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The role of competition and habitat in structuring small mammal communities in a tropical montane ecosystem in southern India

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Abstract

Small mammals were sampled in two natural habitats (montane stunted evergreen forests and montane grassland) and four anthropogenic habitats (tea, wattle, bluegum and pine plantation) in the Upper Nilgiris in southern India. Of the species trapped, eight were in montane evergreen forests and three were in other habitats. Habitat discrimination was studied in the rodents *Rattus rattus* and *Mus famulus* and the shrew *Suncus montanus* in the montane forest habitat. Multivariate tests on five variables (canopy cover, midstorey density, ground cover, tree density, canopy height) showed that *R. rattus* uses areas of higher tree density and lower canopy cover. *Suncus montanus* and *M. famulus* use habitat with higher tree density and ground cover and lower canopy height. Multivariate tests did not discriminate habitat use between the species. Univariate tests, however, showed that *M. famulus* uses areas of higher tree density than *R. rattus* and *S. montanus*. *Rattus rattus* was the dominant species in the montane forest, comprising 60.9% of total density, while the rodent *Millardia meltada* was the dominant species in the grassland. Studies of spatial interaction between these two species in habitats where they coexisted showed neither overlap nor avoidance between the species. *Rattus rattus*, however, did use areas of lower ground cover than did *M. meltada*. The analysis of spatial interactions between the species, habitat discrimination and use, and the removal experiments suggest that interspecific competition may not be a strong force in structuring these small mammal communities. There are distinct patterns in the use of different habitats by some species, but microhabitat selection and segregation is weak. Other factors such as intraspecific competition may play a more important role in these communities.

Key words: habitat selection, habitat segregation, spatial interaction, montane forest, plantation, interspecific and intraspecific competition

INTRODUCTION

Habitat selection has been considered an important factor in community dynamics (MacArthur & Levins, 1964; Rosenzweig, 1974). The view of the niche as multi-dimensional space (Hutchinson, 1958) occupied by each species or individual offered a framework to study resource partitioning and competition between species. Ever since habitat complexity was first linked with species diversity (MacArthur & MacArthur, 1961), there has been a substantial effort to determine the nature of the relationship between habitat and species diversity and other population parameters. The working hypothesis has been that greater habitat diversity leads to more niches, resulting in a higher diversity of bird or small mammal species (Klopfer & MacArthur, 1960). The role of competition has been debated both in the context of the structure of ecological communities and its evolutionary significance in speciation (Schoener, 1984; Walter, Hulley & Craig, 1984; Maurer, 1985). Its role in the structuring of communities has been questioned, with many authors being critical of the purported evidence for competition and the theoretical attention it has received (Connor & Simberloff, 1979; Strong, Szyska & Simberloff, 1979; Connell, 1983). Although evidence of competition may be difficult to demonstrate in field studies (Grant, 1972), much work seems to indicate that interspecific competition for resources occurs in many terrestrial ecosystems (Hairston, Smith & Slobodkin, 1960; Schoener, 1983). Hairston *et al.* (1960) conclude that interspecific competition for resources occurs among producers, carnivores and decomposers, while herbivores are largely predator limited. Amongst herbivores, leaf-eaters and sap-suckers are not likely to show competition, while

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granivores and nectarivores may be expected to do so (Slobodkin, Smith & Hairston, 1967).

Although some studies of small mammals demonstrate the importance of competitive exclusion (e.g. Valone & Brown, 1995), many others point to habitat selection as a more important force in small mammal communities (e.g. Boitani, Loy & Molinari, 1985; Murúa *et al*., 1987; Turner & Grant, 1987; Scott & Dueser, 1992). Though there may be little doubt that interspecific competition occurs in various taxa (Schoener, 1983), the question is how important is this as a force in structuring ecological communities, and in this study, small mammal communities. Extensive work on desert communities (for a review see Kotler & Brown, 1988) seems to indicate that resource partitioning and interspecific competition do play an important role in structuring these communities. However, the role of competition and the relative importance of other factors is not clear in other small mammal communities, especially in tropical forests.

In this study, the role of competition and habitat selection in a small mammal community in a tropical montane ecosystem in southern India was considered. Microhabitat selection and segregation in three common species of small mammals (the common rat *Rattus rattus* L., Bonhote's mouse *Mus famulus* Bonhote, and a shrew *Suncus montanus* Kelaart) were examined in montane evergreen forests. The spatial interactions between these three species in montane forests were also investigated. The community structure of small mammals was studied across a range of montane habitats. *Rattus rattus*, the dominant species in the montane forests, and the soft-furred field rat *Millardia meltada* Gray, the dominant species in the grassland, do not coexist in natural habitats (Shanker, 1998). The interaction between these two species was thus examined in plantations where they do coexist.

METHODS

Study area

The Nilgiris are located between 11°10′–11°30′N and 76°25′–77°00′E at the junction of the Eastern Ghats and the Western Ghats, in southern India. The study was conducted in the higher altitudes (1800–2500 m a.s.l.) of the Nilgiris which have a montane ecosystem, comprising patches of stunted evergreen forest (locally called 'sholas') surrounded by grasslands. Though most grasslands have been replaced by exotic species such as wattle *Acacia* spp., pine *Pinus roxburghii*, tea *Camellia sinensis* and bluegum *Eucalyptus globulus*, the natural ecosystem remains intact in the south-west region of the Nilgiris plateau. The stunted montane evergreen forest patches, usually 1–10 ha with few exceeding 100 ha, are confined to depressions and folds in the mountain. They are extremely dense, with 5000 or more woody plants (> 1 cm d.b.h.) per hectare, and are dominated by the families Lauraceae, Rubiaceae and Symplocaceae. There is a sharply defined ecotone between the montane forest patches and the grasslands, which is maintained by frost and fire (Meher-Homji, 1984). The climate is highly seasonal, with a dry season extending from December to February, a pre-monsoon season from March to May, the south-west monsoon from June to August and a second wet season from September to November. Most of the areas sampled receive annual rainfall of 1500–2000 mm.

