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Community structure and demography of small-mammal populations in insular montane forests in southern India

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Abstract Small mammals were studied in insular montane forest patches in the Upper Nilgiris in southern India from February 1994 to September 1996. Nine patches were selected at two sites, one with a single large 600-ha patch, the other with several small patches ranging in size from 0.2 to 60 ha. The population characteristics and community structure of small mammals were studied in relation to patch size and habitat structure within the patches. The two most abundant species were *Rattus rattus* (2–36 individuals/ha) and *Suncus montanus* (0–11 individuals/ha), while the abundance of seven other species recorded were very low. The population characteristics of *R. rattus* examined were density, biomass, proportions of juveniles, sub-adults and adults, mean weight of all animals, mean weight of adults, sex ratio and persistence. The proportion of adults, sub-adults, mean weight of animals, and mean weight of adult males were correlated with patch size. Persistence of sub-adult females in the large patch was especially high. The density and biomass of other small-mammal species were also studied. Two indices of diversity, species richness and proportion of *R. rattus* were compared as measures of community structure. Seven habitat characteristics were measured; of these, canopy cover, canopy height and tree density were correlated with the size of the patch. Density and biomass of species other than *R. rattus* and proportion of *R. rattus* were correlated with canopy height. Density and biomass of species other than *R. rattus* were highest in smaller patches. While the population characteristics of *R. rattus* may be affected by patch size, the density of rare species may be influenced by factors related to lower canopy height. Migration between patches may be an important factor in maintaining populations in these patches.

Key words *Rattus rattus* · Small mammals · Community structure · Insular populations · Patch size

Introduction

The island biogeography framework (MacArthur and Wilson 1967) has been extended to insular groups of animals (Brown 1971; Lomolino et al. 1989) and plants (Kelly et al. 1989; Kohn and Walsh 1994; Laurance 1991; Leigh et al. 1993) to study theoretical aspects of diversity, community structure and population dynamics. It is also being increasingly used in conservation biology in fields such as population viability analysis (Shaffer and Samson 1985) and in refuge design (for review, see Shafer 1990). Islands have hence served as 'natural laboratories' for studying theories and testing hypotheses in ecology (Diamond 1975). It has long been known that island populations of rodents differ from mainland populations in terms of population dynamics, reproductive behaviour and other life history characteristics (Gliwicz 1980). These characteristics have been called the island effect, the island rule and, most recently, the island syndrome (Adler and Levins 1994).

Some of the major ecological characteristics of island populations of rodents (reviewed by Gliwicz 1980 and Adler and Levins 1994) include higher densities and high stability of numbers (Gliwicz 1980), reduced reproductive output (Stamps and Buechner 1985) and greater body mass (Foster 1964; Lomolino 1985; Angerbjörn 1985). Dispersal is much lower in insular populations than in open populations (Gliwicz 1980). Gliwicz (1980) also reviewed other characteristics such as the social interactions, processes responsible for changes in numbers (reproduction, mortality) and population regulation, in which insular populations differ from mainland or open populations. Adler and Levins (1994) propose that various life history traits will covary with density depending on the degree of isolation, as increased density may be the most significant variable in these populations. However, the distinction is not merely between mainland and island

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populations, because some island effects disappear as the islands become large enough to resemble mainland areas. Hence, population traits may vary not merely between island and mainland populations, but among island populations as well (Adler 1996). Insular rodent diversity is known to vary with a number of ecological correlates including vegetation parameters (Dueser and Brown 1980). There has been some debate about the role of habitat complexity and heterogeneity in structuring small-mammal communities (Adler 1995; August 1983; Bowles and Copsey 1992; Canova and Fasola 1991; Dueser and Shugart 1978), which may be particularly important in the context of fragmentation (Laurance 1994).

We have studied insular populations of small mammals in southern Indian montane forest patches (size range 1–600 ha) separated by grassland. The population characteristics of the most abundant species, the common rat (*Rattus rattus* Hinton) and other small mammals were compared between patches of various sizes to examine if they exhibited the island syndrome. Another aspect that we considered was the species diversity of small mammals in the forest patches. Small islands are expected to have lower species diversity than larger islands due to higher rates of extinction (MacArthur and Wilson 1967). This has been elaborated into the SLOSS (single large or several small) debate with respect to conservation of rare species and refuge design (Wilcox and Murphy 1985; and Wright and Hubbell 1983). We examined differences in diversity and other population traits between these two sites, one with a single large patch, the other with several small patches.

Populations must maintain critical population sizes to avoid extinction in forest fragments (Shaffer 1981; Shaffer and Samson 1985), unless other factors such as the rescue effect (Brown and Kodric-Brown 1977) and migration between fragments (Burkey 1989) play an important role. We discuss the implications of higher island densities for maintaining viable populations of these species in these islands and the possible role of migration and the rescue effect. Finally, we look at the role of habitat in the population characteristics and community structure of the small mammals.

