dense herbaceous growth. The effects of microhabitat availability on small mammal species distributions and the consequences for conservation are discussed.

Department of Biology, Royal Holloway and Bedford New College, University of London, Egham, Surrey, TW20 0EX, UK

Key words: Nesomyinae, Tenrecidae, co-existence, conservation, habitat disturbance

Introduction

Tropical rain forests in Madagascar are under severe threat from deforestation (IUCN/UNEP/WWF 1987, Nicoll and Langrand 1989, Green and Sussman 1990). An understanding of factors affecting co-existence and diversity within this threatened ecosystem is essential if remaining habitats are to be managed effectively. The last remaining large tracts of primary rain forest in Madagascar are found in the northeastern part of the island (Green and Sussman 1990). Within this forest block, Anandrivola may represent one of the few suriviving remnants of lowland rain forest, yet its fauna and flora have been poorly studied (Stephenson *et al.* 1987).

In Madagascar, the native terrestrial small mammal fauna comprises the endemic insectivore subfamilies Oryzorictinae and Tenrecinae (Insectivora: Tenrecidae) and the endemic rodent subfamily Nesomyinae (Rodentia: Muroidea). These taxa may be ideal indicators of faunal and floral diversity within Malagasy rain forests

*Present address: WWF Country Office for Tanzania, PO Box 63117, Dar es Salaam, Tanzania

(Stephenson 1993). The distribution and abundance of endemic small mammals may be affected by human disturbance and the introduction of exotic species (Stephenson 1993) yet the ecology of many species is very poorly understood.

Many studies have demonstrated that the richness, distribution and abundance of co-existing small mammal species are influenced by the availability of microhabitats that can be measured by specific habitat variables (eg M'Closkey and Fieldwick 1975, Barnett *et al.* 1978, Porter and Dueser 1982, Abramsky *et al.* 1985, Kemper and Bell 1985, Fa *et al.* 1992, Laurance 1994). Dueser and Shugart (1978) investigated small mammal microhabitats in more structural detail than other studies by measuring 29 habitat variables around all their forest trap sites. In Madagascar, these techniques have been adapted for use in mid-altitude rain forest (Nicoll *et al.* 1988) and western dry forest (Ganzhorn *et al.* 1990). A replicate study conducted in Anandrivola offers an ideal opportunity to examine small mammal habitat use whilst providing a comparison with previous study sites.

In the present study, the techniques of Dueser and Shugart (1978), adapted for use in Malagasy rain forest (Nicoll *et al.* 1988), were used to address the following questions: (1) Which small mammal species co-exist in Anandrivola Forest? (2) Do sympatric species inhabit significantly different microhabitats? (3) How does anthropogenic habitat disturbance affect the small mammal community?

Study area

The study site was located in Anandrivola Forest (15°46'S, 49°36'E: 450–625 m a.s.l.) about 10 km south-west of Maintimbato. This is a village close to Rantabe on the western shore of Antongil Bay, about 40 km south-west of Maroantsetra, Toamasina Province. Anandrivola is mixed moist semi-evergreen rain forest with a canopy height of around 30 m. The understory comprises saplings, as well as herbaceous angiosperms (eg *Clinogyne comorensis, Impatiens* sp., *Begonia* sp.) and pteridophytes (eg *Asplenium* sp., *Blechnum* sp., *Sphenomeris* sp., *Selaginella* spp.). Epiphytes and lianes are abundant, as are palms and tree ferns. During the study period, local people cleared land on the eastern edge of the forest for agriculture. Further details of the study site and the fauna and flora of Anandrivola are provided elsewhere (Stephenson *et al.* 1987, Raxworthy 1988, Raxworthy and Stephenson 1988).

Materials and methods

Small mammal trapping

A total of 120 trap sites were established in four 0.45 hectare trapping grids. Grids I and II were laid down at randomly selected sites in primary forest where there was no evidence of recent human disturbance such as tree felling. To facilitate a comparison and determine the effects of habitat disturbance, grids III and IV were located on the edge of Anandrivola in forest that had experienced some degree of perturbation in recent years and comprised secondary growth.

In each 30 × 135 m grid, traps were laid in three rows of ten trap sites at 15 m intervals. One large (9 × 7.5 × 23 cm) aluminium Sherman trap (H. B. Sherman Traps Inc., Tallahasee, Florida, USA) was positioned at each trap site and baited with dried fish and coconut flesh ground in vegetable oil. Each trap was placed in a transparent plastic cover to afford protection against the rain. Beside

each Sherman trap was positioned one pitfall trap. Pitfall traps were plastic plant propogators (Stuart Plastics Ltd., Croydon, London, UK), 20 cm in depth and 12 cm in diameter. Each trap was set by carefully digging a hole in the soil, causing minimal disturbance to surrounding vegetation. The propogator was then sunk into the hole below the leaf litter/root mat layer. Holes in the base facilitated water drainage.