Sampling procedures

Small mammal live-trapping was carried out between February 1994 and September 1996. Montane forest patches and grasslands were sampled using 0.49-ha and 1-ha plots. Traps were placed at intervals of 10 m so that each 0.49-ha plot consisted of 49 permanently marked trap stations, in a square grid of 7 × 7 traps (the 1-ha plots had 100 trap stations, in a 10 × 10 configuration). Because of their size and shape, plantations were sampled using 0.45-ha plots (15 × 3 trap stations). A standard Sherman live-trap (22.9 × 7.6 × 8.9 cm) was placed on the ground at each station, close to a tree, log, or any other appropriate runway. The traps were baited with grated coconut and rice. All trapped animals were identified, uniquely marked, sexed, weighed, measured and released. A standard ear-punch (National Band and Tag Co., U.S.A. No. 1538) was used. In the initial part of the study, toe-clipping was briefly used; this method was painful to the animals, but most species were recaptured despite the clipping. Monel tags were also tried (a painless technique), but the method was not useful as animals lost their tags between trapping sessions. The pros and cons of different tagging methods are discussed in Shanker (1998).

The traps were checked once daily between 08:00 and 12:00. The plots were run for 5 consecutive nights during February–October 1994. Trap mortality was found to be particularly high towards the end of the trapping period in some seasons and the trapping duration was thus reduced to 3 nights for the rest of the study (Shanker, 1998).

Six montane evergreen forest patches, ranging from 2 to 600 ha, were extensively sampled using 9 plots of 0.49-ha and 2 plots of 1-ha (see Shanker, 1998; Shanker & Sukumar, 1998). Grasslands were also sampled using 0.49-ha plots. Both forest patches and grasslands were also sampled with 0.45-ha plots, which enabled comparisons with plots in anthropogenic habitats that had a similar design. Anthropogenic habitats (tea, gum, wattle and pine) were sampled using 0.45-ha plots, including wattle plantations of 3 different ages (see Table 1 for sampling details). Additionally, a 0.90-ha plot was established in an old wattle plantation to study the interaction between *R. rattus* and *M. meltada*. Each plot was sampled several times, typically once during each season (= session).

Removal and introduction experiments were conducted on 3 small (0.1–2.2 ha) montane forest patches in

Table 1. Trapping effort and habitat characteristics of the habitat types sampled in the montane regions of the Nilgiris in southern India. Grassland and montane forests were extensively sampled using 0.49-ha and 1-ha square plots (see sampling procedure). They were also sampled using 0.45-ha plots to enable comparisons with the other habitats. Wattle plantations (*Acacia* spp.) were sampled at different stages: young, 3–4 m; intermediate, 4–5 m; old, > 8 m. Each plot was sampled more than once; the number of trapping sessions is the total for the habitat type. All habitat variables were quantified using a qualitative score, which was then normalized for the analysis

Habitat	Plots	Trap sessions	Trap-nights	Canopy cover	Grass	Woody stems	Tree density	Height (m)
Grassland (0.49 ha)	6	16	3381	Open	High	None	None	
Grassland (0.45 ha)	3	3	405	Open	High	None	None	
Wattle, young	3	6	810	Open	Medium	High	None	3.2
Wattle, medium	1	4	540	Medium	High	High	Medium	4.1
Wattle, old	3	9	1800	Closed	Low	Medium	High	9.9
Forest (0.45 ha plots)	4	5	675	Closed	Low	High	Medium	11.5
Forest (0.49 ha, 1 ha)	11	85	~20000	Closed	Low	High	Medium	11.5
Bluegum	2	6	810	Open	Low	Low	Medium	5.3
Tea	2	3	335	Open	Low	Medium	None	
Pine	3	10	1350	Closed	None	None	Low	10.9

Upper Bhavani. Following preliminary sampling at each of these plots, *R. rattus* individuals were removed from these plots until no *R. rattus* individuals were captured for at least 2 days of trapping and the plots were subsequently monitored for responses to the removal. In the second stage, *M. meltada* individuals were introduced into plots from which *R. rattus* had been removed, and their persistence and directional movement was monitored. In 1 experiment, 8 *M. meltada* (4 males + 4 females) were released in a 0.5-ha patch at distances of 10 m from each other and *c*. 30 m from the grassland on either side. In a second experiment, 6 *M. meltada* (3 males + 3 females) were released in a 2.2-ha patch at a central point. The plots were subsequently monitored.

Data analysis

Various capture–recapture models were used for density estimation, but they could not be applied to all plots during all the sampling sessions because of low sample sizes/population densities (Shanker, 1998). Hence, density estimates for small mammals were based on the minimum number alive (Krebs, 1966). Habitat variables (topography, slope, canopy cover, midstorey density, ground cover, woody stem density, tree density, canopy height, log size and log abundance, number of species within 1 and 5 m radius, number of individuals within 1 and 5 m radius) were examined at 11 plots in montane forest patches (modified from Dueser & Shugart, 1978). Following a preliminary analysis, 5 habitat variables (canopy cover, midstorey density, ground cover, tree density and canopy height) were selected and examined across all plots at 641 trap stations. All variables were quantified using a qualitative score, which was then normalized for the analysis: (1) canopy cover, a qualitative estimate on a scale of 0–4; (2) midstorey cover, a qualitative estimate on a scale of 0–4; (3) ground cover, a qualitative estimate on a scale of 0–4; (4) tree density, a classification of the density of trees (> 10 cm d.b.h.) within a radius of 5 m around the trap site on a scale of 0–3 where 1 = low (1–5 stems); 2 = medium (6–10 stems); 3 = high (> 10 stems); (5) canopy height. These 5 habitat variables were also studied in all the plantations.