Materials and 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 and Western Ghats, in southern India. The higher altitudes (1800–2500 msl) of the Nilgiris and other ranges in the Western Ghats have a montane ecosystem, composed of patches of stunted evergreen forest (locally known as 'shola') surrounded by grasslands. In the Nilgiris, most grasslands and much of the forest have been replaced by exotic wattle (*Acacia* spp.), pine (*Pinus roxburghii* Sarg.), tea [*Camellia sinensis* (L.) Kuntze] and bluegum (*Eucalyptus globulus* Labil). The shola patches, usually 1–10 ha in size 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 dbh) per hectare, and are dominated by the families Lauraceae, Rubiaceae and Symplocaceae (H.S. Suresh and R. Sukumar, unpublished data). There is a sharply defined ecotone between the sholas and the grasslands that is maintained by frost and fire (Meher-Homji 1984).

The natural vegetation has remained relatively undisturbed in the Upper Bhavani region, at the southwest corner of the Nilgiris, a part of the Mukurthi National Park (74 km^2) in Tamilnadu state. Thaishola (601 ha), 12 km from Upper Bhavani, is the largest shola patch in the Nilgiris plateau. It is surrounded by tea estates, but the vegetation within the shola has thus far remained intact. Both these areas, on the western slopes of the Nilgiris, receive 1500–2000 mm of annual rainfall, mostly between June and November.

Five patches, ranging in size from 2 to 60 ha, were selected in Upper Bhavani and a single large patch in Thaishola . Eleven plots were established and sampled in these patches; the sampling effort is detailed in Table 1. In addition, three other 0.49-ha plots were sampled in Upper Bhavani. Species removal experiments at two of these plots provided information on immigration of small mammals into patches; the experiments and results are described in detail elsewhere (K. Shanker, in preparation). Data from these three plots (0.1–0.5 ha) were also used for estimating species richness. Three 0.49-ha plots were established in open grasslands and one 0.48-ha plot (120 m × 40 m) was established between two patches.

Sampling procedure

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). 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

Table 1 Summary of sampling effort and capture history of small mammals in 11 plots in six montane forest patches of the Nilgiris. The four small patches were located in Upper Bhavani, the medium patch (Maduppumalai shola) also in Upper Bhavani, while the large patch is in Thaishola

	Size (ha)	Size of plot (ha)	Trap nights	Number of sessions	Total captures	Total individuals	*Rattus rattus* captures	*Rattus rattus* individuals
Small patch 1	~2	0.49	1176	6	106	69	61	31
Small patch 2	2.2	0.49	1715	10	199	110	135	67
Small patch 3	6.8	0.49	1666	9	189	109	117	55
Small patch 4	~11	0.49	1176	6	122	63	85	31
Medium patch (1)	60	0.49	1470	8	132	79	101	52
Medium patch (2)		0.49	1715	9	162	84	133	57
Large patch (1)	600	0.49	1715	9	193	102	170	78
Large patch (2)		0.49	1568	8	181	81	155	57
Large patch (3)		0.49	1470	8	185	101	139	57
Large patch (4)		1.00	2300	7	250	125	194	73
Large patch (5)		1.00	1700	5	142	66	118	45

Table 2 Eleven plots were sampled in six montane forest patches in the Upper Nilgiris. Seven habitat variables were measured at each trap site. Canopy, midstorey and ground cover, and woody stem and tree density were subjective measures (described in Data analysis)

	Canopy cover	Midstorey cover	Ground cover	Woody stem density	Tree density	Distance to nearest tree (m)	Canopy height (m)
Small patch 1	2.24	2.86	1.08	1.13	2.96	1.33	9.36
Small patch 2	2.80	3.07	0.29	0.96	2.82	1.63	10.04
Small patch 3	1.81	2.57	1.86	1.15	3.20	2.09	8.32
Small patch 4	2.38	2.67	2.43	1.22	3.20	1.38	11.96
Medium patch (1)	3.06	1.79	1.76	1.06	2.22	1.17	14.73
Medium patch (2)	2.36	2.70	0.41	1.38	3.25	1.39	8.52
Large patch (1)	3.67	3.24	0.77	0.43	1.92	0.63	13.00
Large patch (2)	2.98	2.41	1.61	1.10	2.20	1.23	12.70
Large patch (3)	3.71	2.02	1.22	0.92	2.06	0.82	11.30
Large patch (4)	3.64	2.71	0.64	1.00	2.11	1.37	12.32
Large patch (5)	3.87	2.26	0.35	1.01	1.65	1.32	13.27

other appropriate runway. The traps were baited with grated coconut and rice. The plots were run for five consecutive nights during January–October 1994 and for three consecutive nights after that until September 1996. All trapped animals were identified, ear-punched, sexed, weighed, measured and released. The traps were checked once daily between 0800 and 1200 hours. Trapping was carried out seasonally over a period of 33 months, from February 1994 to September 1996, for a total of 24 024 trap nights.