The four grids were trapped simultaneously in August and September 1986 for a total of 2640 Sherman trap nights and 2640 pitfall trap nights. Traps were checked daily between 07.00–10.00 h. Captured animals were identified, weighed, measured and examined for sex and reproductive condition. Species nomenclature follows Wilson and Reeder (1993) and Stephenson (1995). Animals were marked with unique ear clips (Twigg 1975) and released at the capture site.

In addition to trapping on the grids, opportunistic trapping was carried out around the study area to reveal the presence of species not caught by systematic methods. Opportunistic traps were set in positions known or suspected to maximize small mammal captures such as alongside fallen logs or tree roots, near burrow openings and on low-hanging branches.

Habitat variables

Twenty-six habitat variables were measured around each trap site (Table 1) to measure floristic composition and architecture at six strata levels of the forest: overstory, understory, shrub level, herbaceous level, forest floor and leaf litter/root mat level. In accordance with the criteria set out by Dueser and Shugart (1978), the variables were quickly and precisely measurable in the field with non-destructive sampling techniques and had "intraseason variation that was small relative to interseason variation". They were used to measure habitat to accurate detail within the immediate vicinity of the trap sites, and concentrated on features that were known or suspected to influence species distribution and abundance. Small mammal microhabitat preferences were then estimated from the frequency of captures at particular trap sites.

Results

Nine species of small mammal were caught in the grids: the oryzorictine tenrecs *Microgale talazaci* Forsyth Major, 1896, *M. pulla* Jenkins, 1988, and *Oryzorictes hova* A. Grandidier, 1870; the tenrecine tenrec *Hemicentetes semispinosus* (G. Cuvier, 1798); the crociduran shrew *Suncus murinus* (Linnaeus, 1766); the nesomyine rodents *Eliurus webbi* Ellerman, 1949, *E. minor* Major, 1896, and *Nesomys rufus* Peters, 1870; and the murid rodent *Rattus rattus* (Linnaeus, 1758) (Table 2). *M. pulla* had never been described before and the individual trapped here represents the type specimen (Jenkins 1988). *O. hova* has been caught infrequently, and details of the individual trapped in the present study are published elsewhere (Stephenson 1994a). Opportunistic trapping did not reveal any additional species.

M. talazaci, *S. murinus* and all rodent species were caught only in Sherman traps which recorded an average of 15.2 individual captures per 1000 trap nights. *M. pulla, O. hova* and *H. semispinosus* were caught only in pitfall traps (1.1 captures per 1000 trap nights). The majority of rodent captures were at sites where no other species were caught. *R. rattus* was never trapped at the same site as an endemic rodent, though it did share one capture site with *M. talazaci*.

Table 1. Descriptions and sampling techniques for 26 variables used to measure habitat composition and architecture. Based on methods developed by Dueser and Shugart (1978) and adapted for rain forest habitats by Nicoll *et al.* (1988). DBH – diameter at breast height.

Variable	Methods
Percent canopy cover	Percentage of points with overstory vegetation out of 21 ocular tube sightings aimed at the canopy, taken at 5 sites around the trap within 1 m radius.
Percent light penetration of canopy	Percentage light intensity measured with light meter at 5 sites around the trap on 2 uniformly cloudy days between 11.00–13.00 h. (100% – measure where no canopy present; 0% – measure where continuous canopy cover present).
Overstory tree size	Mean diameter (cm) of nearest overstory tree (DBH > 10 cm) in quarters around trap.
Overstory tree dispersion	Mean distance (m) from trap to nearest overstory tree in quarters around trap.
Understory tree size	Mean diameter (cm) of nearest understory tree (DBH 5–10 cm) in quarters around trap.
Understory tree dispersion	Mean distance (m) from trap to nearest understory tree in quarters around trap.
Woody stem density (ground = 0 m)	Live woody stem count at ground level (0 m) within 2 m^2 circle centred on trap.
Woody stem density (0.5 m)	Live woody stem count at 0.5 m height within 2 m^2 circle centred on trap.
Woody stem density (1.0 m)	Live woody stem count at 1.0 m height within 2 m^2 circle centred on trap.
Number of woody species	Number of woody plant species within a 2 m^2 circle centred on trap.
Herbaceous stem density (0 m)	Live herbaceous stem count at ground level (0 m) within 2 m^2 circle centred on trap.
Herbaceous stem density (0.5 m)	Live herbaceous stem count at 0.5 m height within 2 m^2 circle centred on trap.
Herbaceous stem density (1.0 m)	Live herbaceous stem count at 1.0 m height within 2 m^2 circle centred on trap.
Number of herbaceous species	Number of herbaceous plant species within a 2 m^2 circle centred on the trap.
Percent herbaceous cover	Percentage of points with herbaceous vegetation out of 21 ocular tube sightings aimed at the ground around the trap within 1 m radius.
Fallen log size	Mean diameter (cm) of nearest fallen log (diameter > 7.5 cm) in quarters around trap.
Fallen log dispersion	Mean distance (m) from trap to nearest fallen log in quarters around trap.
Percent exposed soil	Estimated percentage of exposed soil within 2 m radius of trap.
Percent exposed rock	Estimated percentage of exposed rock within 2 m radius of trap.
Percent exposed leaf litter/root mat (LLRM)	Estimated percentage of exposed LLRM within 2 m radius of trap.
Leaf litter/root mat depth	Mean depth (cm) of litter/soil layer at 4 perpendicular points 1 m from trap.
Tree fern density	Number of tree ferns within 5 m radius of trap.
Liane stem density	Number of liane stems within 3 m radius of trap.
Slope	Slope (°) within immediate vicinity permanent water (measured to nearest 5 m).
Distance from water	Distance (m) from trap to nearest permanent water (measured to nearest 5 m).
Distance from forest edge	Shortest distance (m) from trap to forest edge (measured to nearest 5 m).

