

## A PRELIMINARY STUDY OF TWO SYMPATRIC *MAXOMYS* RATS IN SARAWAK, MALAYSIA: SPACING PATTERNS AND POPULATION DYNAMICS

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**ABSTRACT.** – An ecological study focusing on the spacing patterns and population dynamics of two sympatric rats, *Maxomys rajah* and *M. whiteheadi*, was conducted using wire-mesh live cage traps over eight years in a primary tropical rain forest in Sarawak, Malaysia. Home range size, observed range length, the distribution of home ranges, and fluctuations in abundance of the two species were quantified. No significant differences were found in home range size or observed range lengths between conspecific sexes or between species. Overlaps of home range were mostly detected between heterospecific individuals, but occasionally between conspecific individuals. Populations of both rats fluctuated widely throughout the study period. The similar-sized home ranges of sexes within species and the significantly broad, overlapping home ranges between species respectively suggest a monogamous mating system in *Maxomys* and a mechanism facilitating interspecific coexistence. Natural disturbances such as severe drought or changes in food availability (like mass fruiting) may influence the population dynamics of these rats.

**KEY WORDS.** – Disturbance, general flowering, home range, mating system, observed range length, tropical forest.

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### INTRODUCTION

Social spacing among rodents is important because it reflects their social structure. It is also important because ground-dwelling mammals play an essential role in forest ecosystems as seed dispersers or seed predators and are therefore critical for forest regeneration and dynamics (Compton et al., 1996; Shanahan & Compton, 2000; Vander Wall et al., 2005). The mating system of rodents, which is difficult to determine directly, is generally reflected in social spacing. Broad overlap of home ranges and larger male than female home ranges suggest a promiscuous mating system (Adler et al., 1997; Endries & Adler, 2005). In monogamous systems, there are no intersexual differences in home range size and reproductive pairs usually share a home range (Kleiman, 1977; Oka, 1992). Intra- and interspecific relationships are

also important determinants of social spacing (Abramsky & Tracy, 1980; Morris, 1999). Competition among rodents may promote segregation in habitat use to avoid competition; the size and overlap of home ranges may vary according to the strength of conspecific and heterospecific competition (Ribble & Sanley, 1998; Perri & Randall, 1999; Maitz & Dickman, 2001). However, most studies of the space use, mating systems, and intra- and interspecific relationships of rodents have been conducted in temperate or neotropical regions; information on the spacing patterns of tropical rodents in Southeast Asia are very limited, despite the high diversity of small mammals (Brown et al., 2001; Saiful et al., 2001; Wells et al., 2004; Nakagawa et al., 2006).

The potential for large fluctuations in abundance is another remarkable ecological trait of rodents. Population dynamics

have been reported for various small mammals including rats, voles, lemmings and squirrels (Gurnell, 1996; Saitoh et al., 1998; Adler et al., 2000; Lambin et al., 2000; Selås et al., 2002). Variation in rodent abundance is associated with food supplies (Wolff, 1996; Schnurr et al., 2002; Selås et al., 2002; Abe et al., 2005), predation pressure (Hanski et al., 1991; Norrdahl, 1995), direct and delayed density-dependence (Stenseth, 1999; Saitoh et al., 2003), and climatic forces (Lima et al., 2001; Murúa et al., 2003). A natural disturbance such as drought could also influence rodent populations. For example, during a drought year, a significant decrease in growth and individual body size following a population decline of brush-tailed phascogales was reported in southwestern Australia (Rhind & Bradley, 2002). However, most studies of population dynamics have been conducted in northern Europe and temperate regions, and the population dynamics of rodents in tropical forests are poorly understood (Wood, 1984; Lee, 1997; Adler, 1998). Although long-term research is necessary to elucidate the patterns and mechanisms of rodent population dynamics, reports by Lee (1997) and Adler (1998) were based on observations made over a few years, and Wood (1984) reported the 10-year population dynamics of a rat in an oil palm plantation.

