

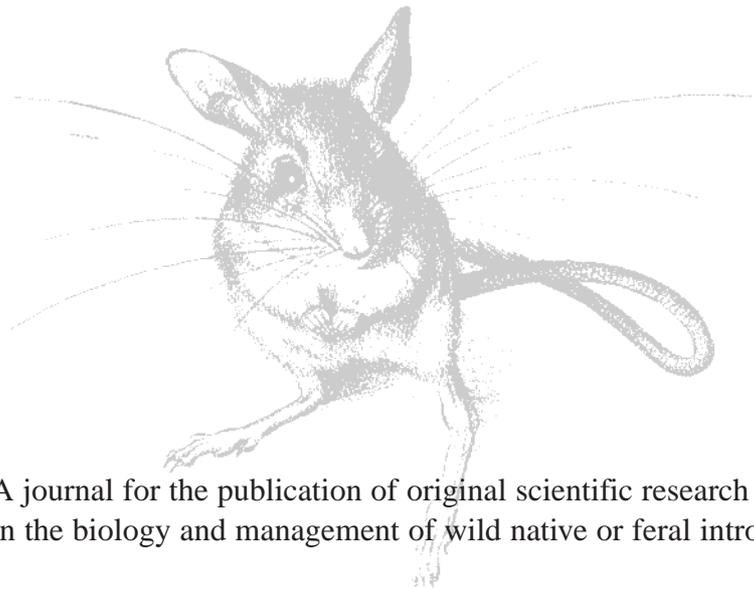
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## Long-term dynamics of a rodent community in an Australian tropical rainforest

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### Abstract

We report on a long-term population study (started in 1969) of three sympatric rodent species in a tropical Queensland (Australia) rainforest. Populations were censused annually using live-trapping and individual marking on two grids in different habitat types. Two of the species, *Melomys cervinipes* and *Uromys caudimaculatus*, are ‘old endemics’ and have slower life-histories than the third species, *Rattus fuscipes*, which invaded Australia more recently. The numbers of all three species fluctuated markedly over the study period. *Rattus* numbers started low, peaked in the early 1980s, and then crashed to zero by 1993. In contrast, *Melomys* climbed gradually throughout the study period but crashed to zero by 1996. *Melomys* numbers increased in drier years whereas *Uromys* numbers decreased, but these results were confounded by autocorrelation over time. When the effects of time (year of study) were removed statistically, the correlations with rainfall disappeared, but the number of *Rattus* remained negatively correlated with the number of *Melomys* on one grid. We discuss the possibility that numbers of these two species are determined by a combination of climate and interspecific competition.

### Introduction

Most studies of population dynamics are of short duration and do not cover the full range of environmental conditions experienced in any one area. Long-term data (relative to generation time) are clearly necessary to understand the combined effects of various ecological forces (e.g. Brown and Zeng 1989; Brown and Heske 1990; Skupski 1995). For example, although numerous studies of rodent communities have teased apart the importance of vegetative structure (e.g. Rosenzweig and Winakur 1969; Hallett 1982; Parmenter and MacMahon 1983), and others have investigated the role of competition (Schoener 1983; Heske *et al.* 1994), few studies have persisted for long enough to examine the interactions between them. The best way to examine these processes is to compare species that coexist in sizeable guilds over long periods (Brown and Zeng 1989), especially when the life-history strategies and systematic relationships among the species are known.

The Australian rodents provide a good opportunity to study the interactions between ecologically similar sympatric species that vary in their evolutionary and life-history traits. All 60 species belong to one family, the Muridae, and most of these are in a single sub-family, the Hydromyinae (Watts *et al.* 1992). Members of this sub-family, called the ‘old endemics’, first invaded Australia from the north as much as 15 million years ago, whereas the remaining 10 species invaded Australia more recently (Strahan 1995). Seven species of *Rattus* (the ‘new endemics’) arrived during the last one million years, and three species (*Rattus rattus*, *Rattus norvegicus*, and *Mus musculus*) were introduced by European humans within the last 200 years. The ‘old’ and ‘new’ endemics differ markedly in their life-history traits, with the old endemics being characterised by smaller litters, longer gestation rates and weaning periods, and late maturity (Lee *et al.* 1981; Yom-Tov 1985). Despite these differences, species from both groups may coexist in superficially similar niches (Wood 1971; Fox 1982; Strahan 1995).