The presence or absence of the 3 common species were examined in relation to the habitat variables at each trap station. The habitat variables were examined in 3 ways. First, the normalized habitat variable measured at each trap site was used without change. Second, the habitat variable for each trap site was taken as the average of variables measured at that site and all sites immediately surrounding the site (i.e. 10 m in 4 directions). Third, principal components analysis was performed on the site scores and averaged site scores, and the derived principal component axes were used for further analysis.

The analysis was performed using univariate ANOVA and multivariate tests. Canonical discriminant analysis was used to distinguish between groups, and significance of the test was derived from the estimate of Wilk's λ. Canonical discriminant analysis is a dimension-reduction technique. It derives canonical variables, which are linear combinations of the quantitative variables which summarizes the between-class variation in the sample (Harris, 1985; SAS/SAT, 1988).

The occurrence of species at particular trap sites was also examined. As a simple approximation, the probabilities of capture of each species were used to calculate the expected number of traps that would capture both species during a sampling session:

$$\text{expected} = a \times b/n \qquad \text{(Equation 1)}$$

where expected = expected number of traps that capture 2 species; a = total number of captures of species a; b = total number of captures of species b; n = number of traps.

This was followed by simulation methods to determine whether the number of traps with 2 species was above or below that expected by chance alone. The simulation relaxes certain assumptions implicit in the above formula and provides an expected distribution from empirical data. In each simulation, captures of 2 species are

Table 2. Seven species of rodents and two species of insectivores were trapped during the study (names and distribution from Ellerman & Morris-Scott, 1951; Ellerman, 1961)

Species	Common name	Distribution
Rodents		
Family Muridae		
Rattus rattus	Common rat	World-wide
Cremnomys blanfordi	White-tailed wood rat	Peninsular India, Sri Lanka
Mus famulus	Bonhote's mouse	Nilgiris in Peninular India, Assam
Mus platythrix	Brown spiny mouse	Indian subcontinent
Vandeleuria oleracea	Long-tailed tree mouse	Southern Western Ghats
Millardia meltada	Soft-furred field rat	Indian subcontinent
Family Muscardinidae		
Platacanthomys lasiurus	Malabar spiny dormouse	Indian subcontinent, Sri Lanka
Insectivores		
Family Soricidae		
Suncus montanus	–	Southern peninsular India, Sri Lanka
Suncus dayi	Days shrew	Southern peninsular India

Table 3. Relative abundance (%) and biomass (%) of *Rattus rattus*, *Millardia meltada* and *Suncus montanus* (the three common species) in various habitats and the proportion of the total that these species comprise in each of the habitats

Plot	*Rattus rattus*		*Millardia meltada*		*Suncus montanus*		Common species	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Grass	0.00	0.00	86.67	94.04	13.33	5.96	100.00	100.00
Wattle, young	0.00	0.00	75.00	83.47	25.00	16.53	100.00	100.00
Wattle, medium	14.29	21.01	73.02	73.08	12.70	5.91	100.00	100.00
Wattle, old	54.22	70.87	27.31	19.88	14.06	4.32	95.58	95.07
Montane forest	69.23	91.66	0.00	0.00	23.08	6.81	92.31	98.47
Montane forest, all	64.78	88.10	0.00	0.00	20.91	7.17	85.69	95.27
Bluegum	28.21	41.35	53.85	50.42	17.95	8.23	100.00	100.00
Tea	54.92	78.14	12.95	13.35	4.79	1.74	72.67	93.23
Pine	45.00	65.24	30.00	23.18	22.50	8.65	97.50	97.07

randomly distributed into *n* traps over a fixed number of days. The sites occupied by the 2 species in the simulated data are compared to compute the number of traps occupied by both species. Each simulation was repeated 100 times. The 3 common species were examined as pairs to check for co-occurrence or avoidance as indicators of competition.

RESULTS

Species composition and population characteristics in various habitats

Of the nine species trapped, eight were in montane evergreen forests, three were in the grassland, three were in wattle, eucalyptus and pine plantations and four were in tea plantations (see Table 2 & Appendix for information on the species). *Rattus rattus* was the dominant species in the montane forest, comprising 60.9% of total density, while *M. meltada* was the dominant species in the grassland. In the natural habitat (forest and grassland), the two species were mutually exclusive. While *R. rattus* was trapped in the forest patches, *M. meltada* was the only rodent trapped in the grassland. An analysis of wattle stands of different ages shows that *Millardia* dominates young stands (grass-like habitat), while *Rattus* dominates the older stands (forest-like habitat). *Suncus montanus*, a shrew, was the only species captured in both habitats. The other common species in the montane forest included *Mus famulus* and *Suncus dayi*.

The total density and biomass of small mammals was highest in the old and middle-aged wattle stands (Fig. 1). While *R. rattus* accounted for the bulk of the density and biomass in the old wattle stands, *M. meltada* was the dominant species in the middle-aged wattle stands (Table 3). Montane forests had intermediate densities and biomass, while grasslands had relatively low density and biomass. The density and biomass of the dominant species were substantially higher in some plantations than in the natural habitats. The density of *M. meltada* was significantly higher in middle-aged wattle stands than grasslands, while the density of *R. rattus* was significantly higher in old wattle plantations than in montane forest patches. *Rattus rattus* attained a maximum density of 34 animals/ha and biomass of 3.3 kg/ha in November 1995 in an old wattle plantation. *Millardia meltada* peaked at 31 animals/ha (1.6 kg/ha) in June 1995 in a middle-aged wattle plantation. The mean weight of adult male *R. rattus* varied between habitats (Kruskal–Wallis, $P < 0.05$) while the weight of adult females was not different (Fig. 2).