*Maxomys* rats are often the most common rodents in Southeast Asian tropical forests, from most of the Malay Archipelago to Sulawesi, Borneo and Palawan (Corbet & Hill, 1992). They are generally terrestrial and nocturnal, and consume a wide range of fruits and seeds as well as insects (Langham, 1983; Payne et al., 1985; Kitamura et al., 2006; Suzuki et al., 2007). Their main habitat is primary and secondary forests, although they are occasionally found in rice fields, gardens or tree plantations, especially those adjacent to forests (Stuebing & Gasis, 1989; Corbet & Hill, 1992). However, little is known about the ecological features of *Maxomys* rats (Yasuda et al., 2000) or their spacing patterns and population dynamics, despite their widespread distribution and common existence. Moreover, interspecific relationships among rats have not been studied, although several *Maxomys* species often occur sympatrically (Langham, 1983; Akbar & Ariffin, 1997; Wells et al., 2004). Maitz & Dickman (2001) reported the occurrence of ecological competition between two sympatric and congeneric *Rattus* rats. Competition between coexisting species is often an important determinant of habitat use and population dynamics (Morris, 1999; Perri & Randall, 1999).

The objective of this study was to reveal the major ecological traits of two sympatric *Maxomys* rats based on long-term field observations using wire-mesh live cage traps. We focused on examining the patterns of space use, i.e. the size and overlap of home ranges, and long-term population dynamics of the *Maxomys* rats over eight years. The mating system, interspecific relationships, and possible factors influencing population dynamics are discussed.

## MATERIALS AND METHODS

**Study site.** – The study was conducted at Canopy Biology Plot in Lambir Hills National Park, Sarawak, Malaysia (Fig. 1; 4°2'N, 113°5'E; approximate elevation: 150 m). The plot covers 8 ha (0.08 km<sup>2</sup>; 200 × 400 m) and was established in 1992 for the long-term monitoring of phenology and plant-animal interactions (Inoue & Hamid, 1994). The most common trees are of the family Dipterocarpaceae in the emergent and canopy layers, and of the Euphorbiaceae, Burseraceae and Myristicaceae in the lower layers (Lafrankie et al., 1995). The climate is aseasonal, with a mean annual temperature of ~ 26 °C, mean annual precipitation of ~ 2700mm, and no clear dry season (Ichie et al., 2005).

**Trapping of *Maxomys* rats.** – In the study area, two *Maxomys* species, the brown spiny rat (*M. rajah*) and Whitehead's rat (*M. whiteheadi*), occur sympatrically (Sato, 1999; Nakagawa et al., 2006). These two species were found to be closely related based on a DNA phylogeny (Ruedas & Kirsch, 1997). The brown spiny rat occurs in primary and secondary forests and tends to favour sandy and lowland sites (Payne et al., 1985). Whitehead's rat is smaller than the brown spiny rat and occurs in tall secondary forests (Payne et al., 1985). The average weight of brown spiny rat and Whitehead's rat were 127.1 and 49.9 g, respectively (see Results).

At the center of the Canopy Biology Plot, 48 wire-mesh live cage traps (15 × 12 × 30 cm), baited with banana and sweet potato, and covered with a sheet of transparent plastic

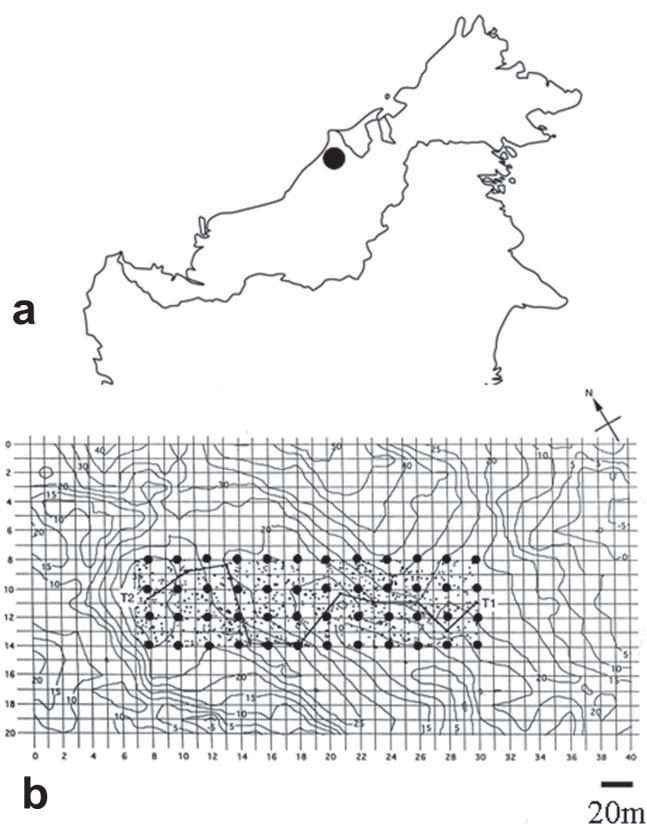


Fig. 1: a) Location of the study area, Lambir Hills National Park, Sarawak, Malaysia (black circle); b) Distribution of wire-mesh live cage traps (black circles) set at the Canopy Biology Plot.