In this paper, we analyse data from 22 continuous years of trapping rodents in a tropical Queensland rainforest, with additional data from earlier years. Of the three species of rodents caught frequently, two, *Melomys cervinipes* and *Uromys caudimaculatus*, are old endemics, and one, *Rattus fuscipes*, is a new endemic. *M. cervinipes* (hereafter called *Melomys*) is the smallest (45–110 g), breeds seasonally, and produces only two young on average per litter (Wood 1971). *R. fuscipes* (hereafter called *Rattus*) is larger (65–225 g), can breed all year, produces about five young per litter, and most members of the population die after their first year of reproduction (Warneke 1971; Lunney *et al.* 1987). *U. caudimaculatus* (hereafter called *Uromys*) is one of Australia's largest rodents (500–890 g) and again is a seasonal breeder with only 2–3 young per litter. It has a relatively long lifespan of up to five years (Moore 1995). Both old endemics are more arboreal than *Rattus*, and *Melomys* is believed to have a more vegetarian diet than the other two (Redhead 1995). We use annual census records to determine the extent of population fluctuations, the effect of changing rainfall patterns, and possible interactions between climate and interspecific competition in shaping the rodent community.

## Methods

### *Study area*

Live-trapping of mammals was carried out on two 1.25-ha grids at Smoko Creek, Kirrama State Forest, Queensland (18°11'S, 145°44'E), within the present Wet Tropics World Heritage Area. This upland rainforest study area (elevation: 610 m) is located toward the western boundary of continuous rainforest in the Cardwell Range. The first grid straddles the creek, and rainforest here is classified as simple mesophyll vine forest (SMVF). The second grid is adjacent to the first, on the hill slopes above the creek where the rainforest grades into simple notophyll vine forest (SNVF: Webb 1959). Both grids have been subjected to disturbance during the study, in particular through selective logging in 1977 when three mature trees were removed, and from a tropical cyclone in 1986 when four mature trees were blown over. Both events increased the amount of debris on the forest floor, including fallen logs, and opened gaps in the canopy. Temporary flooding occurs along Smoko Creek during times of very high rainfall (i.e. the summer wet season, December–April), both washing away and depositing leaf litter. Long-term rainfall records were obtained from the Cardwell weather station on the coast 31 km east south-east of the Smoko Creek study area, and annual rainfall totals were calculated for all years of the study.

### *Live-trapping*

With the exception of 1973, live-trapping was carried out on the study area at least once each year during 1969–97 in the early to middle dry season (April–September). The dry season is the non-reproductive period for each species (Lunney 1995; Moore 1995; Redhead 1995). In 1975, the two adjacent 1.25-ha sampling grids were established. Each had six trap-lines 25 m apart, and each line had five trap sites also spaced 25 m apart. One Elliott trap (10 × 8.5 × 32.5 cm) and one wire cage-trap (21 × 15 × 45 cm) were placed at each of the 60 locations, and each grid was trapped on two consecutive nights. Bait used in the traps consisted of rolled oats, peanut butter and honey. Prior to 1975, the types and numbers of traps used varied, with 50–80 Sherman traps, 9–22 wire cage-traps, and up to 10 Elliott traps used on each occasion. We include census numbers from this period (i.e. 1969, 1971, 1972 and 1974) for illustration purposes, and only when the trapping regime (numbers of traps and sites used) was similar to that used consistently from 1975. We use only data from 1975 onwards for statistical analysis. We analyse the data for each grid separately because the notophyll grid was trapped every year but the mesophyll grid was not (i.e. in 1982, 1983 and 1989), and because numbers were often lower on the notophyll grid. However, because of the close proximity and probable lack of statistical independence between the two grids (i.e. the possibility of catching some of the same animals on each grid), we make no formal comparisons between the two.

### *Handling and marking methods*

Each live-trapped small mammal was weighed, measured, examined, individually marked, sexed and its reproductive status recorded. The smaller rodent species, *Melomys* and *Rattus*, were tagged with numbered monel metal fish fingerling tags using a different number on each ear. We used individually numbered monel metal (fish operculum) ear tags on the the larger *Uromys* from 1969 to 1984. From 1985 to 1995 a small individual number was tattooed onto one or both ears of each *Uromys*. Many ear tags came off between years, but, because at least the puncture holes or tears could be seen, it was always possible to

determine whether the individual had been previously marked. An analysis of the efficacy of the techniques will be presented elsewhere, together with additional demographic information for between-year survival of some individuals (especially *Uromys*).

#### *Data analysis*

Population sizes were summarised for each species on both grids once for each year data were available. All recaptures were excluded and each species was broken into the minimum number of males, females and total individuals 'known to be alive' on the grid. This estimate of population size is conservative and allows a good basis for between-year comparisons (Caughley and Sinclair 1995). We assume that the variation in trapping times between years (April–September) is unimportant because the period covers the dry-season non-reproductive period, and there were no obvious peaks, troughs or trends over any of these months.