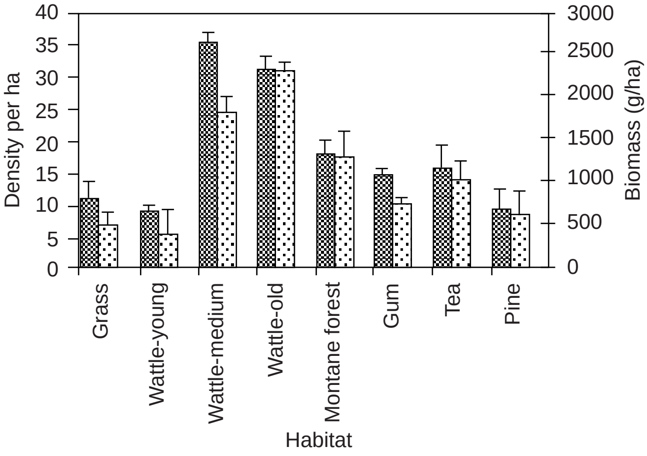

Fig. 1. The total density (▩) and biomass (⬚) of all small mammals in natural and cultivated habitats in the Upper Nilgiris. The abundance is the highest in the medium wattle plantations, while biomass is high in old wattle plantations.

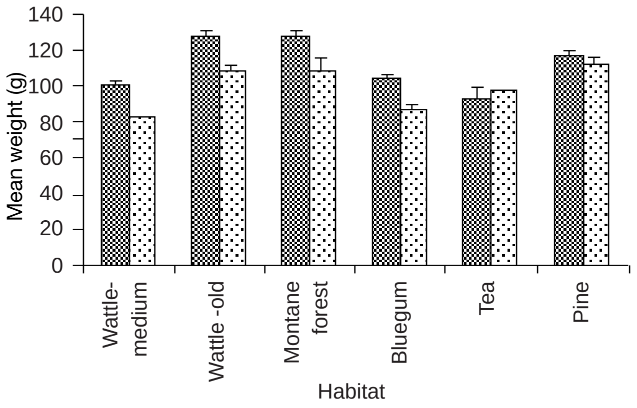

Fig. 2. The mean weight of adult males (▩) and females (⬚) of *Rattus rattus* in various habitats. Adult males are significantly heavier in montane forest and old wattle plantations. There is less variation in the weights of adult females.

In the two *R. rattus* removal experiments carried out in patches of size 0.5 and 0.15 ha, *M. meltada* was not found to enter the forest patches, though they were trapped at the periphery of the patch in the grassland during the period that *R. rattus* was absent from the patch. The first individuals of *R. rattus* were trapped on the 0.15-ha plot 2 weeks after the removal and on the 0.5-ha plot 3 weeks after the removal. In the introduction experiments, *M. meltada* individuals that were introduced into the forest patches were recaptured at the forest–grassland edge and none was recaptured alive within the forest patch.

Interactions in wattle plantations

The interactions between *M. meltada* and *R. rattus* were studied in greater detail at the 0.90-ha plot in an old wattle plantation (canopy height > 8 m). The plot was sampled over five trapping sessions (*c.* 1200 trap-nights). Canonical discriminant analysis was performed on three commonly occurring species, *R. rattus*, *M. meltada* and *Suncus montanus*, based on five habitat variables. *Rattus rattus* was found to discriminate habitat during two of five sampling sessions analysed and when all sessions were pooled (Wilk's $\lambda = 0.8$, $P < 0.05$). *Rattus rattus* was present at sites with higher midstorey cover and lower ground cover (ANOVA, $P < 0.05$). *Millardia meltada* was found to discriminate habitat based on canopy cover and midstorey density (Wilk's $\lambda = 0.86$, $P < 0.05$); it was found in areas of higher canopy cover (ANOVA $P < 0.05$). *Suncus montanus* used the habitat in the same proportion that it was available. *Millardia meltada* used areas of higher ground cover than *R. rattus* (ANOVA $P < 0.05$). The expected number of traps with both species during a sampling session was calculated using Equation 1 and the simulations. The observed number of traps with both species did not differ from the expected number of traps with two species, thus showing no evidence of overlap or avoidance (χ^2, $P < 0.01$). As the density of *S. montanus*

Table 4. Correlations between habitat variables. Pearson's rank order correlation was calculated for all pairs of variables using the normalized score for each variable for each trap site. Correlations were also calculated based on the average site score, which was calculated for each site as the average of variable score of that site and the four sites perpendicular to the site (*significant at $P < 0.001$, # at $P < 0.01$, ** at $P < 0.05$)

	Canopy cover	Midstorey	Ground cover	Tree density	Canopy height
Normalized scores at each trap site					
Canopy	1.00				
Midstorey	0.35*	1.00			
Ground	−0.21*	−0.19*	1.00		
Density	−0.04	$0.09^{\#}$	0.08**	1.00	
Height	$0.12^{\#}$	−0.03	0.05	−0.06	1.00
Averaged site scores					
Canopy	1.00				
Midstorey	0.47*	1.00			
Ground	−0.30*	−0.29*	1.00		
Density	−0.13*	0.04	0.03	1.00	
Height	0.14*	−0.05	$0.12^{\#}$	−0.18*	1.00

was the lowest, the expected interaction with the other species was also very low.