Table 2. Capture data for all small mammals trapped systematically on grids I–IV.

Species	Mean body mass (g)	Number of captures	Number of individuals	Capture sites	Single-species capture sites	Joint-species capture sites
Tenrecidae						
Microgale talazaci	39.2	20 (31%)	19 (48%)	16	7	9
Microgale pulla	4.1	1 (2%)	1 (2%)	1	0	1
Oryzorictes hova	29.5	1 (2%)	1 (2%)	1	0	1
Hemicentetes semispinosus	69.0	1 (2%)	1 (2%)	1	1	0
Soricidae						
Suncus murinus	32.4	1 (2%)	1 (2%)	1	1	0
Nesomyinae						
Eliurus minor	49.0	3 (4%)	2 (5%)	3	2	1
Eliurus webbi	50.0	29 (45%)	9 (23%)	21	14	7
Nesomys rufus	240.0	1 (2%)	1 (2%)	1	1	0
Muridae						
Rattus rattus	96.5	7 (10%)	5 (13%)	7	6	1
Total	–	64	40	52	32	20

The captures for each species were unequally distributed between trapping grids (Table 3). All species except *H. semispinosus*, *R. rattus* and *S. murinus* were found in primary forest. Three endemic species (*O. hova, M. pulla* and *N. rufus*) were not trapped in secondary forest. No animals were trapped in grid III which was subjected to tree-felling by a local farmer who encroached within 15 m of the trapping grid during the study period.

Table 3. Number of individual small mammals captured in primary forest (grids I and II combined) and secondary forest (grids III and IV combined).

Species	Primary forest	Secondary forest
M. talazaci	14	5
M. pulla	1	0
O. hova	1	0
H. semispinosus	0	1
S. murinus	0	1
E. webbi	8	1
E. minor	1	1
N. rufus	1	0
R. rattus	0	5
Total number of individuals	26	14
Total number of endemic species	6	4

Microhabitat selection

Only *M. talazaci, E. webbi, E. minor*, and *R. rattus* were caught more than once on the grids. To determine the habitat variables that distinguish between the microhabitats of different species, the trap sites of the four most commonly caught species were compared. The capture sites of each species were tested against the pooled capture sites of the other species using one-way analysis of variance. Since habitat variable data can deviate from a normal distribution (Dueser and Shugart 1978), the Mann-Whitney *U*-test was also employed. *E. minor* was included in the pooled sample for other species but was not compared with the pooled sample itself as it was caught only three times. "In principle these pooled data represent capture sites where the species was not found against which to test capture sites where it was found" (Dueser and Shugart 1978). These comparisons provide a conservative basis for identifying individual variables on which a particular species appears to be distinguished.

Eleven variables were found to distinguish between microhabitats of different species (Table 4). *M. talazaci* capture sites differed from pooled sites on just three variables compared to seven variables for *E. webbi* and eight variables for *R. rattus*.

Microhabitat characterization

Although univariate analyses are instructive in determining habitat variables by which microhabitats can be characterized, they do not take into account the effects of correlations between variables (Dueser and Shugart 1978). A multivariate test is required to detect and quantify differences between sample groups. Stepwise discriminant analysis (Dixon 1990) was carried out for the three most

Table 4. Differences between pooled and sample means for the 3 most abundant species as determined by the Mann-Whitney *U*-Test (M–W) and one-way analysis of variance (AOV). * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.005$, **** – $p < 0.001$.