Our aims are twofold. First, we describe the nature of the variation of each population over time. We decided to treat males and females separately, as plots of their numbers over time suggested differences in numbers and trends. This has the potential problem of generating too many tests and type 1 statistical error, but, as our aim is primarily exploratory, we consider this risk acceptable and do not make strong conclusions if the number of significant results is only that expected by chance. Second, we explore the possible causes of fluctuating population sizes for each species, including environmental factors and the effects of other species' numbers.

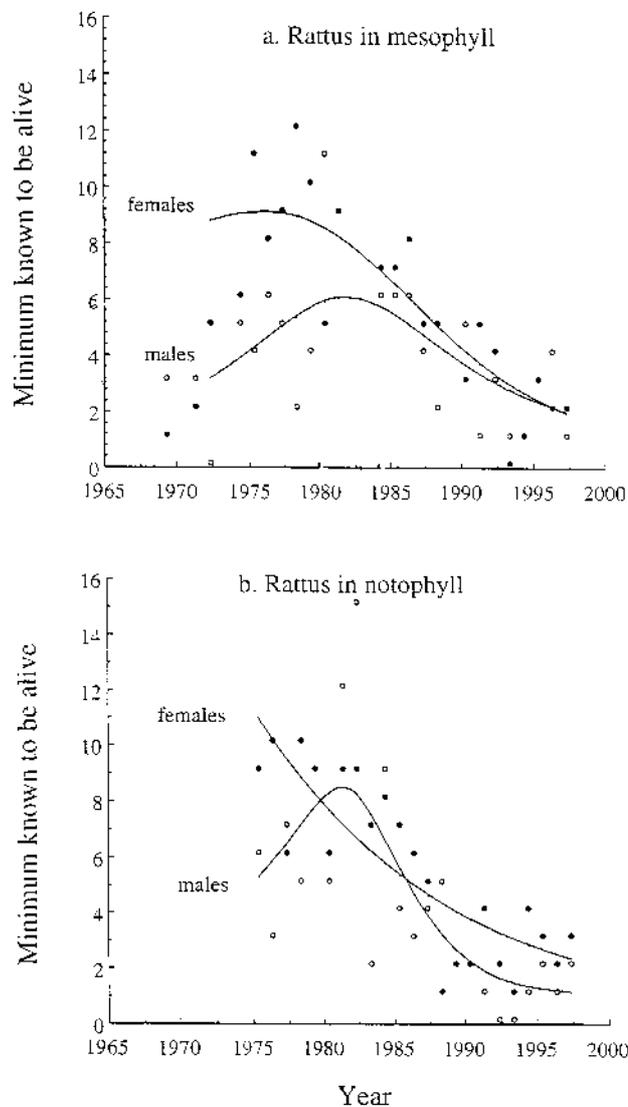
A general problem hampering statistical inference and testing with such time series is the presence of autocorrelation, which will occur in this study in spite of the fact that two of the species have relatively short life-spans that allow their populations to fluctuate quickly. The autocorrelation will arise from community interactions and serial correlation in unmeasured abiotic covariates. We have taken the approach of fitting smoothing splines that describe the relationship between species' numbers and the year of the study. Smoothing splines are complicated functions constructed from segments of cubic polynomials between data points. They have the advantage over ordinary polynomials of being constrained to be smooth at the junctions, and are usually used to investigate the shape of the relationship and to remove 'nuisance' variables (GENSTAT 5 Committee 1993). The smoothing process is effectively nonparametric, and curves of varying complexity are fitted by specifying the degrees of freedom to be used. For example, the smoothing spline with four degrees of freedom has the same effect as fitting a fourth-order polynomial, but does not have the awkward end-effects of the polynomial where the curve tends to bend more sharply than the data would suggest. The most parsimonious splines are found by progressively evaluating the improvement of fit (change in deviance) as the order (degrees of freedom) of the spline is increased. In our case, we use smoothing splines to attain both the most parsimonious description of population numbers over time (Aim 1), and to control for the effect of time so that other variables can be examined (Aim 2) using a statistical modelling approach (GENSTAT 5 Committee 1993). It should be noted that because the data are in the form of counts, all modelling is done on log-transformed data (using the log link function in GENSTAT). The original data are provided in an Appendix.