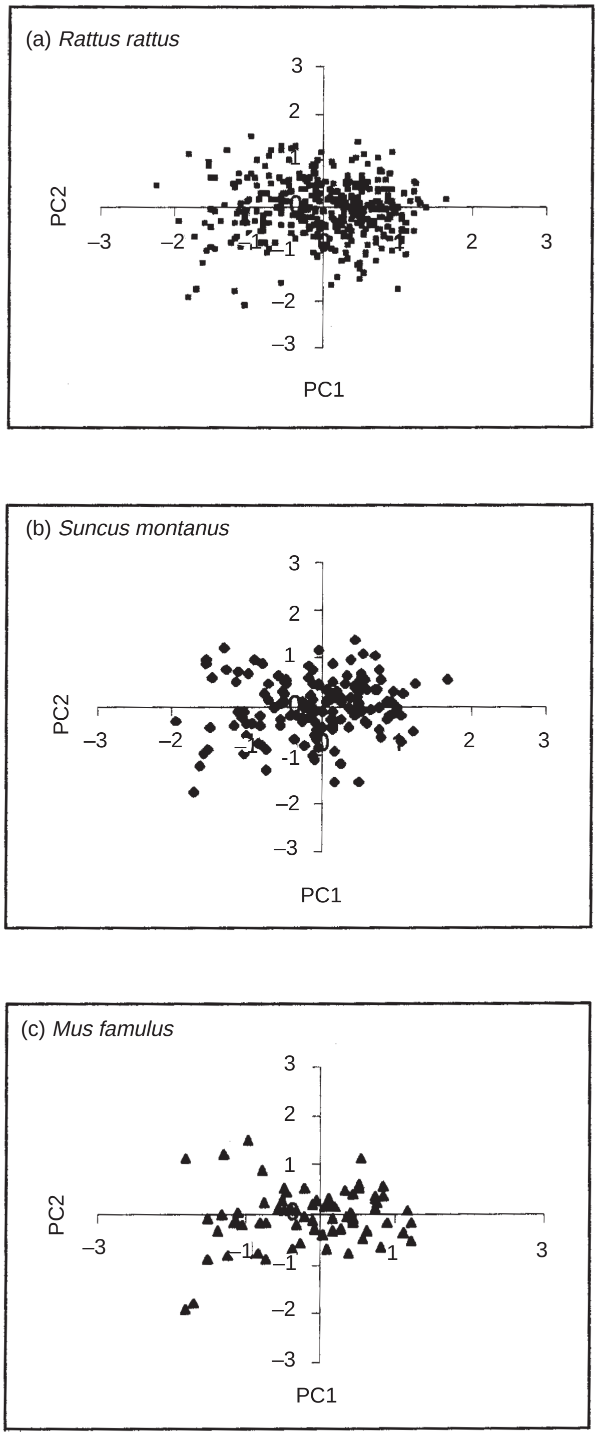

Fig. 3. Habitat use in montane forest patches by three common species: (a) *Rattus rattus*; (b) *Suncus montanus*; (c) *Mus famulus*. PC1, canopy and midstorey cover; PC2, tree density. Though univariate tests indicated that *M. famulus* uses areas of higher tree density, multivariate tests did not distinguish between the species, indicating a wide variation in the use of the habitat by the three most common species.

Habitat structure in montane evergreen forest

Many of the habitat variables were correlated with each other (Table 4). When data from all the montane forest plots were pooled, five variables (canopy cover, midstorey density, ground cover, tree density and canopy height) were analysed at 641 trap sites, PC1 described 34.3% of the variance, while PC2 described 25.1% and PC3 accounted for 17.5%. PC1 is a measure of vertical stratification as it is heavily loaded on canopy cover, midstorey cover and tree density. Here, lower tree density in conjunction with high canopy and midstorey cover implies larger trees, which are likely to have more vertical strata. PC2 essentially describes tree density. Sites with a high density of young trees will also have low ground cover and lower canopy height. PC3 describes variance in ground cover.

Microhabitat selection in montane evergreen forest patches

When the site score data were considered for individual plots, all three species showed habitat discrimination in few plots in few seasons. There was no consistency in the variables that showed significant univariate discrimination between presence–absence sites for each species. Multivariate analysis did not discriminate between presence and absence sites for any of the species, when each season was considered separately. There was also no discrimination between the species (Fig. 3).

However, when data from all the seasons and 641 trap sites were pooled, a clearer pattern emerged (Table 5). *Rattus rattus* was found at sites with higher tree density and lower canopy cover (Wilk's $\lambda = 0.98$, $P < 0.05$). *Suncus montanus* showed a preference for habitats with higher tree density, higher ground cover and lower canopy height with regard to average site scores (Wilk's $\lambda = 0.96$, $P < 0.05$). *Mus famulus* showed a discrimination towards higher tree density, higher ground cover and lower canopy height with regard to individual site scores (Wilk's $\lambda = 0.97$, $P < 0.01$). *Rattus rattus* did not show discrimination based on age or sex.

Spatial interactions in montane evergreen forest patches

Trap overlap is defined here as the number of trap sites (per sampling session) that were occupied by both species. From expected and observed values of trap overlap, there was no evidence of avoidance or overlap in sites between any of the three species that were examined in any of the plots. The analysis of each trapping session individually gave expected values of trap overlap between *R. rattus* and *S. montanus* in the range of 0 to 5 (mean = 0.63) and observed values of 0 to 8 (mean = 0.62). Goodness-of-fit tests showed that

Table 5. The site scores of the habitat variables where the species were present and absent. Canopy, midstorey and ground cover have been converted into percentages. Tree density is a qualitative measure, ranging from 0 to 3 (high density)

		Canopy cover (%)	Midstorey cover (%)	Ground cover (%)	Tree density (5 m radius)	Canopy height (m)
Habitat available		78.5	62.5	24.98	2.4	11.9
Rattus rattus	Absent	85.3	63.2	19.9	2.1	11.9
	Present	76.8	62.4	26.1	2.4	11.9
Suncus montanus	Absent	79.6	61.2	24.8	2.8	12.2
	Present	76.0	65.4	25.3	2.5	11.4
Mus famulus	Absent	80.6	63.4	23.8	2.3	12.2
	Present	64.9	57.3	31.8	2.9	10.2

there was no difference between observed and expected values in any of the sessions in any of the plots (χ^2, $P < 0.01$). The observed values of overlap did not differ from distributions of expected values of trap overlap derived from the simulations.