Habitat sampling

Seven habitat variables that were considered important in affecting rodent distributions were sampled in every plot at each trap site (modified from Dueser and Shugart 1978). (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) Woody stem density: a classification of the density of woody stems (> 1 cm dbh) within a radius of 1 m around the trap site on a scale of 0–3, i.e. 1 low (1–5 stems), 2 medium (6–10 stems), 3 high (> 10 stems). (5) Tree density: a classification of the density of trees (> 10 cm dbh) within a radius of 5 m around the trap site on a scale of 0–3, i.e. 1 low (1–5 stems), 2 medium (6–10 stems), 3 high (> 10 stems). (6) Distance to the nearest tree: in metres. (7) Canopy height.

Data analysis

We analysed the following variables

Population characteristics of R. rattus

(1) Density (minimum number alive/ha). (2) Coefficient of variation of density. (3) Proportion of juveniles, sub-adults, adults and adult females. (4) Mean weight of animals in a trapping session. (5) Biomass per hectare. (6) Mean weight of adults (males, females). (7) Sex ratio (all individuals, juveniles, sub-adults, adults). (8) Persistence of animals in a patch. Two measures of persistence were calculated: (a) the proportion of animals in each age and sex class that was captured at any subsequent trapping session; (b) the average persistence time (in days) of animals in each age and sex class (after assigning a value of 0 days persistence to those animals that were captured in only a single sampling session).

Community structure

(1) Total small-mammal density. (2) Total small-mammal biomass per hectare. (3) Rare-species density (density of species other than *R. rattus*). (4) Rare-species biomass per hectare (biomass of species other than *R. rattus*). (5) Shannon-Wiener index of diversity. (6) Simpson's index of dominance. (7) Species richness. (8) Proportion of the most dominant species, *R. rattus*.

The habitat variables were converted to *z* scores (with a mean of 0 and standard deviation of 1) and averaged for each plot (Table 2). Kendall's ranked correlations were used to test for relationship between patch size, habitat variables and the test variables ($n = 11$ for all comparisons). When more than one independent variable was significantly correlated with a population variable, Kendall's partial correlation was used.

The patches were divided into three different groups based on size. Four patches in Upper Bhavani, ranging in size from 2 to 11 ha were classified as small patches (the total number of data points for the population and community variables, $n = 30$). The 60-ha patch, with two sampling plots, was classified as a medium patch ($n = 17$). Thaishola, the 600-ha patch, with five sampling plots was classified as a large patch ($n = 36$). The Kruskal-Wallis one-way analysis of variance test was used to check for differences in population and community characteristics between the groups; this was followed by multiple comparisons to ascertain which of the groups was different from the other(s) (Siegel and Castellan 1988). The binomial test and a normal approximation were used to test for sex ratio deviations from the expected 1:1. The Wilcoxon matched-pairs signed-rank test was used to compare wet- and dry-season density and biomass estimates (Upper Bhavani $n = 6$, Thaishola $n = 5$) and differences in persistence between age and sex classes.

The Morisita-Horn index of similarity was computed for all pairs of plots. For this analysis, data from nine 0.49-ha plots were used. Six trapping sessions, when all the plots had been sampled, were pooled to compute the index. The Mantel test (Hemelrijk 1990) was used to check for correlation between the similarity index and the geographical distance between the patches. The similarity index was also compared with size difference between the patches (size of smaller patch/size of larger patch; size rank of smaller/larger patch).

Results

Relative abundances, density and biomass

We trapped 1173 individuals of nine species of small mammals in the forest patches, including seven rodents (*R. rattus, Cremnomys blanfordi* Thomas*, Vandeleuria oleracea* Bennett, *Platacanthomys lasiurus* Blyth, *Mus famulus* Bonhote, *M. platythrix* Bennett and *Millardia meltada* Gray) and two shrews (*Suncus montanus* Kelaart and *S. dayi* Dobson). *R. rattus* was the most common species, forming 75.7% of all captures and

Table 3 Density and biomass (per hectare) of *R. rattus* and other species and species richness in the different forest patches