## **Results**

### *Population and rainfall trends*

All three species showed marked fluctuations on both grids over the study period. *Rattus* was initially caught in very low numbers in 1969 and the early 1970s on the mesophyll grid, but rose dramatically during the late 1970s and early 1980s. The trends over time were best expressed by second-order splines for both males and females ( $\chi^2_2 = 19.9$ ,  $P < 0.001$  and  $\chi^2_2 = 30.9$ ,  $P < 0.001$  respectively; Fig. 1a). Numbers decreased again by the late 1980s and early 1990s to the extent that no females and only one male were caught in 1993. Numbers had risen only slightly by 1997. The notophyll grid showed similar trends, except that we have no indication of numbers in the early 1970s. Trends over time were best expressed by a second-order spline for males and a first-order spline for females ( $\chi^2_2 = 41.4$ ,  $P < 0.001$  and  $\chi^2_2 = 27.6$ ,  $P < 0.001$ ; Fig. 1b).

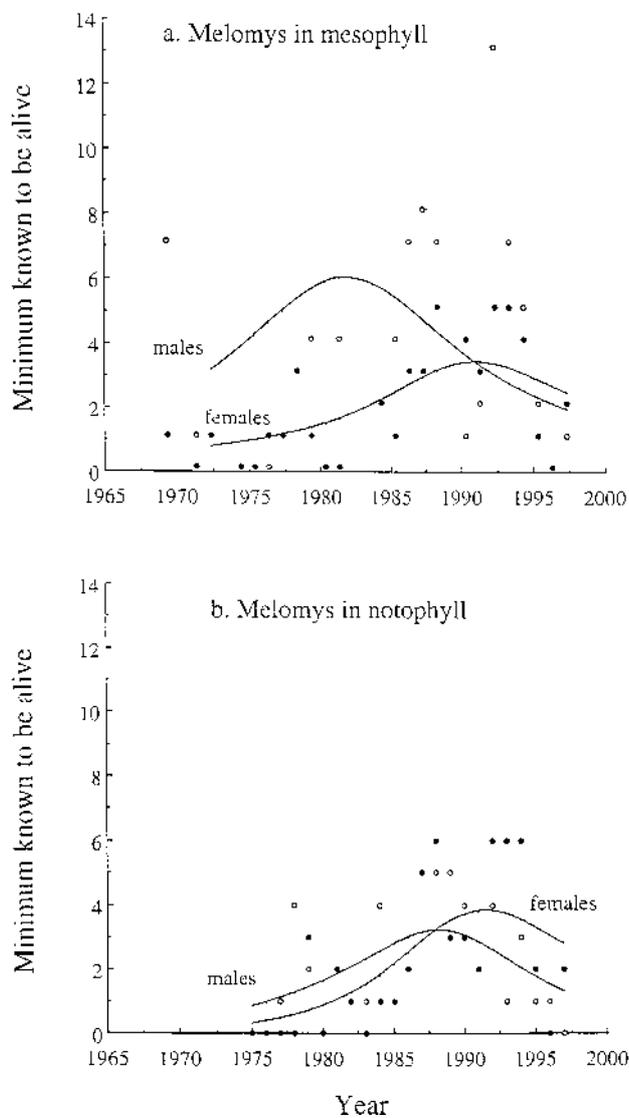
*Melomys* showed different trends. Whereas only a few females were trapped in the early 1970s, numbers increased slowly throughout the 1980s and early 1990s. On the mesophyll grid, data for males and females were best encapsulated by third- and second-order splines respectively ( $\chi^2_3 = 29.4$ ,  $P < 0.001$  and  $\chi^2_2 = 12.9$ ,  $P < 0.005$ ; Fig. 2a). On the notophyll grid, data for males and females were both best encapsulated by second-order splines ( $\chi^2_2 = 12.8$ ,  $P < 0.002$  and  $\chi^2_2 = 25.2$ ,  $P < 0.001$ ; Fig. 2b). However, after 1993 numbers dropped markedly to the extent



**Fig. 1.** Population trends for male (open circles) and female (filled circles) *Rattus fuscipes* on (a) the mesophyll grid and (b) the notophyll grid. Years when males and females had the same value are denoted by a single filled circle.

that no females were caught on either grid in 1996. Two females were again caught on each grid in 1997. Numbers of males fluctuated more widely on the mesophyll grid whereas numbers of females on the two grids were roughly similar.

There are fewer easily detected trends for *Uromys* over the study period, except for a possible increase over the early 1970s and a crash to very low numbers on both grids in 1995 (Fig. 3a, b). Numbers were also generally lower on the notophyll grid where no females were caught in five separate years (1976, 1981, 1991, 1995, and 1996), and no males in three separate years (1983, 1986 and 1996). On the mesophyll grid, we failed to find a significant fit for any spline of first- to fourth-order for either males or females. There was a similar lack of fit for the notophyll grid.



