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Synchrony in small mammal populations of montane forest patches in southern India

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Summary

1. Small mammal populations were studied in montane evergreen forests in the Nilgiris, southern India, using live-trapping from January 1994 to September 1996. Two sites were selected, one with a single large forest patch and adjoining plantations, and the other with several small forest patches separated by grassland.
2. Nine species were recorded, of which eight were trapped in the forest patches, two in the grasslands and five in plantations. *Rattus rattus* was the most abundant species (2–36 individuals ha^{-1}) followed by *Suncus montanus* (0–11 individuals ha^{-1}). Densities of seven other species recorded were very low.
3. Synchrony in various population variables – density, biomass, mean weight, density of adults and adult females, and proportion of adults, adult females and sub-adults – was examined for *Rattus rattus* populations in the forest patches and plantations. Density and biomass were studied in seven other species recorded at these sites. Spearman's rank order correlation was used as a measure of synchrony between the population variables.
4. Within-site synchrony was higher than between-site synchrony in population characters. Synchrony was also higher between plots within the unfragmented site than they were between plots in the fragmented site. Relatively high synchrony in proportions of adults, adult females and juveniles in the forest patches implied that breeding is probably influenced by climate and food availability, which are seasonal in this habitat.
5. Given the small patch sizes ($\approx$ 1–10 ha) and low population sizes, asynchrony is likely to be an outcome of demographic and environmental stochasticity, and low dispersal rates may impede establishment of synchrony.

Key-words: *Rattus rattus*, montane forests, demographic trends, stochasticity, asynchrony.

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Introduction

The theory of island biogeography (MacArthur & Wilson 1967) has been extended to fragmented and insular habitats on land (Brown 1971; Lomolino, Brown & Davis 1989; see Shafer 1990 for a review.). The island metaphor has taken on greater importance in the context of the design of nature reserves for conservation (Wilcox & Murphy 1985; Burkey 1989; Shafer 1990). However, forest fragmentation worldwide has also brought into focus interesting questions in theoretical ecology. These questions involve aspects of population dynamics that may be equally important in understanding the consequences of fragmentation (Holt 1992; Robinson *et al.* 1992). The degree of spatial synchrony between populations may help clarify some of the processes that drive population dynamics (Steen, Ims & Sonerud 1996).

Island populations of rodents have been known to show differences in demography, behaviour and reproduction in comparison with mainland populations (for reviews, see Gliwicz 1980; Adler & Levins 1994). Insular rodent populations have traits that allow individuals in a population to respond rapidly to temporal changes in their habitat (Adler 1996). In this context, the spatial synchrony of population fluctuations between isolated groups becomes an interesting and important question. Synchrony has

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been examined for various taxonomic groups ranging from insects (Pollard 1991) to mammals (Ims & Steen 1990; Mackin-Rogalska & Nabaglo 1990; Steen 1995; Steen *et al.* 1996). Small mammal populations may be out of phase at larger spatial scales, while local populations may show significant synchrony (Steen *et al.* 1996). Tropical forest fragmentation and isolation could promote asynchrony among small rodent populations (Adler 1994).

The Western Ghats in southern India are considered to be one of 18 'hotspots' of biodiversity in the world (Myers 1990). However, much of the natural habitat has been transformed due to human activity. The upper plateau of the Nilgiris and other ranges in the Western Ghats have insular forest patches surrounded by extensive grassland. Although the size and extent of the forest patches may have varied during the Quaternary, it is likely that they have been isolated in the past, as well (Sukumar, Suresh & Ramesh 1995). The isolation of the montane system atop the Nilgiris, and the patchy nature of the forests, provide an ideal opportunity to study plant and animal populations in fragmented forests. Grasslands were even more extensive during the last glacial maximum (≈ 18 000 years BP) and earlier periods (> 40 000 years B.P.) during the Quaternary (Sukumar *et al.* 1993; Rajagopalan *et al.* 1997). The montane forests have thus remained isolated on time scales of thousands of years. The system can thus be expected to be in equilibrium over short time scales (decades), and may be crucial to our understanding of population dynamics in fragmented habitats.

We analysed synchrony among populations of the common rat, *Rattus rattus* (Linnaeus) and other small mammals in these forest patches. Several population variables were examined with a view to answering two questions of primary interest: (1) Are forest patches that are closer to each other more synchronized than more distant ones? (2) Are sites within a single, large unfragmented forest patch more synchronized than several small fragmented patches? In the light of the results, we discuss possible mechanisms of synchrony and asynchrony of small mammal populations in these tropical montane forests.

Methods

STUDY AREA

The Nilgiris are located between 11°10′ and 11°30′N, and 76°25′ and 77°00′E at the junction of the Eastern Ghats and the Western Ghats, the two hill ranges that run almost parallel to the coastlines of peninsular India. The vegetation of the montane (1800–2500 msl) regions of the Nilgiris comprises stunted evergreen forest (hereafter referred to by the local name 'shola') and grassland (Meher-Homji 1984). Although much of the natural vegetation has been replaced by exotic wattle (*Acacia* spp.), pine (*Pinus roxburghii* Sarg.), tea (*Camellia sinensis* (L.) Kuntze) and bluegum (*Eucalyptus globulus* Labil), the original sholas and grasslands are still found in small pockets, particularly in the south-western part of the Nilgiri plateau.