to avoid rainfall, were placed on the ground in a 20 m grid (Fig. 1). The total trapping area was 1.32 ha (0.0132 km<sup>2</sup>; 60 × 220 m) and covered 16.5% of the Canopy Biology Plot. Traps were set for 3–5 consecutive nights at each trapping census, 1–4 times a year from August 1997 to July 2005, except in 2000, for a total of 3245 effective trapnights during the study period. The trapping census was conducted in August and December 1997; January, March, August and September 1998; March and July 1999; May and September 2001; January and March 2002; September 2003; April, July, and November 2004; March and July 2005. We checked all traps once a day in the morning (0700–1100 hours), and all captured rats were toe-clipped for permanent individual identification. After marking and recording the species, sex, weight, reproductive condition and capture point, trapped individuals were immediately released at the site of capture. All procedures met the guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee, 1998). Species identification and nomenclature follow that of Payne et al. (1985).

**Data analysis.** – Home range size was estimated by a minimum convex polygon using the capture points of individuals recaptured at more than 3 points (Mohr, 1947). Because many rats were recorded at only 2 capture points, precluding the calculation of home range size using the minimum convex polygon method, we also determined observed range length (ORL), i.e. the linear distance between the most extreme capture points, for each individual to reinforce the home range size data (Stickel, 1954; Laidlaw et al., 1996). The population dynamics of the 2 *Maxomys* species were calculated as the number of each species captured per 100 effective trapnights, excluding the traps accidentally closed by strong rainfall or fallen twigs. Means of home range size and ORL were compared between sexes and species using Mann-Whitney U-tests. A chi-squared test, using a 2 × 2 contingency table, was used to detect differences in total overlapping home range area within and among species. All statistical analyses were performed using STATISTICA 5.1 (StatSoft, 1995).

## RESULTS

### *Maxomys* rats

In total, 117 *M. rajah* and 58 *M. whiteheadi* were captured during the study period. We captured 64 male and 52 female *M. rajah*; one additional individual escaped before its sex was determined. We captured 22 male and 33 female *M. whiteheadi*; we could not determine the sex of three additional individuals. The average body weight of *M. rajah* and *M. whiteheadi* were 127.1 and 49.9 g, respectively (Table 1).

### Spacing patterns

Of the 117 *M. rajah* and 58 *M. whiteheadi*, 17 *M. rajah* and nine *M. whiteheadi* individuals were recorded at more than three different capture points. The home ranges of the

two *Maxomys* rats covered most of the study plot, although those of *M. whiteheadi* could not be detected after July 1999 because of extremely low densities (Fig. 2).

The average home range size and ORL of all *M. rajah* were 670.6 m<sup>2</sup> (range: 200–1400 m<sup>2</sup>) and 55.0 m (20.0–61.2 m), respectively (Table 1). The mean home range size and ORL of male *M. rajah* were 671.4 m<sup>2</sup> (200–1400 m<sup>2</sup>) and 58.6 m (20.0–134.0 m), respectively; those of female *M. rajah* were 666.7 m<sup>2</sup> (600–800 m<sup>2</sup>) and 49.6 m (20.0–161.2 m), respectively. For all *M. whiteheadi*, home range size was 200 to 1400 m<sup>2</sup>, the average being 644.4 m<sup>2</sup>; the ORL ranged from 20.0 to 181.1 m, with an average of 52.7 m (Table 1). The average home range size and mean ORL of male *M. whiteheadi* were 400 m<sup>2</sup> and 34.9 m (20.0–44.7 m), respectively; those for female *M. whiteheadi* were 675.0 m<sup>2</sup> (200–1400 m<sup>2</sup>) and 57.2 m (20.0–181.1 m), respectively. A Mann-Whitney U-test revealed no significant differences in home range size or ORL between the sexes for either species, or between the two species.

Whereas the home ranges of conspecifics rarely overlap, most home ranges overlapped between *M. rajah* and *M. whiteheadi* from August 1997 to July 1999, when home ranges of both species were detected. During this period, the population density of *M. rajah* and *M. whiteheadi* was 2.3–8.3 and 1.5–9.8 individuals/ha, respectively. The overlapping home range area between the *Maxomys* species was significantly larger than that of overlapping home ranges within species ( $P < 0.001$ ). Within a species, all overlapping home range areas belonged to pairs of different sexes.