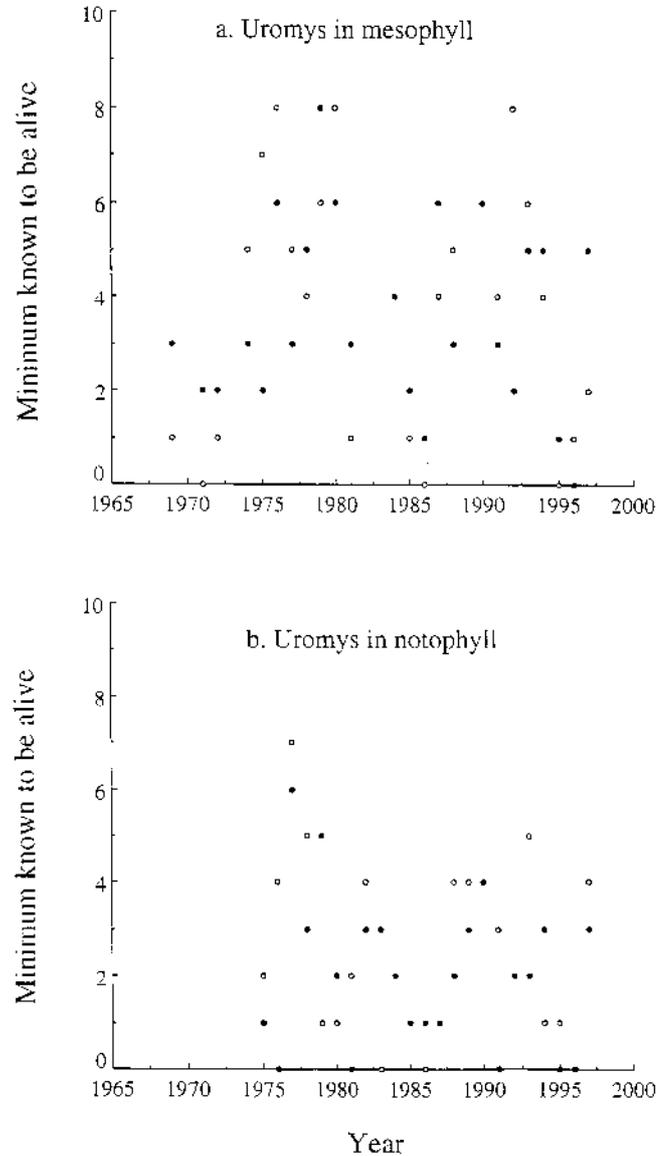
**Fig. 2.** Population trends (splines) for male (open circles) and female (filled circles) *Melomys cervinipes* on (a) the mesophyll grid and (b) the notophyll grid. Years when males and females had the same value are denoted by a single filled circle.

The general lack of fit for male and female *Uromys* on both grids suggests that time lags and autocorrelation are less straight-forward in this species.

The mean annual rainfall over the study period was 2123 mm (s.e. = 116). The wettest year was 1981 with 3650 mm, and the driest was 1986 with 1350 mm. The best fit to the rainfall data over time was a fourth-order spline ( $\chi^2_4 = 929.0$ ,  $P < 0.001$ ; Fig 4). Annual rainfall was generally lower from 1985 onwards.

#### *Initial correlations*

In the mesophyll habitat, numbers of *Rattus* (males, females, and total) were not significantly correlated with rainfall (Spearman-rank correlation,  $0.20 < P < 0.95$ ). In contrast, numbers of



**Fig. 3.** Population trends (splines) for male (open circles) and female (filled circles) *Uromys caudimaculatus* on (a) the mesophyll grid and (b) the notophyll grid. Years when males and females had the same value are denoted by a single filled circle.

both male and female *Melomys* were negatively correlated with total rainfall for the preceding wet season (December–April) ( $r = -0.41$ ,  $P = 0.041$  and  $r = -0.43$ ,  $P = 0.027$ , respectively). Numbers of *Melomys* males were also negatively correlated with total rainfall from the previous year ( $r = -0.44$ ,  $P = 0.026$ ). Further, numbers of *Uromys* males were positively correlated with total rainfall for the previous year ( $r = 0.49$ ,  $P = 0.012$ ). In the notophyll habitat, none of the species' numbers were correlated with rainfall for the preceding wet season, and only *Melomys* females ( $r = -0.41$ ,  $P = 0.040$ ) and *Uromys* males ( $r = 0.45$ ,  $P = 0.025$ ) show significant correlations with rainfall from the previous year