DISCUSSION

Competition and habitat selection in montane evergreen forests

Resource partitioning has been demonstrated in some small mammal communities, such as desert rodents (reviewed by Kotler & Brown, 1988). It has been suggested that interspecific competition may serve to increase habitat selection (Dueser & Brown, 1980; Rosenzweig, 1981), but it is possible that despite the ubiquity of competitive relationships, the effects of competition may be fairly weak (Dueser & Porter, 1986). Structural habitat complexity has been found to influence rodent communities and densities (Dueser & Shugart, 1978; Dueser & Brown, 1980) and numerous studies have dealt with the role of habitat complexity and heterogeneity in structuring small mammal communities (Dueser & Shugart, 1978; August, 1983; Canova & Fasola, 1991; Bowles & Copsey, 1992; Adler, 1995). Scott & Dueser (1992) found evidence that habitat selection may be more important than interspecific competition. Murua *et al.* (1987) did not find evidence of competition using reciprocal removal experiments in a Chilean temperate rainforest.

In our study, the absence of significant discrimination in each of the montane forest plots during each individual session suggests that there is a lot of variation in the use of the habitat by these species. Multivariate tests also failed to discriminate in microhabitat use between the species. However, univariate analysis of the entire sample showed that all three species discriminate microhabitat based on tree density. Hence, it would seem that, though habitat selection occurs at the microhabitat scale, the patterns are weak. While habitat segregation between species could have been caused by interspecific competition, there are no compelling reasons to believe that this is so. The three common species in the montane forest, *R. rattus*, *S. montanus* and *Mus famulus*, do not show spatial overlap or avoidance. *Rattus rattus* is substantially larger than the other two, and as *S. montanus* is an insectivore, it is expected to have different food habits from the others. Chance observations indicate that *S. montanus*, though much smaller, is an aggressive animal, and has been seen to attack *R. rattus* (though in weak condition after a night in the trap). Theoretical distributions of trap overlap indicate that the encounter rate between the species at the densities at which they occur in these forests may be too low for the species to evolve a response to each other.

It has been suggested that competition would be a strong force in low-dimensional communities, i.e. those with few species. Many studies of tropical forests have shown that species richness is quite low, rarely over seven species, and even amongst these communities, a few species are extremely common (Walker & Rabinowitz, 1992; Chandrasekhar-Rao & Sunquist, 1996; Wu, Luo & Fox, 1996; Meena, 1997). At lower elevation (1000 m a.s.l.) forests of the Nilgiris, Meena (1997) found that the distributions of *R. rattus* and *Cremnomys blanfordi* were strongly negatively correlated. *Rattus rattus* was more dominant in semi-evergreen forests, while *C. blanfordi* was more dominant in dry deciduous forests. In another study in a different range in the Western Ghats, *R. rattus* was found to be dominant in moist deciduous forest and deciduous forest (*Tectona grandis* plantation) (Chandrasekhar-Rao & Sunquist, 1996). These results and those from this study indicate that there are strong patterns in the use of different habitats by different species. There seems to be widespread evidence for habitat selection at the scale of the macro-habitat, which could be the result of the influence of food availability. However, the results from this study indicate that there are weak or no patterns at the micro-habitat scale.

Interactions between *R. rattus* and *M. meltada* in montane habitats

Competition can be said to occur if two (or more) species show an inverse numerical or spatial relationship (Grant, 1972). Schroder & Rosenzweig (1975) suggested that two coexisting species of *Dipodomys* avoid competition by habitat selection. However, they felt that competition might still be important in the system, and in the absence of its ‘threat’, the habitat specialization would disappear. The first pattern that is discernible in the small mammal communities of the Upper Nilgiris is the distribution of *M. meltada* and *R. rattus*. Their mutually exclusive occurrence in natural habitat implies competitive forces, past or present. There is nothing in the natural history or distribution of these species that suggests, *a priori*, that such a pattern may be expected. In fact, in Rajasthan in arid north-west India, neither *M. meltada* nor *R. rattus* are found above 1000 m (Prakash, Partap Singh & Saravanan, 1996). The absence of *M. meltada* is especially notable in the hilltop grasslands, despite its great abundance in the foothills. *Millardia meltada* is generally found in heavy scrub and agricultural ecosystems (Prater, 1988). It was also found in various plantations surrounded by montane forests and grasslands in the Nilgiris in this study. It may to a certain extent be considered a commensal species, since it is strongly associated with habitats which are anthropogenic. In the Nilgiris, it has successfully colonized the grassland, which no other rodent species has been able to do. *Rattus rattus*, on the other hand, has been found in forests of various types in southern India including scrub and thorn, dry and moist deciduous, semi-evergreen and evergreen. It seems to be most dominant in evergreen forests (Chandrasekhar-Rao & Sunquist, 1996; Meena, 1997). Though the distribution of the two species implies competition, removal and introduction experiments offered no evidence that it is taking place at present.

Interestingly, both *R. rattus* and *M. meltada* coexist in the plantations. Since the plantations were introduced in Nilgiris in the last 150 years, one may expect that competition, if present, can be discerned. However, analysis of the interactions between the species and discriminant analysis of habitat use indicate that the species do not compete. Since *R. rattus* is considerably larger than *M. meltada*, it is not unreasonable to suppose that their food habits are sufficiently different to preclude competition. In North America, Scott & Dueser (1992) did not find competition between the rodents *Peromsycus leucopus* and *Mus musculus* in shrub and grassland habitats, and argued against the reduction of competition by competitive coevolution since the species had coexisted for only 300 years. They suggest that habitat selection and intraspecific interactions may be more important.