	R. rattus density (per hectare)			Standard deviation	*R. rattus* biomass (g/ha)	Mean weight (g)	Rare species density	Rare species biomass (g)	Species richness
	Minimum	Maximum	Mean						
Small patch 1	4	14	4.8	1.7	493.3	98.4	5.3	118.2	3.3
Small patch 2	2	26	7.5	3.7	778.5	101.0	4.5	104.3	2.3
Small patch 3	6	22	6.1	2.7	623.3	103.3	5.3	143.2	3.8
Small patch 4	4	26	5.5	3.9	534.0	101.3	2.9	74.9	2.7
Medium patch (1)	6	24	7.3	2.8	733.9	98.3	2.0	38.8	2.3
Medium patch (2)	4	18	6.1	2.4	616.4	103.3	4.6	111.9	3.2
Large patch (1)	10	28	8.6	3.1	808.0	92.9	2.2	54.0	2.0
Large patch (2)	10	36	8.6	3.9	712.0	87.0	2.6	72.4	2.6
Large patch (3)	4	30	7.8	4.0	681.3	87.4	4.9	126.0	3.6
Large patch (4)	6	20	6.7	2.2	628.0	94.2	3.4	80.2	3.0
Large patch (5)	3	16	5.0	2.7	434.8	86.3	2.3	50.3	2.6

60.9% of all individuals, followed by *S. montanus* (25.3% of all individuals) and *M. famulus* (10.2%). The other species represented less than 5% of the captures, with *C. blanfordi* and *V. oleracea* being represented by single captures (see Table 3 for details of captures). *M. meltada* was trapped exclusively in grasslands, both in open grasslands and along the forest edges. Other rodent species were never captured in the grassland, and marked individuals of both rodents and shrews were rarely found to move between patches, implying that these small-mammal populations were largely insular, despite the small distances separating the patches. Eight species were recorded in the large patch (8753 trap nights), six in the medium patch (3185 trap nights), and four in the seven small patches (1000–2000 trap nights in each patch). In addition to the trapped species, two species of squirrel (*Funambulus* sp. and *Ratufa indica*) were sighted in the large and medium patches. The latter is a much larger species and would not have been caught in the Sherman traps used here (Fig. 1).

The density of *R. rattus* varied from 2 to 36 individuals/ha, while that of *S. montanus* varied from 0 to 11 individuals/ha. The numbers of other species were consistently very low, of the order of 1–2 individuals/ha. Total small-mammal density ranged from 6 to 42 individuals/ha. The total small-mammal biomass ranged from 370 to 2852 g/ha, with an average of 1453 g/ha. *R. rattus* biomass ranged from 274 to 2716 g/ha, with an average of 1280 g/ha (see Table 3 for details). *R. rattus* formed 60.9% of the total density and 87.9% of the total biomass of trapped animals. This was also the only species that was trapped in all patches in all trapping sessions. *S. montanus* and *M. famulus* were trapped in all plots, and in 90.6% and 54.1% of the trapping sessions, respectively. *S. dayi* was trapped in five of the six patches in 25.8% of the trapping sessions.

Following removal of *R. rattus* from two small plots, the first individuals of this species were trapped 2–3 weeks after the removal, and several individuals, including a marked individual from an adjoining patch, were trapped at one of these plots 3 months after removal.

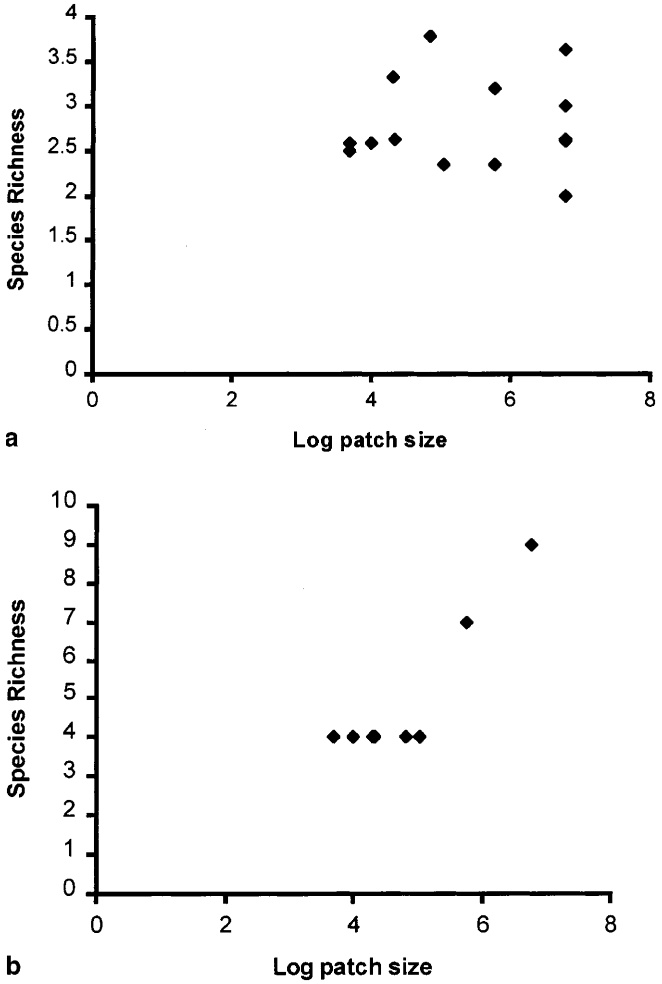

Fig. 1 a Mean small-mammal species richness at each plot against $\log_{10}$ patch size (m^2). There is no relationship between patch size and species richness. **b** All plots in the range of 0.5–11 ha have four small mammal species, the 60-ha patch has seven species and the 600-ha patch has nine species (species include eight trapped species and one recorded by visual sighting)