The sholas, usually confined to depressions and folds in the mountain, are characterized by medium sized (15–20 m) and small (7–15 m) trees (von Lengerke & Blasco 1989). They are usually extremely dense, with 5000 or more woody plants (> 1 cm d.b.h.) per hectare, dominated by the families Lauraceae, Rubiaceae and Symplocaceae (H. S. Suresh & R. Sukumar, unpublished data). The ecotone between the sholas and the grasslands is sharply defined and maintained by frost and fire (Meher-Homji 1984). Most sholas are small (0·1–10 ha), and though some are larger (10–100 ha), very few are greater than 100 ha in size.

The Upper Bhavani region, at the south-west corner of the Nilgiris, forms a part of the Mukurthi National Park (74 km^2) in Tamilnadu state. The natural vegetation has remained more or less intact in this park. Thaishola (601 ha), 12 km east of Upper Bhavani is the largest shola in the Upper Nilgiris. Thaishola and Upper Bhavani, on the western slopes of the Nilgiris, receive 1500–2000 mm annual rainfall, mostly between June and November.

SAMPLING PROCEDURE

Eight sholas were selected in two areas, Upper Bhavani and Thaishola (Fig. 1). Seven sholas were selected in Upper Bhavani, ranging in size from 0·2 to 60 ha. Eleven plots were laid within the shola patches; a single 0·49-ha plot (70 × 70 m) was laid in each of the smaller sholas, two 0·49-ha plots were laid in the 60-ha shola and, three 0·49-ha plots at Thaishola. Two 1-ha plots (100 × 100 m) were added in Thaishola 6 months later. In addition, the plantations adjacent to Thaishola were sampled, with one 0·49-ha plot at the edge of the shola, extending into a blue gum plantation, and one 0·90-ha plot (150 × 60 m) in a wattle plantation. In Upper Bhavani, two small sholas (0·5 and 0·2 ha) were sampled, with traps extending into the grassland. Each plot was sampled six to 11 times, for a total of 11 186 trap nights in Upper Bhavani and 11 144 trap nights in Thaishola.

Open grasslands (2009 trap nights) and grasslands between shola patches (1392 trap nights) were sampled to check species composition and small mammal movement between patches. Removal experiments were conducted on one of the small shola patches (0·5 ha) and an adjacent patch (0·15 ha). The two patches were within 100 m of other small and large patches. Individuals of *Rattus rattus* were removed from the two patches (> 1 ha) over 6 days of trapping; no new individuals were caught in either patch over the last two days. Both plots were sampled for 2 days each week for 3 weeks following the removal. The