Variable	*M. talazaci*		*E. webbi*		*R. rattus*	
	M–W	AOV	M–W	AOV	M–W	AOV
% canopy cover		*				
% light penetration					*	**
Overstory tree size					*	*
Understory tree dispersion				*		
Woody species number			*	*	*	
Herbaceous stem density (0.5 m)	*	*	***	***	*	*
Herbaceous stem density (1.0 m)	*	*	**	***		*
% herbaceous cover					*	*
Fallen log dispersion			***	***		
Liane stem density			*	*	*	*
Distance to forest edge			*	***	****	****

commonly caught species using trap site variables previously identified (Table 4). Again, *E. minor*, although included in pooled samples, was excluded from analysis itself due to small sample size. The value of *F* determined by stepwise discriminant analysis provides a measure of the relative contribution of the variable to discriminate between species' microhabitats. With *M. talazaci*, relatively high herbaceous stem density and low canopy cover discriminate its microhabitat from the microhabitats of other species (Table 5). Low herbaceous stem densities at 0.5 m are the strongest characteristic by which to distinguish the microhabitat of *E. webbi* which is found in areas far from the forest edge where fallen logs are highly dispersed, woody species richness is high and lianes are abundant. *R. rattus* was never caught more than 40 m inside forest and a small distance to the forest edge is the most important microhabitat characteristic in this species. It was found where overstory trees were more dispersed than at other capture sites, lianes were relatively scarce and light penetration of the canopy was high. Herbaceous cover at *R. rattus* trap sites was lower than for other capture sites but herbaceous stem counts were high. This discrepancy arose because the dominant herbaceous species at many *R. rattus* capture sites was *Aframomum angustifolium* (Zingiberaceae).

Table 5. Microhabitat variables of each species compared with pooled values of other species as determined by stepwise discriminant analysis (see text).

Variable	*F*	Sample means ± SD	
		Species	Pooled
Microgale talazaci			
Herbaceous stem density (0.5 m)	5.11	2.9 ± 2.79	1.5 ± 1.63
% canopy cover	3.31	77.6 ± 14.77	84.5 ± 7.59
Herbaceous stem density (1.0 m)	2.17	1.4 ± 1.71	0.6 ± 1.10
Eliurus webbi			
Herbaceous stem density (0.5 m)	11.53	0.9 ± 0.75	2.8 ± 2.54
Fallen log dispersion	7.83	5.7 ± 2.19	3.8 ± 2.16
Distance from forest edge	6.24	474.8 ± 206.06	259.4 ± 267.53
Understory tree dispersion	4.83	2.1 ± 0.79	2.5 ± 1.58
Woody species number	3.87	5.1 ± 2.25	4.0 ± 1.77
Herbaceous stem density (1.0 m)	3.16	0.2 ± 0.41	1.4 ± 1.65
Liane stem density	2.64	4.6 ± 2.10	3.0 ± 1.93
Rattus rattus			
Distance from forest edge	20.38	7.1 ± 14.96	384.5 ± 236.81
Overstory tree size	17.06	16.7 ± 5.28	20.8 ± 4.62
% herbaceous cover	12.86	35.9 ± 8.51	48.5 ± 15.59
Liane stem density	10.28	2.0 ± 1.29	4.0 ± 2.10
Herbaceous stem density (0.5 m)	8.29	3.6 ± 2.07	1.7 ± 2.12
% light penetration	6.89	23.4 ± 17.19	11.3 ± 9.08
Herbaceous stem density (1.0 m)	5.82	1.9 ± 1.68	0.7 ± 1.28
Woody species number	4.97	3.1 ± 1.35	4.7 ± 2.06

This species reaches heights in excess of 2 m so was omitted from the ocular counts of ground herbs used to determine herbaceous cover.

Differences between primary and secondary forest

Habitat variables measured in primary and secondary forest were compared using both parametric and non-parametric tests to determine differences even when data were not normally distributed. Twelve habitat variables were found to differ between the two forest types (Table 6). Seven of these variables (percentage light penetration of the canopy, woody species number, herbaceous stem density at 0.5 m, percentage herbaceous cover, fallen log dispersion, liane stem density

Table 6. Mean habitat variable measurements (± SD) for grids I and II combined (primary forest) and grids III and IV combined (secondary forest). Differences between grids determined by Mann-Whitney *U*-Test (M–W) and oneway analysis of variance (AOV). * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.005$, **** – $p < 0.001$.