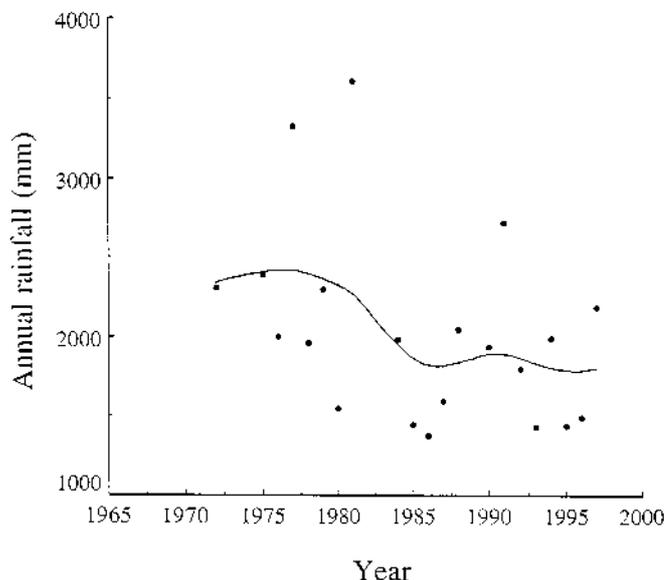


Fig. 4. Total rainfall for each year of the study with fourth-order spline showing trends.

There were no significant correlations between species' numbers on the mesophyll grid, but on the notophyll grid there was a negative relationship between the number of *Melomys* and *Rattus* females ( $r = -0.52$ ,  $P = 0.008$ ).

#### Corrections for year effects

When a modelling approach was adopted in which 'Year' is explicitly controlled for (i.e. retained in the model), none of the species on any grid are dependent on rainfall. This is possibly due to some collinearity between rainfall and year ( $r = 0.33$ ,  $P = 0.099$ ), with rainfall decreasing over the study period (Fig. 4). This suggests that when the effects of one are removed there is insufficient variation left for the other to show a significant effect. Thus it is impossible to state conclusively whether population numbers are truly dependent on rainfall, as was suggested by the initial correlations.

Only two significant effects remain when Year is included in the model. First is a strong dependence of the number of female *Melomys* on the total number of *Rattus* on the mesophyll grid. When number of female *Melomys* is treated as the dependent variable, it is dependent on both Year ( $\chi^2_2 = 12.9$ ,  $P = 0.009$ ) and total number of *Rattus* ( $\chi^2_1 = 5.3$ ,  $P = 0.034$ ). A split-variable plot illustrating the negative relationship between the two species is shown in Fig. 5. In contrast, the number of female *Rattus* is not dependent on the total number of *Melomys* when Year is included in the model ( $\chi^2_1 = 0.1$ ).

Second, male *Rattus* are dependent on the total number of *Melomys* ( $\chi^2_1 = 5.361$ ,  $P = 0.02$ ), although male *Melomys* show no significant relationship with total *Rattus* when Year is included in the model. ( $\chi^2_1 = 1.2$ ). A split-variable plot illustrating the negative relationship between male *Rattus* and total *Melomys* on the mesophyll grid is shown in Fig. 6.

#### Discussion

Fluctuations in both climate and community structure are more likely to be detected over long-term studies (Davis 1986; Pimm 1991). Most studies of small mammals in tropical forests have revealed that populations are susceptible to seasonal changes (e.g. Langham 1983; Happold

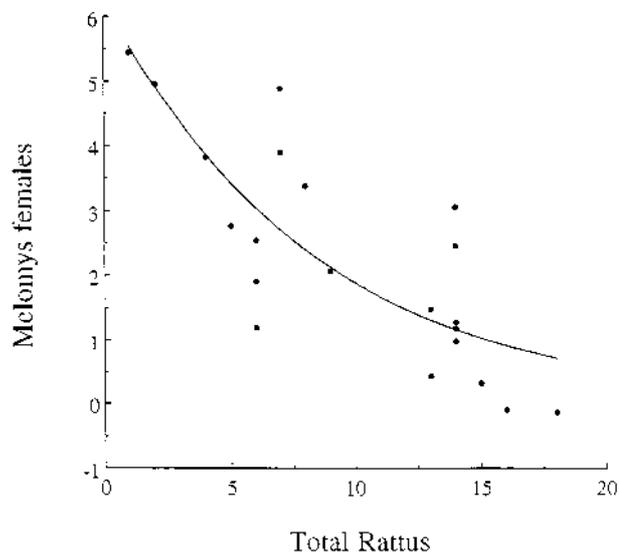


Fig. 5. Split-variable plot showing relationship between the number of female *Melomys* and total number of *Rattus* on the mesophyll grid.