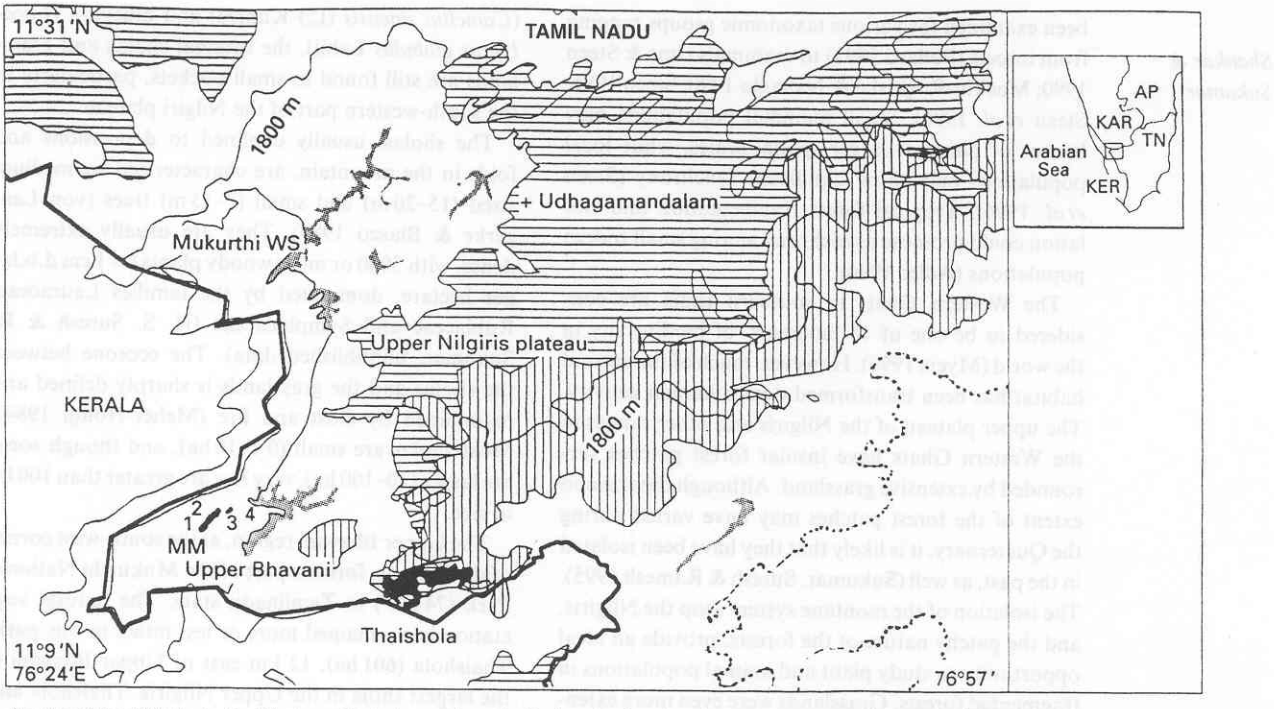

Fig. 1. A map of the Nilgiris in the Western Ghats in southern India (inset), showing the present extent of montane forests and grasslands (clear area, largely within 1800 m contour line), tea (vertical lines), cultivation (horizontal lines) and reservoirs (lightly shaded). Seven plots at the unfragmented site were at Thaishola (601 ha), the largest shola in the Nilgiris. These included five plots (two 1-ha plots and three 0·49-ha plots) within the shola and two plantation plots towards the western boundary of Thaishola. Eight sampling plots at the fragmented site were at Upper Bhavani in the Mukurthi Wildlife Sanctuary. There were two 0·49-ha plots in MM-shola (60 ha). Sholas 1–4, ranging in size from 2 to 11 ha, had one 0·49-ha plot each. The removal plots (0·5 and 0·2 ha) were located at the northern tip of MM-shola. The 0·2-ha shola was between Shola 3 and MM-shola.

plots were sampled again after 3 and 6 months, for a total of 1350 trap nights.

Each 0·49-ha plot consisted of 49 permanently marked trap stations, in a square grid of 7 × 7 traps, at an interval of 10 m each (the 1-ha plots had 100 trap stations, in a 10 × 10 configuration, while the 0·90-ha plot had 90 traps in a 15 × 6 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 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. Plots were generally sampled once during each season. All sampling within a season was considered as one cycle of sampling. In all sampling cycles barring the first season, plots were sampled within about 1 month of each other. All trapped animals were identified, ear-punched, sexed, weighed, measured and released. The traps were checked once daily between 08·00 hours and 12·00 hours.

We recognized four seasons for this study, taking rainfall, temperature and occurrence of frost at both sites into consideration (Fig. 2).

1. Winter (November–January): some rain occurs from north-east (winter) monsoon during November, while occurrence of frost is common during December–January which are mostly dry.

2. Dry (February–April); very low rainfall during these months.

3. First wet (May–July): premonsoon showers begin in May and south-west (summer) monsoon breaks in June, with peak rainfall in July.

4. Second wet (August–October); this marks the end of south-west monsoon in August and the onset of north-east monsoon in October.

Geographical distances between the plots were measured using a 1:50 000 Survey of India topographical map (58 A/12 and 58 A/8) on which the locations of the plots were marked by ground based mapping. The plots in Upper Bhavani were 150 m to 2·3 km from each other, while those in Thaishola were 50 m to 2 km from each other. The Thaishola and Upper Bhavani sites were about 12 km from each other. Patch sizes were estimated using digitized data, perimeter traverses and photographs of the shola patches (Fig. 1).

DATA ANALYSES

The following population variables were considered for analysis.

For *Rattus rattus*

1. Density: the 'minimum number alive' per ha during a sampling session (Krebs 1966). When population sizes and capture probabilities are very low, capture-

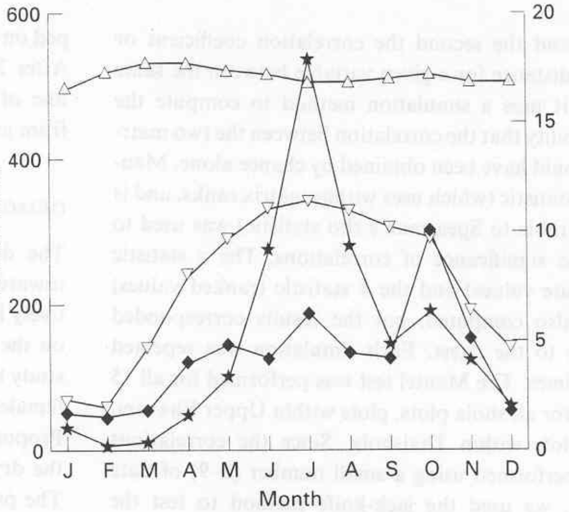

Fig. 2. Average monthly rainfall (1941–1970) in Upper Bhavani (opened squares) and Thaishola (closed diamonds) (1986–1996), and average maximum and minimum temperatures (1962–1972) in Korakundah (open triangles) which is halfway between Thaishola and Upper Bhavani. (data from von Lengerke 1977).

recapture models can not be applied (White *et al.* 1982). Since population sizes were frequently very low in all plots and appropriate models could not be applied to all sampling sessions, MNA was used to derive density estimates.

2. Biomass: the total weight of all animals captured during a session per ha

3. Mean weight of animals: biomass/MNA: this was used as measure of age structure, based on biomass rather abundance.

4. Density of adults: males with scrotal testes plus females who were pregnant or lactating or had a perforate vagina per ha.