Variable	Grids I and II ($n = 60$)	Grids III and IV ($n = 60$)	M–W	AOV
% light penetration	10.3 ± 10.98	16.5 ± 15.80	*	*
Woody stem density (1.0 m)	4.6 ± 2.76	5.9 ± 3.76		*
Woody species number	4.8 ± 1.91	4.1 ± 1.41		*
Herbaceous species number	2.8 ± 1.23	2.0 ± 0.96	****	****
Herbaceous stem density (0.5 m)	2.6 ± 3.34	1.7 ± 2.62	*	
% herbaceous cover	48.9 ± 15.33	41.7 ± 12.99	*	**
Fallen log dispersion	6.2 ± 2.56	5.3 ± 2.95	*	
% exposed rock	7.3 ± 13.91	1.5 ± 6.64	***	***
Tree fern density	2.5 ± 3.50	4.3 ± 5.35	*	*
Liane stem density	3.9 ± 2.15	2.8 ± 1.96	**	**
Distance to water	55.1 ± 35.62	66.3 ± 25.80	*	*
Distance to forest edge	371.3 ± 200.50	50.9 ± 47.00	****	****

and distance to forest edge) were among the 11 variables that distinguished between small mammal microhabitats (Table 4). Therefore, habitat disturbance and deforestation in lowland forests such as Anandrivola, which result in forest loss and subsequent secondary growth, will be expected to alter significantly the availability of favoured small mammal microhabitats and consequently affect species distributions.

Discussion

Small mammal species richness and abundance

Studies employing similar trapping protocols in Analamazaotra rain forest recorded 11 species of small mammals (Nicoll *et al.* 1988, Stephenson 1993). The lower number of species recorded in the present study may be due to seasonality

effects since fewer small mammal species are captured in Malagasy forests during winter months (Stephenson 1994b). Tenrec species such as *Tenrec ecaudatus* and *Setifer setosus* would have been in torpor at the time of the present study (Eisenberg and Gould 1970, Stephenson *et al.* 1994a) yet are widespread throughout eastern rain forests (Nicoll and Langrand 1989) and are probably present in Anandrivola.

In the present study, endemic small mammal species richness was greatest in undisturbed forest. In mid-altitude rain forest (Stephenson 1993), species richness was also found to be greatest in primary habitat though individual species abundance was reduced. Small mammal abundance (ie the number of individual animals captured) was generally lower in the present study than in any other forest site trapped in Madagascar. Sherman traps recorded 15.2 captures per 1000 trap nights compared with 25.1 (Nicoll *et al.* 1988), 36.7 (Stephenson 1993) and 83.8 (Stephenson *et al.* 1994b) captures in other studies. When pitfall traps of identical size were used successfully elsewhere, captures rates were 2.4 (Nicoll *et al.* 1988) and 2.5 (Stephenson 1993) individuals per 1000 trap nights, more than twice the rate of the present study. Considering trapping protocols were similar and the recorded number of individual small mammals usually increases in winter months (Stephenson 1994c), it must be concluded that small mammal abundance at Anandrivola is lower than in forests at higher altitudes. Further studies of lowland sites are required to ascertain whether or not this difference is a function of altitude.

Small mammal microhabitat use

Eleven habitat variables differentiated between small mammal microhabitats. Interspecific differences in microhabitat utilization may be greater than predicted because: (1) the range of categories defined (ie the habitat variables measured) are unlikely to coincide with all those factors discriminated by the animals and additional variables may provide further bases for segregation (Price 1978, Dueser and Shugart 1979); (2) trapping methods do not measure foraging microhabitat precisely because an animal can be captured whilst travelling through an inappropriate habitat patch to reach an appropriate one (Schroder and Rosenzweig 1975), especially in high dispersal seasons (Carnes and Slade 1982). Alternatively, an individual may venture into an unfavourable microhabitat to investigate the trap bait placed there.

Therefore, the identified microhabitat differences are a conservative basis for interspecific comparisons. The model may be improved in the future by including additional variables. For example, soil composition can affect elements of the habitat such as overstory tree distribution (Austin *et al.* 1972).

The use of multivariate discriminant analyses in ecological studies, particularly for characterizing differences among sympatric species, is discussed by numerous authors (eg Green 1971, Rotenberry and Wiens 1980, Carnes and Slade 1982, Van Horne and Ford 1982, Williams and Titus 1988). In all studies it is important to accept that statistical and biological significance are not necessarily related

(Rexstad *et al.* 1988) and that statistical significance alone is insufficient to establish even a likelihood of causality (Green 1974). As proposed by Abramsky *et al.* (1985), one way of determining the efficacy of such an analysis is to compare the results with information available from other trapping studies.