## Population dynamics

The populations of both rodents fluctuated widely. We found three peaks in abundance for *M. rajah* and two peaks in abundance for *M. whiteheadi* during the eight years of the study (Fig. 3). Although the two species had similar population densities (*M. rajah*: 0.0–9.63, *M. whiteheadi*: 0.0–8.99 per 100 trapnights), the coefficient of variation (CV) was 0.81 in *M. rajah* and 1.43 in *M. whiteheadi*.

## DISCUSSION

### Home range sizes of *Maxomys* rats

Although the body weight of *M. rajah* is nearly double of that of *M. whiteheadi*, neither the home range size nor the ORL was significantly different between the species. While larger species are thought to have larger home ranges (Don, 1983), our results do not support this hypothesis.

Radiotelemetry, in addition to live trapping, is a common method for studying the home ranges of rodents. Although the live-trapping technique is thought to underestimate home range size (Frank & Heske, 1992; Ribble & Stanley, 1998), overestimation by live trapping and similar results using the two methods have also been reported (Laidlaw et al., 1996;

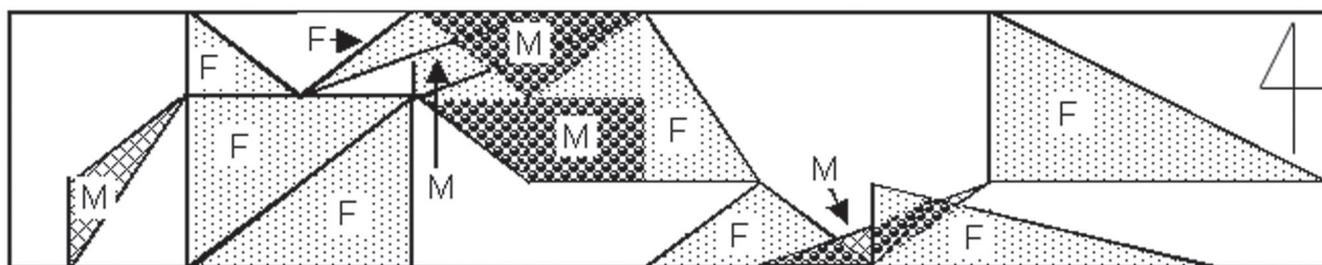
Endries & Adler, 2005). *Maxomys* tend to have smaller home ranges than other rodents of similar weight. *Rattus rattus* in Hawaii and *R. argentiventer* in West Java, whose weight are ~ 125 and ~ 140 g, respectively, have three- to fifty-times larger home range sizes than *M. rajah* (Tobin et al., 1996; Brown et al., 2001). The home range sizes of two *Dipodomys* rats (~ 50 g) are slightly larger than that of *M. whiteheadi* (Perri & Randall, 1999). Although these results were obtained using radiotelemetry, the home range sizes of two *Apodemus* mice and *Microtus agrestis* estimated by live trapping were nearly same as those of *Maxomys* measured here, despite their extremely small size (Erlinge et al., 1990; Oka, 1992). The main factors influencing home range size are population density (Erlinge et al., 1990; Ribble & Stanley, 1998), food supply (Mares et al., 1982) and breeding condition (Oka, 1992; Tew & Macdonald, 1994). Home ranges at high densities are smaller than those at low densities (Erlinge et al., 1990; Ribble & Stanley, 1998), but

the densities measured here were not very high. When the food supply increases, home range size decreases (Mares et al., 1982). The plausible food resources for *Maxomys*, i.e. figs, fruits of shrubs, mushrooms and invertebrates, may be sufficient, and *Maxomys* may not need to forage over a wide area. The massive and abrupt fruit supply caused by general flowering and fruiting events (see below) may also regulate their home range size. However, further research on *Maxomys* is necessary for an in-depth understanding of home range dynamics related to the breeding season or the food supply.