5. Density of adult females.

6. Proportion of adults: number of adults/number of individuals captured.

7. Proportion of adult females: number of adult females/number of individuals captured.

8. Proportion of sub-adults: number of sub-adults/number of individuals captured.

For all small mammal species: these estimates were derived from the 11 plots that covered shola habitat exclusively since the community structure and relative abundance of small mammals is considerably different in other habitats.

9. Total density.

10. Total biomass.

11. Rest density: density of all species apart from *Rattus rattus*.

12. Rest biomass: biomass of all species apart from *Rattus rattus*.

Density and biomass were derived from the first three nights of trapping for the entire study to standardize the estimates. Proportions of adults and adult females, and mean weights were calculated using all individuals captured during the sampling session.

Spearman's rank order correlation coefficients were calculated for all variables using the Pearson's product-moment correlation formula on ranked data (Siegel & Castellan 1988). Pearson's correlation coefficients were also computed for all the population variables considered. However, since the parametric correlations were virtually identical to those obtained from rank order correlations, the former have been mentioned only where they differ significantly from the latter. For each variable, correlation coefficients were calculated for all pairs of plots. The coefficient for each pair was calculated using data points from all seasons in which both plots were sampled (in each season, plots were sampled within a month of each other). Pairs were sampled in the same season three to nine times. Spearman's correlation coefficient was used as a measure of synchrony between each pair of plots for a particular variable. The distance between the sites in multi-dimensional space with regard to the population variables was also used to examine the relationship between the population variables and geographical distance between the sites. The chord distance between the sites was derived from the Pearson's correlation coefficient using the following formula:

$$\text{Chord distance} = \sqrt{(2-2r)}$$

where r is the Pearson's product moment correlation coefficient (Ludwig & Reynolds 1988).

The mantel test was performed to test the significance of the correlation between synchrony in population variables (chord distance and Spearman's correlation coefficient) and geographical distance. The program MANTEL (Hemelrijk 1990) was used to compute the test statistic. The test compares two matrices, one the geographical distances between all pairs of plots, and the second the correlation coefficient or chord distance for a given variable between the same pairs. It uses a simulation method to compute the probability that the correlation between the two matrices would have been obtained by chance alone. Mantel's r statistic (which uses within-matrix ranks, and is comparable to Spearman's rho statistic) was used to test the significance of correlations. The z statistic (absolute values) and the k statistic (ranked values) were also computed, but the results corresponded closely to the r-test. Each simulation was repeated 2000 times. The Mantel test was performed for all 15 plots, for all shola plots, plots within Upper Bhavani, and plots within Thaishola. Since the correlations were performed using a small number (3–9) of data points, we used the jack-knife method to test the robustness of the result. The jack-knife was performed by removing one plot at a time from the computation of the mantel, giving pseudo-values of the test statistic, r. All results were tested for significance at $P < 0{\cdot}05$, unless specifically mentioned otherwise.

Results

SPECIES COMPOSITION

We trapped 1310 individuals of nine species of small mammals in the sholas, plantations and grasslands with an overall trapping success of 10·6%. The mammals trapped included rodents (*Rattus rattus*, *Cremnomys blanfordi* Thomas, *Vandeleuria oleracea* Bennett, *Platacanthomys lasiurus* Blyth, *Mus famulus* Bonhote, *Mus platythrix* Bennett and *Millardia meltada* Gray) and shrews (*Suncus montanus* Kelaart and *Suncus dayi* Dobson). *Rattus rattus* was the most abundant (737 individuals), followed by *Suncus montanus* (310), *Mus famulus* (125), *Suncus dayi* (28), *Millardia meltada* (93), *Platacanthomys lasiurus* (12) and *Mus platythrix* (3). *Cremnomys blanfordi and Vandeleuria oleracea* were represented by single captures. The density of *Rattus rattus* varied from 2 to 36 individuals ha^{-1}, while *Suncus montanus* varied from 0 to 11 individuals ha^{-1}. The numbers of other species were consistently very low, of the order of 1–2 individuals ha^{-1}.

Millardia meltada is a grassland species that was trapped occasionally on the periphery of the sholas. *Suncus montanus* was the only other species trapped in grasslands. *Rattus rattus*, *Millardia meltada*, *Suncus montanus*, *Suncus dayi* and *Mus famulus* were trapped in the bluegum and wattle plantations. The shola-grassland edge is very sharply defined and the forest rodent species were never captured in the grassland, even within metres of the forest edge. Marked individuals of both rodents and shrews were rarely found to move between sholas, implying that the small mammal populations were largely insular, despite the small distances separating the sholas. In the removal experiments, the first individuals of *Rattus rattus* were trapped on the removal plots 2–3 weeks after the removal. After 3 months, several individuals were trapped in one of the patches, including a marked individual from an adjacent patch.