Seasonality

In Upper Bhavani, there was no seasonality in wet- and dry-season density and biomass. However, in Thaishola, the density and biomass of *R. rattus* were higher during the wet season than in the dry season (Wilcoxon $P < 0.05$). The density and biomass of other species did not show any seasonality in Thaishola. The density of *R. rattus* was higher in 1994 than in 1995 (Fig. 2a), and there were indications that densities were relatively high in 1996 although fewer plots were sampled.

R. rattus showed distinct seasonality in breeding (Fig. 2b). The proportion of adults was highest during the dry season (January–April), while the proportion of juveniles peaked between April and June. The proportion of sub-adults was highest between June and October. This pattern, however, was clearer in Thaishola than in Upper Bhavani. There were no discernible annual patterns in breeding in the other species in any of the study areas.

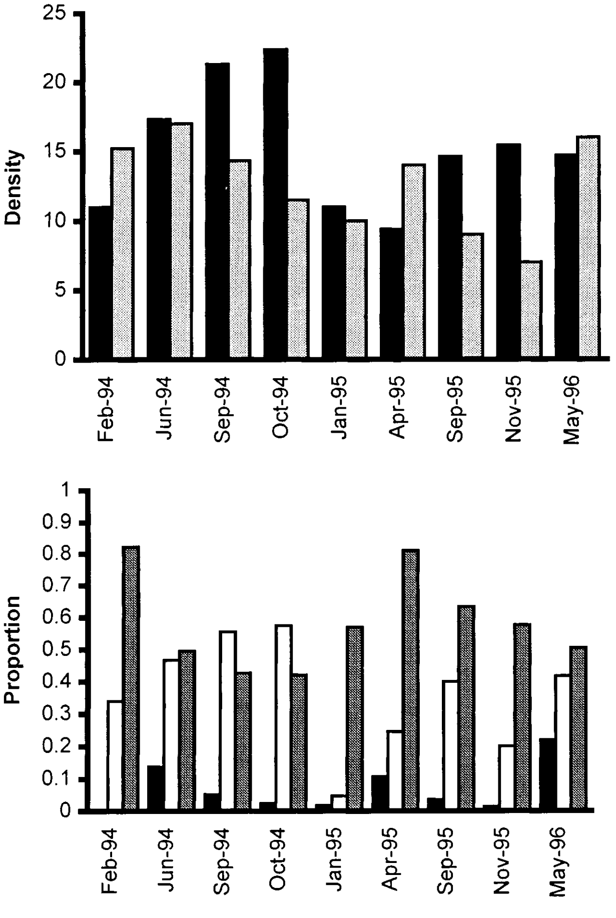

Fig. 2 a Mean abundances of *Rattus rattus* at Thaishola (*black*) and Upper Bhavani (*grey*) from February 1994 to May 1996. **b** Proportions of juveniles (*black*), sub-adults (*white*) and adults (*grey*) in all the plots

Similarity

The Morisita-Horn similarity index was calculated for all pairs of plots. All values of the similarity index were high, ranging from 0.825 to 0.999, with 86% lying between 0.9 and 1. The similarity between plots within Thaishola, within Upper Bhavani, and between Thaishola and Upper Bhavani were not significantly different from each other. There was no difference between small patches and large patches with regard to within-group and between-group similarities. Similarity was also not related to the size ratio between the patches.

Population characteristics, habitat variables and patch size

Canopy cover (Kendall's ranked correlation, $T = 0.88$, $n = 11$, $P < 0.001$) and canopy height ($T = 0.55$, $n = 11, P < 0.01$) were positively correlated with patch size, while tree density ($T = -0.76, n = 11, P < 0.001$) was negatively correlated with patch size. Canopy cover was negatively correlated with tree density ($T = -0.82$, $n = 11$, $P < 0.05$), while woody stem density and tree density were positively correlated ($T = 0.64$, $n = 11$, $P < 0.05$).