Eisenberg and Gould (1970) generally caught *M. talazaci* in mature second growth or multistratal primary evergreen forest, often in tangled ground cover. Nicoll *et al.* (1988) found the species widespread in mid-altitude forest, with a tendency to frequent areas with deep leaf litter and dense herbaceous growth. These observations correlate closely with the findings of the present study. Eisenberg and Gould (1984) noted that many species of *Microgale* appear highly specialised for "discrete micro-environments", making them vulnerable to habitat destruction. They found that *Microgale* species were more easily trapped in areas remote from human habitation and disturbance and were captured in greatest abundance in those areas where *Rattus* and *Suncus* were absent (Eisenberg and Gould 1970). Stephenson (1993) found endemic small mammal species richness reduced in areas where *R. rattus* was abundant. Heim de Balsac (1972) questioned whether or not the rarity of *Microgale* species was a direct result of introduced rats and shrews. In the present study, *M. talazaci* was only once captured at the same site as an introduced species (*R. rattus*).

In Anandrivola, *R. rattus* was found only in secondary forest, never more than 40 m from the forest edge and never at the same sites as endemic rodents which were generally more abundant in primary forest. Most other small mammal surveys in Malagasy rain forest have also recorded *R. rattus* in disturbed habitats and only endemic rodents deep within primary forest (eg Thompson *et al.* 1987, Raxworthy and Rakotondraparany 1988, Stephenson 1993). Nicoll *et al.* (1988) found *R. rattus* had a strong association with open herbaceous areas of forest and riparian habitats. Although a solitary individual was recorded in northern Madagascar in primary cloud forest (Raxworthy and Nussbaum 1994), the proximity of the capture site to disturbed habitat or water is not mentioned. Therefore, the present study further supports the suggestion (Nicoll *et al.* 1988, Stephenson 1993) that cutting or otherwise disturbing native forest will provide microhabitats favourable to *R. rattus*. In such instances, however, it is still unclear whether endemic small mammals are most threatened by the loss of appropriate microhabitats or by competition from invading exotic species. Since introduced rats and shrews appear to prefer microhabitats unfavourable to most endemic species, this question cannot be answered without removal experiments.

Comparison with other microhabitat studies in Madagascar

In mid-altitude rain forest, eight habitat variables differentiated between the microhabitats of the six small mammal species studied (Nicoll *et al.* 1988). Only two of these eight variables (light penetration of the canopy and understory tree dispersion) were found to be significant in the present study. Explanations that may account for the difference in microhabitat segregation between study sites

include: (1) Altitude. Within tropical rain forest, floral and faunal species composition varies with altitude (Lieberman *et al.* 1985, Carleton and Schmidt 1990). Microhabitat availability and utilization will therefore also be expected to vary as a function of elevation. (2) Community composition. The small mammal community studied at mid-altitude included four species not found in the present study. Since the spatial use of habitat may be influenced by competitive interactions with other species (Hallett *et al.* 1983, Moss and Croft 1988, Busch and Kravetz 1992), a particular species may use microhabitats differently in a different small mammal community. (3) Species abundance. Relative species abundance can affect microhabitat use (Rosenzweig 1981, Abramsky *et al.* 1985, Rosenzweig and Abramsky 1985) and lower small mammal densities were recorded in the present study. (4) Seasonality. The mid-altitude study was conducted between April and June. Seasonality may affect either the fauna or flora in such a way as to influence habitat use.

A full understanding of small mammal microhabitat use and co-existence within a given habitat type will come only through year-round concurrent studies at a range of sites.

In dry forest in western Madagascar, six habitat variables were found to influence the distribution of the tenrecine tenrecs *Echinops telfairi* and *Tenrec ecaudatus* (Ganzhorn *et al.* 1990). Four of these variables (overstory tree size, understory tree dispersion, woody species number and distance to the forest edge) were also influential in the present study. Ganzhorn *et al.* (1990) concluded that selective logging had limited effects on these variables and was not therefore a direct threat to tenrec populations. This contrasts with the results of the present study where seven variables influential in determining small mammal distributions were altered by habitat disturbance. It has been demonstrated that small oryzorictine tenrecs are more sensitive to habitat disturbance than tenrecine tenrecs (Stephenson 1993) so the conclusions of the present study may differ from those of Ganzhorn *et al.* (1990) due to the differential susceptibility of species to logging. Nonetheless, in both eastern and western studies, logged or secondary forest was associated with a reduction in plant species richness. Woody species diversity differentiated between rodent microhabitats in the present study and is also correlated with lemur abundance (Hawkins *et al.* 1990). Therefore the long-term consequences of habitat disturbance may include a decrease in floral diversity and an associated reduction in mammalian species richness.