DEMOGRAPHIC TRENDS

The density and biomass of *Rattus rattus* peaked towards the end of 1994 (year 1) and remained relatively low throughout 1995. Densities appeared to be on the rise again towards the end of 1996 when our study terminated (Fig. 3). Proportions of adults, adult females, sub-adults and juveniles fluctuated annually. Proportions of adults and adult females peaked during the dry season between February and April (Fig. 3). The proportion of juveniles peaked at the end of the dry season and the beginning of the first wet season between April and June in all three years (Fig. 4), while the proportion of sub-adults peaked towards the end of the year (Fig. 5). Mean weight, which reflected the age structure of the population, also seemed to fluctuate annually. Fluctuations in total density and biomass of all species were very similar to patterns seen in *Rattus rattus*, and this could be attributed to the fact that *Rattus rattus* forms a very large proportion of the total. The other species showed very little fluctuation in Upper Bhavani, while in Thaishola the fluctuations were of low amplitude.

SYNCHRONY IN POPULATION VARIABLES

Correlation coefficients were positive for most *Rattus rattus* population variables within Thaishola, with the positive values ranging between 50 and 100% of all computed values for the variables. On the other hand, correlation coefficients for comparisons within Upper Bhavani plots and those for the Upper Bhavani–Thaishola plot comparisons were biased towards positive values only for variables describing age structure. Overall comparisons of all plots at both sites again indicated positive trends in correlation for variables pertaining to age structure including the proportions of adults, adult females and sub-adults and mean weight (Table 1). Synchrony between plots within Thaishola was greater than that between plots in Upper Bhavani and Upper Bhavani–Thaishola plot comparisons for *Rattus rattus* abundance and biomass (Kruskal–Wallis $P < 0{\cdot}05$). While other correlation coefficients were not significantly different between groups, mean values were generally highest in Thaishola (Table 2). Variables describing *Rattus rattus* age structure had higher correlation coefficents than *Rattus rattus* density and biomass (Friedman $P < 0{\cdot}01$).

When the 11 shola plots alone were considered, synchrony was significantly different between the groups, with most of the *Rattus rattus* population variables, and total density and biomass being more correlated within Thaishola than between the sites

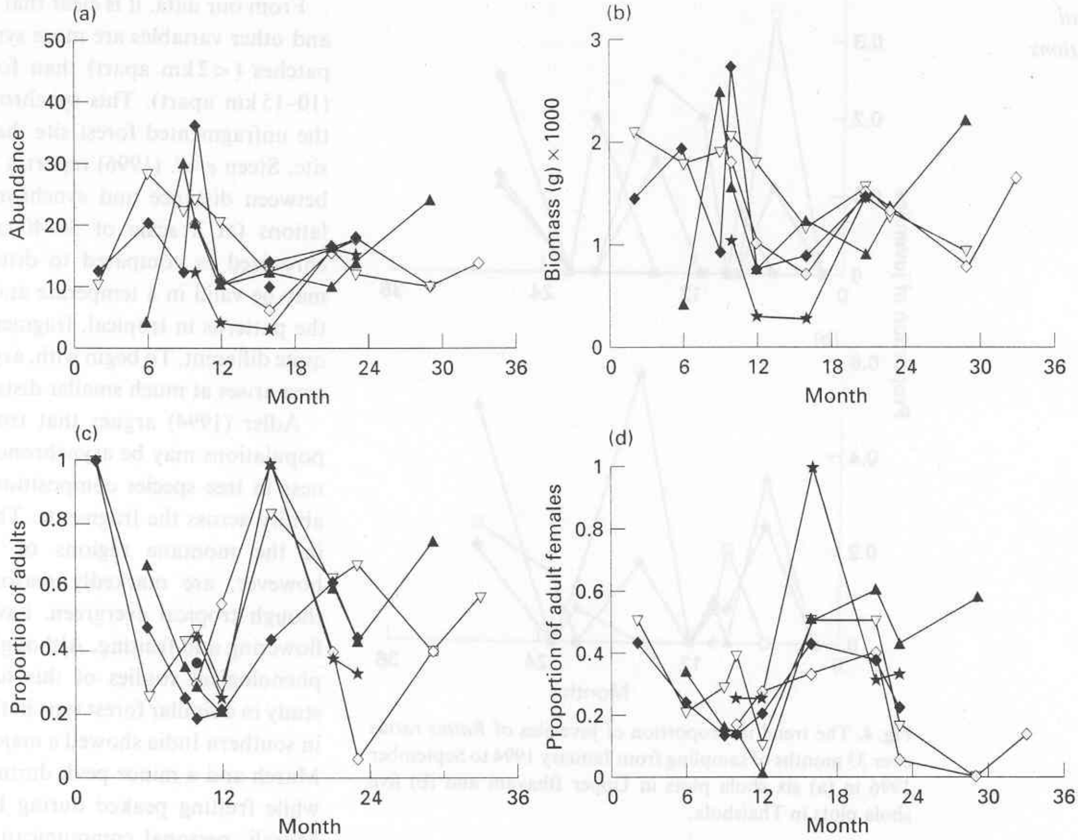

Fig. 3. The trend in population variables for *Rattus rattus* over 33 months of sampling from January 1994 to September 1996, in the five shola plots in Thaishola, a single large unfragmented patch. Each symbol represents data points from a particular plot. Spearman's rank order correlation coefficients (r_s) were calculated for all pairs of plots. (a) density (minimum number alive ha^{-1}) – mean r_s: 0·29; (b) biomass ha^{-1} – mean r_s: 0·35; (c) proportion of adults – mean r_s: 034 (d) proportion of adult females – mean r_s: 0·5.