Population characteristics of *R. rattus* and community structure variables were correlated with patch size and habitat variables (Kendall's correlation coefficients are detailed in Table 4). Partial correlations were used to detect the significant variable in the correlations when more than one variable was correlated with the variable

Table 4 Kendall's correlation coefficients (Tau) for comparisons between population variables and patch size and three habitat variables ($n = 11$ for all comparisons) that showed significant correlations with the population variables. All reported correlations were significant at $P < 0.05$. Asterisks indicate $^*P < 0.01$, $^{**}P < 0.001$

	Population variable	Patch size	Canopy cover	Tree density	Canopy height
1	Rare-species abundance	−0.473			−0.709**
2	Rare-species biomass				−0.673*
3	Proportion of *R. rattus*				0.606*
4	Proportion of adult *Rattus*	−0.514			
5	Proportion of sub-adult *Rattus*	0.790**	0.585	−0.472	0.585
6	Proportion of female subadults	0.775**	0.574	−0.537	
7	Proportion of females (all)	0.524			
8	Proportion of females (sub-adults)	0.555	0.491		
9	Mean weight of *R. rattus*	−0.455	−0.596		
10	Mean weight of adult males	−0.637*	−0.491	0.455	

Table 5 Persistence times (days) of different age and sex classes of *R. rattus* in small, intermediate and large patches

	Juvenile males	Juvenile females	Sub-adult males	Sub-adult females	Adult males	Adult females
All patches	17.70	14.06	21.19	46.75	20.94	20.53
Standard deviation	17.37	21.71	13.58	44.25	15.41	14.73
Small patches	24.59	3.13	21.40	5.67	30.25	20.20
Intermediate patch	13.50	37.33	20.74	25.68	18.71	24.79
Large patch	11.31	13.35	21.24	88.05	14.37	19.09

of interest. Rare-species density and canopy height were correlated with each other when patch size was fixed ($T_{xy,z} = 0.61$, $n = 11$, $P < 0.05$). Mean weight of *R. rattus* was correlated with patch size when canopy cover was fixed ($T_{xy,z} = 0.46$, $n = 11$, $P < 0.05$). The mean weight of adult *R. rattus* was also correlated with patch size when canopy cover ($T_{xy,z} = 0.50$, $n = 11$, $P < 0.05$) and tree density ($T_{xy,z} = 0.50$, $n = 11$, $P < 0.05$) were fixed. The proportion of sub-adults was correlated with size when canopy cover ($T_{xy,z} = 0.71$, $n = 11$, $P < 0.05$), tree density ($T_{xy,z} = 0.75$, $n = 11$, $P < 0.05$) and canopy height ($T_{xy,z} = 0.69$, $n = 11$, $P < 0.05$) were fixed. Similarly, the proportion of female sub-adults was correlated with patch size when canopy cover ($T_{xy,z} = 0.70$, $n = 11$, $P < 0.05$) and tree density ($T_{xy,z} = 0.67$, $n = 11$, $P < 0.05$) were fixed. In summary, population characteristics of *R. rattus* were primarily correlated with patch size, while community structure variables were correlated with canopy height.

Rare-species density and biomass differed significantly (Kruskal-Wallis, $P < 0.001$) between small and medium, and between small and large patches. All indices of diversity – Shannon-Wiener ($P < 0.05$), Simpson's ($P < 0.05$), species richness ($P < 0.05$) and proportion of *R. rattus* ($P < 0.001$) – differed between the patches, with small patches having the highest average diversity. Small patches also differed from the large patch with regard to the proportion of adults ($P < 0.05$), the proportion of female sub-adults ($P < 0.01$), mean weight ($P < 0.01$) and weight of adult males ($P < 0.05$) of *R. rattus*.

There was no difference in stability (coefficient of variation of *R. rattus* abundance) between small, large and medium patches. There was no correlation in the abundance of the two most common species, *R. rattus* and *S. montanus*.

Sex ratios

The sex ratio of *R. rattus* juveniles did not differ from the expected 1:1 ($n = 51$). The sex ratio of sub-adults was also not different when all plots were considered ($n = 306$). However, the proportion of male sub-adults (0.64, $n = 76$) was significantly higher than for females in Upper Bhavani. The proportion of adult females was significantly greater than expected in all plots (0.57, $n = 386$) combined and in Thaishola (0.6, $n = 177$) (Fig. 3).