Both *M. meltada* and *R. rattus* populations achieve higher densities in habitats other than their natural habitats. *M. meltada* increases by a factor of 2.5 in middle-aged wattle plantations as compared to grasslands, while *R. rattus* increases 1.5 times in old wattle plantations. This suggests that food is limiting for these species in the natural habitats. If food is limiting in the wild, and the food habits of the species are sufficiently different, intraspecific competition would be a much stronger force in regulating the population. The increase in body weight of males in smaller patches and in old wattle and montane forests as compared to other habitats also indicates that intraspecific competition might be an important force.

To summarize, there is no evidence of interspecific competition at the present time in any of the montane habitats studied. There are distinct differences in the species composition and densities of individual species in different habitats, but within the habitats, patterns of microhabitat selection and segregation are weak. These results imply that these communities of small mammals are not driven strongly by either competition or habitat selection. If interspecific competition and microhabitat selection do not structure these communities, they may be driven by other forces such as predation. Intraspecific competition may also be a strong force and, as Connell (1983) points out, many other studies of small mammals have found that this is at least as important a force in small mammal populations. There is, in fact, some evidence for intraspecific competition in the *R. rattus* populations in these montane forest patches (Shanker & Sukumar, 1998). Predation may also play a role in the synchrony of small mammal populations between montane forest patches, and coupled with dispersal may strongly affect population processes in the ecosystem (Shanker & Sukumar, 1999); potential predators include many small carnivores, raptors and owls (Shanker & Sukumar, 1999). The results of this study seem to support a growing body of evidence that interspecific competition need not be an important force in all small mammal communities. They also suggest that microhabitat selection may not be a very strong factor either. In the light of these results, it would seem that intraspecific competition and predation may need to be examined more closely as key forces in structuring and regulating small mammal communities in similar habitats.

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REFERENCES

Adler, G. H. (1995). Habitat relations within lowland grassland communities in Taiwan. *J. Zool. (Lond.)* **237**: 563–576.

August, P. V. (1983). The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* **64**: 1495–1507.

Boitani, L., Loy, A. & Molinari, P. (1985). Temporal and spatial displacement of two sympatric rodents (*Apodemus sylvaticus* and *Mus musculus*) in a Mediterranean coastal habitat. *Oikos* **45**: 246–252.

Bowles, J. B. & Copsey, A. D. (1992). Small mammal abundance as a function of herbaceous cover type in South Central Iowa. *Prairie Nat.* **24**: 109–119.

Canova, L. & Fasola, M. (1991). Communities of small mammals in six biotopes of Northern Italy. *Acta Theriol.* **36**: 73–86.

Chandrasekhar-Rao, A. & Sunquist, M. E. (1996). *Ecology* of small mammals in tropical forest habitats of southern India. *J. trop. Ecol.* **12**: 561–571.

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**: 661–696.

Connor, E. F. & Simberloff, D. (1979). The assembly of species: chance or competition. *Ecology* **60**: 1132–1140.

Dueser, R. D. & Brown, W. C. (1980). Ecological correlates of insular rodent diversity. *Ecology* **61**: 50–56.

Dueser, R. D. & Porter, J. H. (1986). Habitat use by insular small mammals: relative effects of competition and habitat structure. *Ecology* **67**:195–220.

Dueser, R. D. & Shugart, H. H. Jr (1978). Microhabitats in a forest floor small mammal fauna. *Ecology* **59**: 89–98.

Ellerman, J. R. (1961). Fauna of India including Pakistan, Burma and Ceylon. In *Mammalia* **3**: *Rodentia* (parts 1 & 2). Roonwal, M. L. (Ed.). New Delhi, India: Manager of Publications, Government of India.

Ellerman, J. R. & Morris-Scott, T. C. S. (1951). *Checklist of Palaearctic and Indian mammals 1758 to 1946*. London: British Museum (Natural History).

Grant, P. R. (1972). Interspecific competition among rodents. Experimental studies of competitive interaction in a two-species system. V. Summary of the evidence for rodent species, and some generalisations. *Annu. Rev. Ecol. Syst.* **3**: 79–106.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960). Community structure, population control and competition. *Am. Nat.* **94**: 421–425.

Harris, R. J. (1985). *A primer of multivariate statistics*. Orlando: Academic Press.

Hutchinson, G. E. (1958). 'Concluding remarks'. *Cold Spring Harbor Symp. Quant. Biol.* **22**: 415–427.

Klopfer, P. & MacArthur, R. H. (1960). Niche size and faunal diversity. *Am. Nat.* **94**: 293–300.

Kotler, B. P. & Brown, J. S. (1988). Environmental heterogeneity and the coexistence of desert rodents. *Annu. Rev. Ecol. Syst.* **19**: 281–307.

Krebs, C. J. (1966). Demographic changes in fluctuating populations of *Microtus californicus*. *Ecol. Monogr.* **36**: 239–273.

MacArthur, R. H. & Levins, R. (1964). Competition, habitat selection and character displacement in a patchy environment. *Proc. Natl Acad. Sci. USA* **51**: 1207–1210.

MacArthur, R. H. & MacArthur, J. W. (1961). On bird species diversity. *Ecology* **42**: 594–598.

Maurer, B. A. (1985). On the ecological and evolutionary roles of interspecific competition. *Oikos* **45**: 300–302.

Meena, V. (1997). *Small mammal communities of Mudumalai Wildlife Sanctuary, southern India*. MSc thesis, Pondicherry University, India.

Meher-Homji, V. M. (1984). Udhagamandalam (Ootacamund): a biogeographic perspective. *Indian Geogr. J.* **59**: 205–213.

Murua, R., Meserve, P. L., Gonzalez, L. A. & Jofre, C. (1987). The small mammal community of a Chilean temperate rain forest: lack of evidence of competition between dominant species. *J. Mammal.* **68**: 729–738.