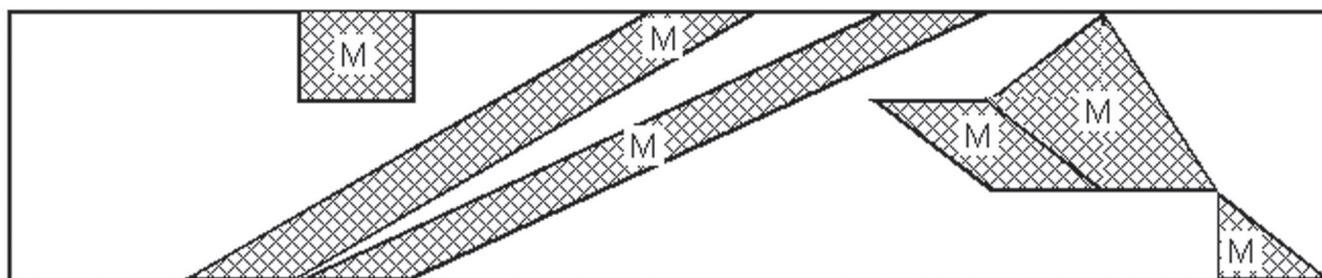
### Interspecific relationships

We detected substantial overlap of home ranges between *M. rajah* and *M. whiteheadi*. Our average home range sizes and population densities results also indicate constant overlap

(a) *M. rajah* and *M. whiteheadi*; August 1997 – July 1999



(b) *M. rajah*; May 2001 – July 2004



(c) *M. rajah*; November 2004 – July 2005

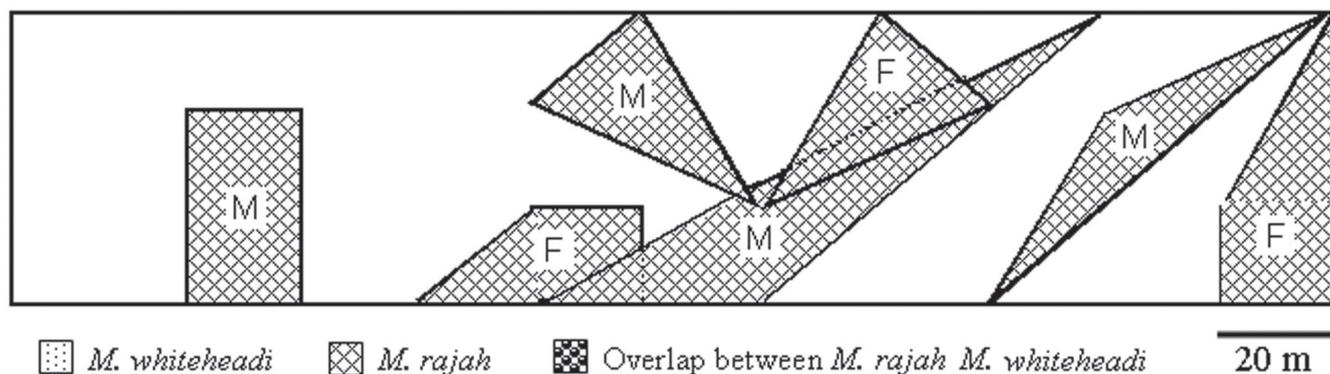


Fig. 2. Distribution of the home ranges of *Maxomys rajah* and *M. whiteheadi* during: a) August 1997–July 1999; b) May 2001–July 2004; and c) November 2004–July 2005. M, male; F, female.

Table 1. Averages and ranges of body weight  $\pm$  SDE (g), observed range length (ORL, m), and home range size (m<sup>2</sup>) of two *Maxomys* rats at Lambir Hills National Park, Sarawak, Malaysia.

Species	Sex	N <sup>1</sup>	Ave. weight $\pm$ SDE (g)	Ave. ORL (range) (m)	Ave. home range (range) (m <sup>2</sup> )
<i>M. rajah</i>	M	19 (14)	141.9 $\pm$ 60.4	58.6 (20.0-134.0)	671.4 (200-1,400)
	F	13 (3)	94.9 $\pm$ 22.1	49.6 (20.0-161.2)	666.7 (600-800)
	Total	32 (17)	127.1 $\pm$ 55.1	55.0 (20.0-161.2)	670.6 (200-1,400)
<i>M. whiteheadi</i>	M	3 (1)	54.3 $\pm$ 17.6	34.9 (20.0-44.7)	400.0
	F	12 (8)	48.8 $\pm$ 14.8	57.2 (20.0-181.1)	675.0 (200-1,400)
	Total	15 (9)	49.9 $\pm$ 14.8	52.7 (20.0-181.1)	644.4 (200-1,400)

<sup>1</sup>Numbers in the parenthesis = individual numbers for the analysis of home range size.