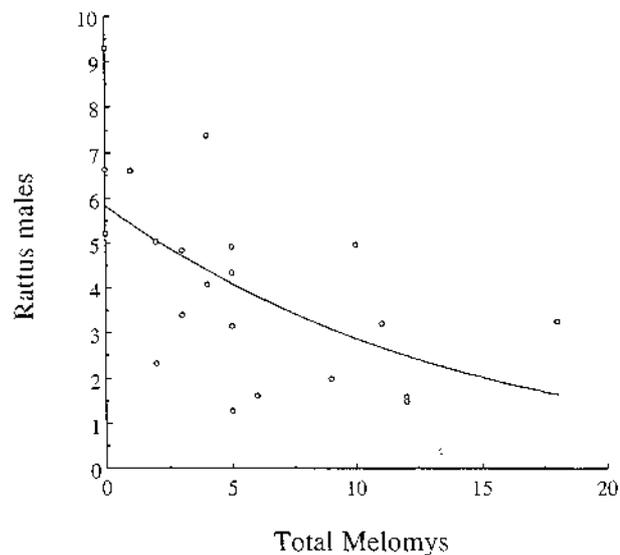


Fig. 6. Split-variable plot showing relationship between the number of male *Rattus* and the total number of *Melomys* on the mesophyll grid.

and Happold 1989; Iyawe 1989; Walker and Rabinowitz 1992), but few have been carried out over long enough periods to detect fluctuations due to long-term weather or habitat change. The long-term nature of this study revealed that marked population fluctuations can occur over the

space of many years. Such fluctuations are contrary to the view that tropical rainforests are marked by stability (e.g. Elton 1958), and support instead the more recent realisation that climatic factors (e.g. drought) can cause periodic reductions in species numbers and diversity even in these environments (e.g. Condit *et al.* 1992). The variation in species composition over time shown in Figs 1–3 also provides a dramatic demonstration of the potential inadequacy of short-term studies. For example, a three-year trapping study carried out at Kirrama in the late 1970s would have yielded a dramatically different picture to one carried out in the early 1990s.

We identified three factors that influence population levels for the three species of rodents. First, both *Rattus* and *Melomys* showed trends over time that were easily described by fitting first-, second- or third-order splines. This suggests autocorrelation or lag effects from one year to the next, i.e. that population levels were not responding independently each year to environmental factors, but were at least partially dependent on numbers from previous years. This result is interesting for both species, but perhaps more so for *Rattus*, which, because of its high rates of reproduction and annual mortality, has the potential for fast increases and decreases that might obscure lag effects. In contrast, there were no discernible trends over time for *Uromys*. This species is larger and longer-lived than the other two and appears to persist in low, relatively stable numbers, although its population numbers did crash in two periods of low rainfall (1985–86 and 1995–96; Figs 3, 4).

Second, the data initially showed that *Melomys* numbers decreased when rainfall was high in both the current and previous years and that *Uromys* numbers increased if the preceding year had been wet. However, these correlations disappeared when the effect of time on population numbers was removed statistically. This may be due to high colinearity between year of study and annual rainfall, with the latter showing an overall decrease with time (Fig. 4), and creates the dilemma of being unable to distinguish between rainfall and other environmental attributes as likely causes of population fluctuations. In the absence of other evidence, we suggest that the marked changes in rainfall observed over this study were probably important.

The best predictor of rodent numbers is often the extent of vegetation cover or foliage (e.g. Abramsky 1981), both of which may relate to rainfall. However, in our study, the fluctuations in population size were sometimes dramatic between years (Figs 1–3). This period is probably too short for plant composition to change markedly, suggesting that rainfall may be a better indicator of food availability (e.g. foliage or invertebrates) or physical change to the environment. For example, that *Uromys* responds positively to high rainfall in preceding years may indicate that these are the best conditions for fruiting trees. It is more difficult to understand why the largely arboreal *Melomys* increases when the present and preceding years were dry. One possibility is that flooding washes away the leaf litter and other debris on the forest floor that they appear to need for terrestrial movements (Wood 1971). This could either lead to a genuine reduction in their numbers, or it may encourage them to stay off the ground. If the latter is true, then *Melomys* numbers may not fluctuate as much as the trapping data indicate.