Acknowledgements: In Madagascar I am grateful to the Ministère des Eaux et Forêts, Ministère de l'Enseignement Supérieur, Ministère de la Recherche Scientifique et Technologique pour le Développement, Parc Botanique et Zoologique de Tsimbazaza, and WWF – Aires Protégées. Field assistance came from N. Quansah, F. Rakotondraparany, C. Raxworthy and D. Cemmick. I would also like to thank the following individuals for advice and assistance at various stages of the project: S. Alibhai, D. Bellamy, M. Carleton, L. Durrell, M. Gorman, J. Ingles, P. Jenkins, O. Langrand, W. Muster, M. Nicoll, P. Racey, D. Shreeve and A. Wroot. The project was funded by grants from The Conservation Foundation, WWF-US, Royal Geographical Society (Silver Spoon Award), University of London Union, The Twenty-Seven Foundation, and the Royal Holloway and Bedford New College Driver Award.

References

Abramsky Z., Rosenzweig M. L. and Brand S. 1985. Habitat selection of Israel desert rodents: comparison of a traditional and a new method of analysis. Oikos 45: 79–88.

Austin M. P., Ashton P. S. and Greig-Smith P. 1972. The application of quantitative methods of vegetation survey III. A re-examination of rain forest data from Brunei. Journal of Ecology 60: 305–324.

Barnett J. L., How R. A. and Humphreys W. F. 1978. The use of habitat components by small mammals in eastern Australia. Australian Journal of Ecology 3: 277–285.

Busch M. and Kravetz F. O. 1992. Competitive interactions among rodents (*Akodon azarae, Calomys laucha, Calomys musculinus* and *Oligoryzomys flavescens*) in a two-habitat system. II. Effect of species removal. Mammalia 56: 541–554.

Carleton M. D. and Schmidt D. F. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): an annotated gazetteer of collecting localities of known forms. American Museum Novitates 2987: 1–36.

Carnes B. A. and Slade N. A. 1982. Some comments on niche analysis in canonical space. Ecology 63: 888–893.

Dixon W. T. 1990. BMDP Statistical Software. University of California Press, Berkeley.

Dueser R. D. and Shugart H. H., Jr 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59: 89–98.

Dueser R. D. and Shugart H. H., Jr 1979. Niche pattern in a small mammal fauna. Ecology 60: 108–118.

Eisenberg J. F. and Gould E. 1970. The tenrecs: a study in mammalian behaviour and evolution. Smithsonian Contributions to Zoology 27: 1–127.

Eisenberg J. F. and Gould E. 1984. The insectivores. [In: Key environments, Madagascar. A. Jolly, P. Oberlé and R. Albignac, eds]. Pergamon Press, Oxford: 155–166.

Fa J. E., Romero F. J. and Lopez-Paniagua J. 1992. Habitat use by parapatric rabbits in a Mexican high-altitude grassland system. Journal of Applied Ecology 29: 357–370.

Ganzhorn J. U., Ganzhorn A. W., Abraham J.-P., Andriamanarivo L. and Ramananjatovo A. 1990. The impact of selective logging on forest structure and tenrec populations in western Madagascar. Oecologia 84: 126–133.

Green G. M. and Sussman R. W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. Science 248: 212–215.

Green R. H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. Ecology 52: 543–556.

Green R. H. 1974. Multivariate niche analysis with temporarily varying environmental factors. Ecology 55: 73–83.

Hallett J. G., O'Connell M. A. and Honeycutt R. L. 1983. Competition and habitat selection: test of a theory using small mammals. Oikos 40: 175–181.

Hawkins A. F. A., Chapman P., Ganzhorn J. U., Bloxham Q. M. C., Barlow S. C. and Tonge S. J. 1990. Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. Biological Conservation 54: 83–110.

Heim de Balsac H. 1972. Insectivores. [In: Biogeography and ecology in Madagascar. R. Battistini and G. Richard-Vindard, eds]. Dr W. Junk B. V. Publishers, The Hague: 629–660.

IUCN/UNEP/WWF 1987. Madagascar: an environmental profile. [M. D. Jenkins, ed]. IUCN, Gland and Cambridge: 1–439.

Jenkins P. D. 1988. A new species of *Microgale* (Insectivora: Tenrecidae) from northeastern Madagascar. American Museum Novitates 2910: 1–7.

Kemper C. and Bell D. T. 1985. Small mammals and habitat structure in lowland rain forest of Peninsular Malaysia. Journal of Tropical Ecology 1: 5–22.

Laurance W. F. 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biological Conservation 69: 23–32.

Lieberman M., Lieberman D., Hartshorn G. S. and Peralta R. 1985. Small-scale altitudinal variation in lowland wet forest vegetation. Journal of Ecology 73: 505–516.