of home ranges between the two *Maxomys* species. Both species are nocturnal and terrestrial, and their diets are almost identical (Payne et al., 1985; Sato, 1999; Wells et al., 2006). Their food requirements, estimated using stable isotopes, are similar (Nakagawa et al., unpublished data). The home range size did not differ between species; hence, the ecological habitat requirements of the two sympatric *Maxomys* seem to be almost identical. However, the body weight of the two species was quite different, with *M. rajah* approximately twice the weight of *M. whiteheadi*. These results indicate that the two *Maxomys* species are likely to interact and that *M. whiteheadi* might be at a disadvantage. Nonetheless, their home ranges sometimes overlapped, suggesting a mechanism facilitating interspecific coexistence. In sympatric and competitive rats, nondominant species give the dominant species access priority to preferred habitats and tolerate temporally restricted access to preferred habitats to avoid encounters (Maitz & Dickman, 2001). A similar relationship might exist between the two *Maxomys* species; *M. whiteheadi* might move in when *M. rajah* is absent. Fine partitioning of active time is another plausible mechanism facilitating coexistence. Pre-dawn and post-dusk activity levels of the rice rat increase with the density of a coexisting rat (Harris et al., 2006). There may also be differentiation in food preferences. Variation in visits to fruit species among coexisting rats occurs in a tropical forest in Thailand (Suzuki et al., 2007).

### Mating system

We found no significant differences in home range size or ORL between males and females of either species, suggesting

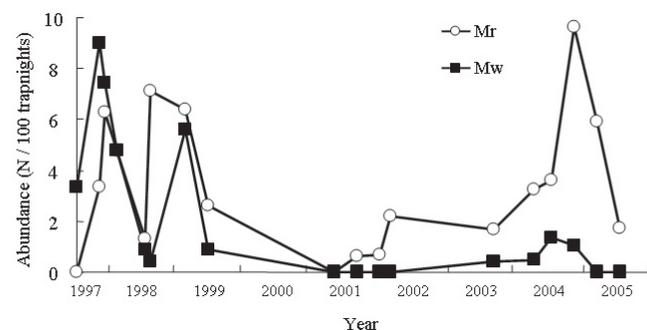


Fig. 3. Population dynamics of *Maxomys rajah* (open circles) and *M. whiteheadi* (black squares) from August 1997 to July 2005 at Lambir hills National Park, Sarawak, Malaysia.

that they have a monogamous mating system. In monogamous mating systems, breeding pairs generally share a home range and guard against conspecific individuals (Kleiman, 1977). Although conspecific *Maxomys* rats in the study population seldom had overlapping home ranges, these overlaps always occurred between individuals of different sexes. *Maxomys* pairs may have individual home ranges, but may share a small portion of their home ranges.

### Factors affecting population dynamics

The populations of the two *Maxomys* species fluctuated throughout the study period. Although the fluctuations were similar between the species, there was less variation in *M. rajah* than in *M. whiteheadi*. This might reflect the relatively constant presence of *M. rajah*, even during the low-density period. One possible factor affecting rat abundance is fluctuation in food availability. In the study plot, fruit production largely varied in supra-annual and irregular cycles at the community level, known as general flowering and fruiting (Sakai, 2002). General fruiting occurred in 1997, 1998, 2001, 2004 and 2005, with large fluctuations in fruiting intensity (Sakai et al., 2006; Nakagawa, unpublished data). *Maxomys* populations seemed to increase after general flowering and then decreased. However, a population increase was not always detected. In 2001, we found no evidence of a population increase, although this may have been due to sampling frequency. In the case of general flowering and fruiting in 2004, the population of *M. rajah* increased, whereas the *M. whiteheadi* population barely changed, indicating the existence of complicated mechanisms controlling population dynamics.

In early 1998, an extremely severe drought associated with the strong El Niño event of 1997–1998 occurred in the study area, and tree mortality was significantly higher than during the non-drought period (Nakagawa et al., 2000; Potts, 2003). Phenological changes in figs and local extinction of pollinators also resulted from this drought (Harrison, 2000, 2001). Such a severe drought might affect the population dynamics of rodents. Indeed, the population of *M. whiteheadi* surpassed or equaled that of *M. rajah* before the drought (until March 1998), whereas *M. rajah* was always more abundant than *M. whiteheadi* after the drought. After the drought, many small trees and shrubs in the study area

withered (Delissio & Primack, 2003), possibly causing a serious decline in food availability. Although the mechanism of drought-induced population decline is still unclear, food shortages may cause a reduction in growth and size of young individuals through poor maternal nutrition or an increase in predation due to a lack of ground cover (Fisher et al., 2001; Rhind & Bradley, 2002).

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