Third, the negative relationship between numbers of *Rattus* and *Melomys*, once the effects of year have been removed (Figs 5, 6), may simply mean that both species responded differently to some unmeasured environmental variable. It may also suggest that competitive exclusion is a factor determining the composition of the rodent community. Our removal of the year effect is similar to the multiple regression method suggested by Crowell and Pimm (1976), who removed habitat variables statistically to examine the residual effect of one species on another. Abramsky (1981) used this technique to conclude that the negative relationship between two similar rodents on 12 Mediterranean sites was due primarily to habitat variables. It should be noted, however, that this technique has been questioned (e.g. Rosenzweig *et al.* 1985; Abramsky *et al.* 1986; but see Fox and Luo 1996) chiefly because competition coefficients and population variance ratios may be correlated, creating an artificial association between competitive ability and habitat specialisation. However, Pfister (1995) has shown that data that incorporate population change through time, but not habitat variables, may be amenable to this approach. In either case, our study can at best be suggestive owing to the lack of data on other variables (e.g. vegetation and food) to test as causative factors.

If competition does occur the conditions under which one species would exclude the other are not clear, although limited observations of the two species suggest that *Melomys* may be more aggressive both to conspecifics and to *Rattus* (Redhead 1995). Further, the largely arboreal *Melomys* requires a thick layer of leaf litter and debris for its terrestrial movements (Wood 1971), and both grids lose their leaf litter during periods of heavy rainfall. During wet conditions, this may encourage *Melomys* to spend less time on the ground where it interacts aggressively with *Rattus*. Under these conditions, *Rattus*, with its ability for very fast colonisation and reproduction, may occupy these areas. Thus *Melomys*, which presumably colonised the rainforest before *Rattus* in evolutionary time (Yom-Tov 1985; Rich 1991), might drive the system, despite its smaller size and slower rate of reproduction. Although our data do not provide definitive answers they do provide intriguing evidence that the rodent community in the Wet Tropics rainforest is prone to large fluctuations that may be driven by both highly variable rainfall patterns and interspecific competition.

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**Appendix. Minimum known to be alive on each grid for both sexes of each species**

Year	Month	Grid	Male <i>Rattus</i>	Female <i>Rattus</i>	Male <i>Melomys</i>	Female <i>Melomys</i>	Male <i>Uromys</i>	Female <i>Uromys</i>
1997		mesophyll	1	2	1	2	2	5
		notophyll	2	3	0	2	4	3
1996		mesophyll	4	2	0	0	0	1
		notophyll	1	2	1	0	0	0
1995	4	mesophyll	3	3	2	1	0	1
		notophyll	2	3	1	2	1	0
1994	4	mesophyll	1	1	5	4	4	5
		notophyll	1	4	3	6	1	3
1993	7	mesophyll	1	0	7	5	6	5
		notophyll	0	1	1	6	5	2
1992	7	mesophyll	3	4	13	5	8	2
		notophyll	0	2	4	6	2	2
1991	9	mesophyll	1	5	2	3	4	3
		notophyll	1	4	2	2	3	0
1990	9	mesophyll	5	3	1	4	6	6
		notophyll	2	2	4	3	4	4
1989	5	mesophyll	*	*	*	*	*	*
		notophyll	2	2	5	3	4	3
1988	8	mesophyll	2	5	7	5	5	3
		notophyll	5	1	5	6	4	2
1987	9	mesophyll	4	5	8	3	4	6
		notophyll	4	5	5	5	1	1
1986	7	mesophyll	6	8	7	3	0	1
		notophyll	3	6	2	2	0	1
1985	9	mesophyll	6	7	4	1	1	2
		notophyll	4	7	1	1	1	1
1984	9	mesophyll	6	7	2	2	4	4
		notophyll	9	8	4	1	2	2
1983	4	mesophyll	*	*	*	*	*	*
		notophyll	2	7	1	0	0	3
1982	5	mesophyll	*	*	*	*	*	*
		notophyll	15	9	1	1	4	3
1981	8	mesophyll	9	9	4	0	1	3
		notophyll	12	9	2	2	2	0
1980	8	mesophyll	11	5	0	0	8	6
		notophyll	5	6	0	0	1	2
1979	9	mesophyll	4	10	4	1	6	8
		notophyll	9	9	2	3	1	5
1978	7	mesophyll	2	12	3	3	4	5
		notophyll	5	10	4	0	5	3
1977	9	mesophyll	5	9	1	1	5	3
		notophyll	7	6	1	0	7	6
1976	4	mesophyll	6	8	0	1	8	6
		notophyll	3	10	0	0	4	0
1975	7	mesophyll	4	11	0	0	7	2
		notophyll	6	9	0	0	2	1