(Table 3). Synchrony in the proportion of adults (mean r_s – 0·34) and adult females (mean r_s – 0. 5) were particularly high within the five shola plots in Thaishola with the 80% of the former and 100% of the latter being positive. Correlation coefficients for the proportion of sub-adults were the highest of all variables tested with 50% of the coefficients being significant in Thaishola, and 100% of the coefficients being positive in Upper Bhavani and Thaishola. Correlation coefficients for the rest of the small mammals were not biased towards positive or negative values; there were also no differences between the two sites (Tables 1 and 2).

SYNCHRONY AND DISTANCE

The Mantel test showed no significant correlation between geographical distance and synchrony in any population variable within the units of Thaishola and Upper Bhavani. However, when all plots were considered together, synchrony in *Rattus rattus* density and biomass was negatively correlated with distance, while the chord distance between the sites for the same variables was positively correlated with distance (Mantel *r*-test $P < 0{\cdot}01$). When the 11 shola plots alone were considered, several of the population variables showed a negative correlation between geographical distance and synchrony. *Rattus rattus* density, biomass, density of adults and adult females, proportions of adults and sub-adults, and total density and biomass were more correlated within sites than between sites (Mantel *r*-test. $P < 0{\cdot}05$). Population distance (chord distance based on population variables) was positively correlated with geographical distances for the same variables and in addition, for the proportion of adult females (Mantel *r*-test, $P < 0{\cdot}05$). We used the jack-knife method to test the robustness of the significant results. Most of the pseudo-values of the Mantel test statistic *r* were significant at $P < 0{\cdot}05$. The significance of the remaining values of *r* ranged from 0·05 to 0·11.

Discussion

Synchrony between populations has thus far been studied primarily in the context of multi-annual cycles in northern Fennoscandian small mammals (Mackin-Rogalska & Nabaglo 1990; Steen 1995; Steen *et al.*

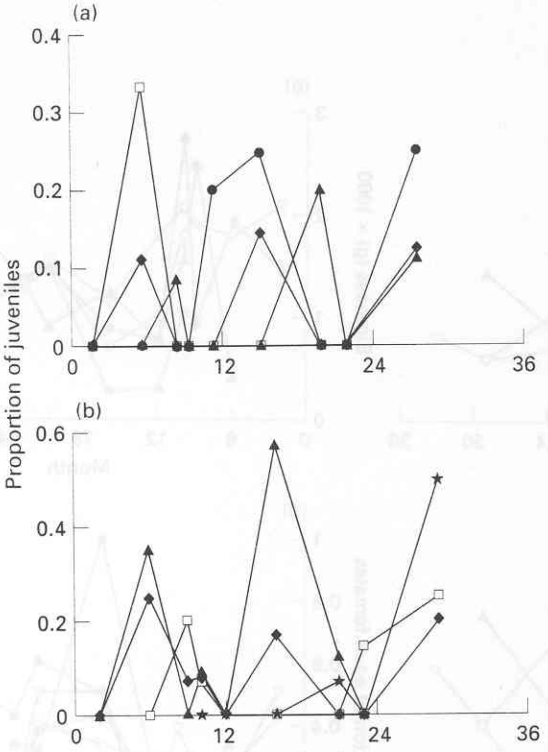

Fig. 4. The trend in proportion of juveniles of *Rattus rattus* over 33 months of sampling from January 1994 to September 1996 in (a) six shola plots in Upper Bhavani and (b) five shola plots in Thaishola.

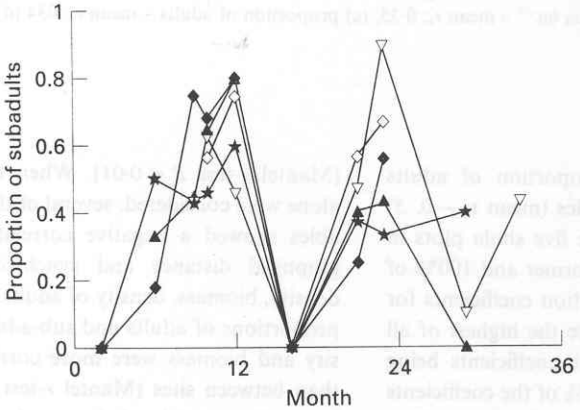

Fig. 5. The trend in proportion of subadult *Rattus rattus* in five shola plots in Thaishola over 33 months of sampling from January 1994 to September 1996; mean r_s: 0·66.

1996). Predation is believed to be important in regulating small mammal populations (Henttonen 1985; Sinclair, Olsen & Redhead 1990; Hanski, Hansson & Hentonnen 1991; Akcakaya 1992; Hanski & Korpimäki 1995) It is generally expected that nomadic predators will synchronize small mammal populations by tracking the relative abundance of prey within the region (Ydenberg 1987; Korpimäki & Norrdahl 1989; Ims & Steen 1990). While this may work in the larger, contiguous habitats, the same may not be true of fragmented habitats.