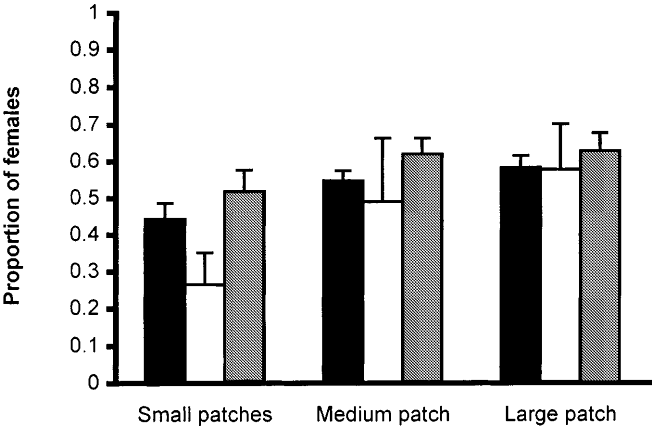

Fig. 3 Proportion of females in the three age classes, juvenile (*black*), sub-adult (*white*) and adult (*grey*) in small, medium and large patches. The proportion of female sub-adults was significantly lower in the small patches, while the proportion of adult females was significantly greater than expected in the large patch

There was no difference in the persistence between different age or sex classes of *R. rattus*. The persistence time of sub-adult females was particularly high in the large patch, while the persistence time of juvenile and sub-adult females was particularly low in the small patches (Table 5). The measures of persistence were used as indices for comparison between age and sex classes in patches of various size, and the absolute values may be biased by the preponderance of individuals with 0 days of persistence.

Discussion

Density and seasonality

Densities of small mammals in tropical evergreen forests show a great deal of variation, ranging from about 0.5 to 25 rodents/ha (Isabirye-Basuta and Kasenene 1987; Jeffrey 1977; Mares and Ernest 1995; O'Connell 1989). Other studies have found lower variation, but the range of densities is roughly the same, such as 4.1–4.9/ha in Malaysia (Harrison 1969) and 0.7–4.9/ha in Venezuela (August 1983). High densities were found in the Brazilian gallery forests with densities ranging from 32–53/ha (Nitikman and Mares 1987). Adler (1996) found extremely high average densities (12–43/ha) of *Proechimys semispinosus* on islands in the Panama Canal. In southern India, Chandrasekar-Rao and Sunquist (1996) reported mean densities of 15 rodents/ha for mid-elevation moist evergreen forests in the Anamalais, a hill range to the south of the Nilgiris. Other studies have shown much lower densities of rodents in mid- and low-elevation evergreen forests (Meena 1997; K. Shanker, unpublished data; D. Mudappa, personal communication).

The wet-season densities and biomass of small mammals in the Upper Nilgiris (peaking at 42 individuals/ha and 2852 g/ha) are comparable to the highest small-mammal densities and biomass recorded for most tropical evergreen forests in the world. They also seemed to be significantly higher than densities of small mammals in lower-elevation evergreen forests in southern India. This could be a consequence of the patchy nature of the habitat, since insular rodent populations are expected to attain higher densities than comparable 'mainland' populations (Gliwicz 1980).

Seasonality in density and biomass were more pronounced in the contiguous patch than in the fragments. This may be due to the fact that synchrony within the contiguous large patch was greater than synchrony between the fragments (Shanker and Sukumar, in press). Reproduction was found to be seasonal in *R. rattus*, with the proportion of breeding adults peaking in the dry season. This would be the best time for breeding due to extensive rains throughout the rest of the year. The dry season is also the peak fruiting season in montane forests (K.S. Murali, personal communication). Though the density of *R. rattus* was higher in 1994 and 1996 than in 1995, long-term studies need to be carried out before any larger-time-scale patterns can be discerned.

Population characteristics of *Rattus rattus*

Some population characteristics may be affected by insularity, while others are not; Adler and Seamon (1991) found that rat occurrence was correlated with island size and isolation, while rat density was not. They proposed that this might be due to the patchy nature of tropical forests and the differing floristic compositions of their study islands. Adler and Levins (1994) suggest that higher densities may be the most important characteristic of insular rodent populations. In the Upper Nilgiris, the evidence from the removal experiments suggests that individuals do not move even short distances (> 50 m) across patches on a daily basis, implying that these populations are insular. The degree of insularity would depend on the immigration rates, and grasslands may be less of a barrier for dispersal than other barriers like water. In our study area, smaller patches did not have higher densities than larger ones, which may be due to high immigration rates. However, it is interesting that the island syndrome was still discernible in other population characteristics.

Island populations of rodents are believed to self-regulate by lowering reproduction (Gliwicz 1980). This effect may be more pronounced in the smaller patches, leading to lower reproductive rates, and consequently, a higher proportion of older animals. This was evident in our study, with the proportion of adults and the mean weight of *R. rattus* both being negatively correlated with patch size. Further, there was a trend towards a lower proportion of juveniles in smaller patches.

Stability was not higher in the smaller patches when compared to the larger patches; however, despite substantial fluctuations in densities which fell to as low as 2/ha, *R. rattus* did not go extinct in any of the patches during the course of the study. This suggested that declining populations in small patches may be 'rescued' by immigration from nearby patches. This was supported by evidence from removal experiments, with new individuals being trapped at the removal plots within 2–3 weeks.