M'Closkey R. T. and Fieldwick B. 1975. Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). Journal of Mammalogy 56: 119–129.

Moss G. L. and Croft D. B. 1988. Behavioural mechanisms of microhabitat selection and competition among three species of arid zone dasyurid marsupial. Australian Journal of Ecology 13: 485–493.

Nicoll M. E. and Langrand O. 1989. Madagascar: Revue de la conservation et des aires protégées. WWF, Gland: 1–374.

Nicoll M. E., Rakotondraparany F. and Randrianasolo V. 1988. Diversité des petits mammifères en forêt tropicale humide de Madagascar: analyse préliminaire. [In: L'Equilibre des ecosystèmes forestiers à Madagascar: Actes d'un séminaire international. L. Rakotovao, V. Barre and J. Sayer, eds]. IUCN, Gland and Cambridge: 241–252.

Porter J. H. and Dueser R. D. 1982. Niche overlap and competition in an insular small mammal fauna: a test of the niche overlap hypothesis. Oikos 39: 228–236.

Price M. V. 1978. The role of microhabitat in structuring desert rodent communities. Ecology 59: 910–921.

Raxworthy C. J. 1988. Reptiles, rainforest and conservation in Madagascar. Biological Conservation 43: 181–211.

Raxworthy C. J. and Nussbaum R. A. 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. Biological Conservation 69: 65–73.

Raxworthy C. J. and Rakotondraparany F. 1988. Mammal Report. [In: Manongarivo Special Reserve (Madagascar) 1987/88 expedition report. N. Quansah, ed]. MERG, The Conservation Foundation, London: 122–130.

Raxworthy C. J. and Stephenson P. J. 1988. Lemur observations in the lowland rainforest of Anandrivola, Madagascar. Primate Conservation 9: 118–120.

Rexstad E. A., Miller D. D., Flather C. H., Anderson E. M., Hupp J. W. and Anderson D. R. 1988. Questionable multivariate statistical inference in wildlife habitat and community studies. Journal of Wildlife Management 52: 794–798.

Rosenzweig M. L. 1981. A theory of habitat selection. Ecology 62: 327–335.

Rosenzweig M. L. and Abramsky Z. 1985. Detecting density-dependent habitat selection. American Naturalist 126: 405–417.

Rotenberry J. T. and Wiens J. A. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228–1250.

Schroder G. D and Rosenzweig M. L. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia 19: 9–28.

Stephenson P. J. 1993. The small mammal fauna of Réserve Spéciale d'Analamazaotra, Madagascar: the effects of human disturbance on endemic species diversity. Biodiversity and Conservation 2: 603–615.

Stephenson P. J. 1994a. Notes on the biology of the fossorial tenrec, *Oryzorictes hova* (Insectivora: Tenrecidae). Mammalia 58: 312–315.

Stephenson P. J. 1994b. Seasonality effects on small mammal trap success in Madagascar. Journal of Tropical Ecology 10: 439–444.

Stephenson P. J. 1994c. Small mammal species richness in a Madagascar rain forest. African Journal of Ecology 32: 255–258.

Stephenson P. J. 1995. Taxonomy of shrew-tenrecs (*Microgale* spp.) from eastern and central Madagascar. Journal of Zoology, London 235: 339–350.

Stephenson P. J., Quansah N., Raxworthy C. J. and Cemmick D. 1987. University of London Expedition to Madagascar 1986 Report. University of London, Egham: 1–92.

Stephenson P. J., Racey P. A. and Rakotondraparany F. 1994a. Maintenance and reproduction of tenrecs (Tenrecidae) in captivity at Parc Tsimbazaza, Madagascar. International Zoo Yearbook 33: 194–201.

Stephenson P. J., Randriamahazo H., Rakotoarison N. and Racey P. A. 1994b. Conservation of mammalian species diversity in Ambohitantely Special Reserve, Madagascar. Biological Conservation 69: 213–218.

Thompson P. M., Raxworthy C. J., Murdoch D. A., Quansah N. and Stephenson P. J. 1987. Zahamena forest (Madagascar) expedition 1985. ICBP Study Report no. 20. ICBP, Cambridge: 1–92.

Twigg G. I. 1975. Marking mammals. Mammal Review 5: 101–116.

Van Horne B. and Ford R. G. 1982. Niche breadth calculation based on discriminant analysis. Ecology 63: 1172–1174.

Williams B. K. and Titus K. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. Ecology 69: 1275–1285.

Wilson D. E. and Reeder D. M. (eds) 1993. Mammal species of the world. Second edition. Smithsonian Institution Press, Washington DC: 1–1206.

Received 23 August 1994, accepted 4 September 1995.