From our data, it is clear that *Rattus rattus* density and other variables are more synchronized for closer patches (<2 km apart) than for more distant ones (10–15 km apart). This synchrony is also greater in the unfragmented forest site than in the fragmented site. Steen *et al.* (1996) report a negative relationship between distance and synchrony, with local populations (at a scale of 30–40 km) being more synchronized as compared to distant ones. While this may be valid in a temperate and contiguous habitat, the patterns in tropical, fragmented habitats may be quite different. To begin with, asynchrony in our study area arises at much smaller distances.

Adler (1994) argues that tropical small mammal populations may be asynchronous due to the patchiness in tree species composition and resource availability across the fragments. The climatic conditions in the montane regions of the Western Ghats, however, are markedly seasonal and the forests, though tropical evergreen, have distinct periods of flowering and fruiting. Although there have been few phenological studies of this habitat type, a 3-year study in a similar forest type in the Biligirirangan Hills in southern India showed a major peak in flowering in March and a minor peak during August–September, while fruiting peaked during February–May (K. S. Murali, personal communication). We have similar qualitative observations in the Nilgiris. The synchrony across 3 years in the proportions of adults, adult females, sub-adults and juveniles of *Rattus rattus* shows that there is distinct seasonality in reproductive behaviour. This is likely to be associated with weather conditions and the availability of food. Breeding appears to take place in the dry season (February–April). The rains are especially heavy in July and continue through to December, and therefore the short dry season would seem to offer the best chances for the survival of young. This is also a peak fruiting season, which would offer the best conditions for foraging. Furthermore, the age structure variables were highly synchronized in the shola plots in Thaishola, but the plantation plots at the same site were not in synchrony with the shola plots. This could be due to differences in food availability in plantations or in the use of plantations by different age classes of *Rattus rattus*.

There was a negative relationship between synchrony in *Rattus rattus* abundance and biomass, and geographical distance, with synchrony being higher in the unfragmented site than the fragmented site. This indicates that population processes in *Rattus rattus* are related in contiguous populations. Small mammal densities may be correlated due to dispersal and other density dependent processes (Steen *et al.* 1996). If seasonal climatic conditions and food availability synchronize breeding, and density-dependent processes maintain synchrony in densities, why are *Rattus rattus*

Table 1. Percentage of positive values of Spearman's Rank Order correlation coefficient for (1) plots within Upper Bhavani, (2) plots within Thaishola, (3) Upper Bhavani–Thaishola plot comparisons, and (4) all plots combined. * indicates that the percentage varies significantly from the expected 50% using the binomial test for (1) and (2), and the normal approximation for (3) and (4). *N* refers to the number of comparisons (i.e. the number of correlation coefficients)

	Population variables	(1) Upper Bhavani	(2) Thaishola	(3) Upper Bhavani–Thaishola	(4) All
	Rattus rattus	*N* = 28	*N* = 21	*N* = 56	*N* = 105
1	Density	50·0	71·4*	41·1	49·5
2	Biomass	53·6	80·9*	44·6	54·3
3	Mean weight	71·4*	17·1	67·9*	66·7*
4	Proportion: adult	57·1	71·4*	57·1*	60·8*
5	Proportion: adult females	50·0	85·7*	67·9*	66·7*
6	Proportion: subadult	67·9*	71·4*	71·4*	70·5*
		N = 15	*N* = 10	*N* = 30	*N* = 55
7	Density of adults	53·3	500·0	40·0	45·4
8	Density of adult females	53·3	50·0	50·0	50·9
	All species	*N* = 15	*N* = 10	*N* = 30	*N* = 55
9	Total density	40·0	80·0*	46·7	50·9
10	Total biomass	53·3	70·0	40·0	49·1
11	Rest density	66·7	70·0	43·3	54·5
12	Rest biomass	66·7	60·0	60·0	61·8

Table 2. Mean value of Spearman's Rank Order correlation coefficient for 15 plots in Upper Bhavani and Thaishola. The groups are (1) plots within Upper Bhavani, (2) plots within Thaishola, (3) Upper Bhavani–Thaishola plot comparisons, and (4) all plots combined. The Kruskal–Wallis one-way analysis of variance was used to test for significant differences between groups, followed by multiple comparisons between pairs. In column (2), * denotes a significant difference between (2) and (3)

	Population variables	(1) Upper Bhavani	(2) Thaishola	(3) Upper Bhavani–Thaishola	(4) All plots
	Rattus rattus	*N* = 28	*N* = 21	*N* = 56	*N* = 105
1	Density	−0·02	0·30*	−0·12	−0·11
2	Biomass	−0·05	0·31*	−0·11	−0·01
3	Mean weight	0·36	0·07	0·14	0·18
4	Proportion: adult	0·11	0·16	0·15	0·14
5	Proportion: adult female	−0·03	0·32	0·14	0·14
6	Proportion: subadult	0·26	0·37	0·19	0·26

densities asynchronous in fragmented habitats? Demographic and environmental stochasticity may both play an important role in the dynamics of small populations (Shaffer 1981; Wright & Hubbell 1983; Wilcox & Murphy 1985). It is likely that demographic stochasticity, irrespective of other considerations, will cause large population fluctuations and extinctions when populations sizes are small, especially in species with high turnover rates. Predation will add to inherent demographic stochasticity and enhance the likelihood of populations in different patches becoming asynchronous. For example, in small patches such as those encountered in our study site, a single predator may be able to substantially reduce the number of small mammals in a patch (e.g. a population of 5–10 rats ha^{-1} in a 1–2 ha patch), and the population may not recover immediately because dispersal rates from surrounding patches are low. Potential predators in our study area include several mammals (felids, canids and mustelids) and birds (raptors and owls; see Appendix).