Gigantism in island rodents is believed to result from factors. Angerbjorn (1985) reported differences in body size between two islands, but suggested that competition and predation are the important factors, not island area and isolation per se. The absence of predators on islands as opposed to mainlands is believed to be an important factor causing gigantism in insular rodents (Foster 1964). In the Upper Nilgiris, predation should not vary in the different fragments. However, the body size of *R. rattus* (i.e. mean weight of adults) was larger on smaller patches. Males showed a more marked difference in body size, suggesting that intraspecific competition may be a factor causing an increase in body size. Since insularity places constraints on dispersal, an increase in competition between males might lead to an increase in body size. The constraint placed by insularity should act on females as well (there was a trend towards an increase in the body size of females), but the effect may be less pronounced because of factors such as spacing behaviour (Gliwicz 1980).

Territoriality and behaviour towards subordinates tend to differ between high-density insular populations and mainland populations (Stamps and Buechner 1985). The sex ratio of sub-adults was significantly biased towards males in the smaller patches (Fig. 3). The persistence of juvenile and sub-adult males was also significantly higher in these patches. This suggests that female juveniles and sub-adults may have been dispersing or subject to higher mortality in these fragments. Both male and female dispersal is known from other rodent species (Wolff 1993). In the smaller patches, dispersal of female sub-adults could lead to higher mortality or emigration to sub-optimal habitats, where they are less likely to be trapped. This would also lead to reduced competition between resident females as opposed to males, leading to a more pronounced body size effect in males, as was observed earlier. In Thaishola, however, the persistence of female subadults was significantly greater than that of males. In fact, this group showed markedly higher persistence times than any other group in any of the patches. As expected, the sex ratio of adults in Thaishola was significantly biased towards females. Since the sex ratio of sub-adults was not biased, this implied higher male mortality at the subadult stage.

The question that arises here is whether these apparent differences between small and large patches arise due to stochastic variations in small populations or are due to varying strategies adopted by a highly adaptable rodent species driven strongly by local conditions such as patch size, edge effect and habitat availability. Adler (1996) reported that island populations of *P. semispinosus* have traits such as a high reproductive rate and the ability to adjust reproductive effort, which allow individuals in a population to respond rapidly to temporal changes in their habitat. *R. rattus*, a ubiquitous species whose adaptability is generally acknowledged, may equally well be equipped to vary its reproductive and dispersal strategies in response to local conditions.

Community structure

Species diversity was low in our study area compared to that of neotropical evergreen forests (Mares and Ernest 1995; O'Connell 1989; Woodman et al. 1995). However, it was high compared to lower-elevation evergreen forests in southern India, such as Anamalais with three species (Chandrasekar-Rao and Sunquist 1996), Kalakkad-Mundanthurai with four species (D. Mudappa, personal communication) and Mudumalai with four species (Meena 1997). Other studies in evergreen forests in south-east Asia reported five species (Wu et al. 1996) and seven species (Walker and Rabinowitz 1992). Although a total of eight species were captured in this study, only four were common and two were represented by single captures. Overall species richness was greater in the larger patches, as expected.

However, average diversity in a given trapping session was higher in the smaller patches. This essentially implies that rare species were more likely to be caught in smaller patches because densities are higher in the smaller patches. Small populations in small insular fragments will have a fairly high probability of going extinct (Wilcox and Murphy 1985; Wright and Hubbell 1983; Shaffer 1981) In insular forest patches such as those encountered in our study area, the populations of rare species on small islands are so low that periodic extinctions can be expected. Given the mosaic of montane patches in the Upper Nilgiris landscape, migration between patches probably plays an important role in reestablishing and rescuing the populations as discussed earlier in the case of *R. rattus*. This reiterates the importance of immigration or the rescue effect in extinction processes and species richness in insular habitats.

Species richness has been shown to be positively correlated with habitat complexity (August 1983) and structural diversity. In our study area, variables that described community structure of small mammals were most strongly correlated with canopy height. However, the correlation between height (which one would expect to be positively correlated with vertical stratification) and species richness was negative. Most of the rare species (*S. montanus, S. dayi,* and *M. famulus*) are known to be ground-dwelling species. *R. rattus* is, on the other hand, believed to be highly arboreal, and may be more dominant in habitats with greater canopy height. There was, however, no significant negative correlation between *R. rattus* and the other species, particularly *S. montanus*. The density of species other than *R. rattus* on small patches is probably determined by the lower canopy height in these patches. Lower canopy may be related to diversity of forest floor niches, which were not adequately measured in our study.

In conclusion, insular small-mammal populations of the Upper Nilgiris have many features that distinguish them from contiguous populations. While some of these characteristics are different even between patches of varying sizes ranging from 2 to 600 ha, others may be different when compared to similar 'mainland' populations. Variables related to demography were influenced by patch size, while community structure varied in relation to certain habitat structure variables, particularly canopy height.

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