Prakash, I., Partap Singh & Saravanan, A. (1996). Ecological distribution of small mammals in Aravalli ranges. *Proc. Ind. Natl Sci. Acad. Part B Biol. Sci.* **61**: 137–148.

Prater, S. H. (1988). *The book of Indian animals*. Bombay, India: Bombay Natural History Society.

Rosenzweig, M. L. (1974). On the evolution of habitat selection. *Proc. 1st Int. Cong. Ecol.*: 401–404.

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

SAS/STAT (1988).*User's guide release*. 6. 03 edn. Cary: SAS Institute Inc.

Schoener, T. W. (1983). Field experiments on interspecific competition. *Am. Nat.* **122**: 240–285.

Schoener, T. W. (1984). Counters to the claim of Walters *et al.* on the evolutionary significance of competition. *Oikos* **43**: 248–250.

Schroder, G. D. & Rosenzweig, M. L. (1975). Perturbation analysis of competition and overlap in habitat utilisation between *Dipodomys ordii* and *Dipodomys merriami*. *Oecologia (Berl.)* **19**: 9–28.

Scott, D. E. & Dueser, R. D. (1992). Habitat use by the insular populations of *Mus* and *Peromsycus*: what is the role of competition. *J. Anim. Ecol.* **61**: 329–338.

Shanker, K. (1998). *Community ecology of small mammals in montane ecosystems of the Upper Nilgiris, southern India*. PhD thesis, Indian Institute of Science, Bangalore, India.

Shanker, K. & Sukumar, R. (1998). *Community ecology and demography of small mammal communities in insular montane forests in southern India*. *Oecologia (Berl.)* **116**: 243–251.

Shanker, K. & Sukumar, R. (1999). Synchrony in small mammal populations of montane forest patches of southern India. *J. Anim. Ecol.* **68**: 50–59.

Slobodkin, L. B., Smith, F. E. & Hairston, N. G. (1967). Regulation in terrestrial ecosystems and the implied balance of nature. *Am. Nat.* **101**: 109–124.

Strong, D. R., Szyska, L. A. & Simberloff, D. (1979). Tests of community wide character displacement against null hypotheses. *Evolution* **33**: 897–913.

Turner, C. L. & Grant, W. E. (1987). Effect of *Sigmodon hispidus* on microhabitat utilisation by *Baiomys taylori* and *Reithrodontomys fulvescens*. *J. Mammal.* **68**: 80–85.

Valone, T. J. & Brown, J. H. (1995). *Effects of competition, colonization and extinction on rodent species diversity*. *Science* **267**: 880–883.

Walker, S. & Rabinowitz, A. (1992). The small-mammal community of a dry-tropical forest in central Thailand. *J. trop. Ecol.* **8**: 57–71.

Walter, G. H., Hulley, P. E. & Craig, A. J. F. K. (1984). Speciation, adaptation and interspecific competition. *Oikos* **43**: 246–248.

Wu, D. L., Luo, J. & Fox, B. J. (1996). A comparison of ground dwelling small mammal communities in primary and secondary tropical rainforests in China. *J. trop. Ecol.* **12**: 215–220.

Appendix

Rattus rattus (L.)
The most common and well known of murid rodents is the common rat, *R. rattus*, also known as the black, roof, house or ship rat. *Rattus rattus* is found worldwide, and owes much of its ubiquity to accidental human introduction. It is highly arboreal in the wild; the females are territorial, while the males seem to be free ranging. Each female occupies a nest on her own and has three to four pups. The adult is *c.* 15–20 cm long with a 20–25 cm long tail; large males weigh *c.* 150 g, while adult females weigh 100–120 g.

***Millardia meltada Gray* (Muridae)**
The soft-furred field rat, found in cultivated fields throughout India, has also adapted successfully to the grasslands of the Upper Nilgiris. The general colour is pale brownish-grey, greyish-white on the underside. It has large rounded ears and a hairy tail, has a head–body length of 13–15 cm, a tail nearly as long, and weighs 50–70 g.

***Mus* spp.**
Mus famulus Bonhote, Bonhote's field mouse, is small with a brown coat and a yellow underside, found at *c.* 1500 m and above in the Nilgiris. It is 5–8 cm long and weighs *c.* 20 g, and is probably less arboreal than the other rats and mice. *Mus platythrix* Bennett, the spiny field mouse, a species common all over India, is brownish above and white below. The fur in this species is composed of flattened spines.

***Platacanthomys lasiurus* and other rare rodents**
Platacanthomys lasiurus Blyth is light rufous brown above and a dull white below. The muzzle is pointed, the ears are thin and naked and the hind feet are broad and elongated. It is 13–20 cm long and weighs *c.* 70 g. The spiny dormouse inhabits rocky hills and forests at altitudes of 600 m and above. It lives mainly in the cavities of trunks and branches and in clefts in rocks. The long tail, covered with hair, serves as a balancing organ, as the animal is highly arboreal.

Cremnomys blanfordi Thomas, the white-tailed wood rat is very similar to the common rat in appearance, except for the tail, which is brown for three-quarters of its length, but white towards the tip. In forests, this too is highly arboreal, makes a large and untidy nest and has litters of two to three young. *Vandeleuria oleracea* Bennett, the long-tailed tree mouse, can be distinguished by the fact that the first and fifth toe on all four feet are partially opposable and have a flat nail instead of a claw. The animal is *c.* 7 cm long with a tail that is slightly longer. It has a reddish coat and white underparts.

***Suncus* spp.**
Suncus murinus (L.), the common or grey musk shrew, is found all over India in all kinds of habitats, and is also common in cities. It is *c.* 10–12 cm long with a slightly shorter tail, and weighs *c.* 20 g. In the Nilgiris, *Suncus montanus* Kelaart, a similar looking shrew, is more common. *Suncus dayi* Dobson, a much smaller shrew, weighing 6–10 g, is also found in the Nilgiris.