Since *Rattus rattus* was never resident in the grasslands, the fragments may be considered insular and population processes in different fragments may, to some extent, be independent of each other. While there is evidence for migration between patches, the time taken for a population to recover from depletion (weeks or months) may differ between patches. The patches selected in our removal experiments were very close to other large and small shola patches, and dispersal to more distant patches may be even slower. The difference in time taken for populations in different patches to recover from stochastic fluctuations and depletion may lead to asynchrony in densities between these populations. Insularity places constraints on dispersal, preventing small populations in fragments from becoming synchronized, promoting asynchrony even at small spatial scales. This is sup-

Table 3. Mean values of Spearman's Rank Order correlation coefficient (r_s) for the 11 shola plots in Upper Bhavani and Thaishola. The groups are (1) plots within Upper Bhavani, (2) plots within Thaishola, (3) comparisons between Upper Bhavani and Thaishola plots, and (4) for all plots. The Kruskal–Wallis one-way analysis of variance was used to test for significant differences between groups, followed by multiple comparisons between pairs. In column (1), # denotes a significant difference between (1) & (2); * denotes a significant difference between (1) & (3). In column (2), * denotes a significant difference between (2) and (3)

	Population variables	(1) Upper Bhavani (n = 15)	(2) Thaishola (n = 10)	(3) Thaishola–Upper Bhavani (n = 30)	(4) All plots (n = 55)
	Rattus rattus				
1	Density	0·08*	0·29*	−0·23	0·05
2	Biomass	−0·05	0·35*	−0·19	0·04
3	Mean weight	0·31	0·24	0·12	0·19
4	Density of adults	0·06	0·04	−0·11	−0·04
5	Density of adult females	0·04	0·15	−0·07	−0·02
6	Proportion: adult	0·19	0·34*	0	0·11
7	Proportion: adult female	0·04#	0·5*	0·18	0·2
8	Proportion: subadult	0·48*	0·66*	0·14	0·34
	All species				
9	Total density	0	0·29*	−0·13	−0·02
10	Total biomass	0·01	0·27*	−0·18	−0·05
11	Rest density	0·17	0·19	−0·01	0·08
12	Rest biomass	0·14	0·14	0·07	0·1

ported by the evidence that synchrony is significantly higher in Thaishola than in Upper Bhavani. The plots in Thaishola lie in different parts of an unfragmented patch, while rats have to disperse across grasslands in the fragmented forest site at Upper Bhavani.

Hence, given the small population and fragment sizes in our system, we believe that stochasticity may be a more important factor in causing asynchrony in these forests than patchiness in resource availability. The implication of synchronous and asynchronous population dynamics in these tropical habitats needs to be examined very closely. The Western Ghats has a large number of endemic species of animals, many of which are endangered because of fragmentation of forests. A better understanding of the processes that drive these populations would be important to planning for their conservation.

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Appendix

POTENTIAL MAMMALIAN AND AVIAN PREDATORS OF SMALL MAMMALS IN THE UPPER NILGIRIS IN SOUTH INDIA

Mammals (personal observation; names from Prater 1971)

Felidae
1. Jungle cat *Felis chaus* Guldenstaedt
2. Leopard cat *Felis bengalensis* Kerr
3. Leopard *Panthera pardus* (Linnaeus)

Viverridae
4. Small Indian civet *Viverricula indica* (Desmarest)
5. Common palm civet *Paradoxurus hermaphroditus* (Pallas)

Herpestidae
6. Ruddy mongoose *Herpestes smithi* Gray

Canidae
7. Jackal *Canis aureus* Linnaeus

Mustelidae
8. Nilgiri marten *Martes gwatkinsi* Horsfield

Birds (personal observation; names from Ripley 1982)

Accipitridae
1. Buzzard? *Buteo* sp.
2. Brahminy kite *Haliastur indus* (Boddaert)
3. Bonnelli's eagle *Hieraaetus fasciatus* (Vieillot)
4. Black eagle *Ictinaetus malayensis* (Temminck)
5. Crested serpent eagle *Spilornis cheela* (Latham)
6. Black-winged kite *Elanus caeruleus* (Desfontaines)

Falconidae
7. Kestrel *Falco tinnunculus* Linne

Strigidae
8. Barn owl *Tyto alba* (Scopoli)
9. Forest eagle owl *Bubo nipalensis* Hodgson
10. Mottled wood owl *Strix ocellata* (Lesson)
11. Brown wood owl *Strix leptogrammica* Temminck

Corvidae
12. Jungle crow *Corvus macrorhynchos* Wagler