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Population Ecology of the Southeast Asian House Mouse (Muridae: *Mus musculus castaneus*) Inhabiting Rice Granaries in Taiwan

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Shu-Yu Wu, Yu-Teh K. Lin, and Hon-Tsen Yu (2006) Population ecology of the Southeast Asian house mouse (Muridae: *Mus musculus castaneus*) inhabiting rice granaries in Taiwan. *Zoological Studies* **45**(4): 467-474. We studied the population ecology of a house mouse subspecies, *Mus musculus castaneus*, in northeastern Taiwan. Populations living in rice granaries offer a unique opportunity to understand the house mice in a commensal habitat. Environments in rice granaries fluctuate both spatially and temporally in terms of food and habitat availability, and mortality risk, due to the pulsed removal of rice sacks and the practice of poisoning. The results indicated that the pulsed removal of rice sacks in individual rooms did not noticeably reduce the size of the house mouse population in granary 1, whereas the total removal of rice sacks from granary 2 severely altered the habitat and precipitated a sharp decline in the mouse population size. In contrast, poisoning considerably altered population structures. The age structure changed from ones with a high proportion of young animals to a clearly inverted triangular structure, indicating a strong effect of poisoning on recruitment of the young. However, poisoning did not change the sex ratio, nor disrupt breeding activities of breeders. Continuous breeding activities throughout the year and rapid reproductive rates apparently have allowed *M. m. castaneus* to successfully persist in rice granaries. We also discuss the body growth patterns and spatial distribution patterns of the house mouse in granaries. http://zoolstud.sinica.edu.tw/Journals/45.4/467.pdf

Key words: *Mus musculus castaneus*, Commensal habitats, Rice granary, Population structure, Poisoning.

The house mouse (*Mus musculus castaneus*) is a commensal rodent closely associated with human activities. In Taiwan, they exclusively inhabit granaries in rice-producing townships in the lowlands (Chou et al. 1998), and are an important pest species. Feral populations are extremely rare and sporadic. Thus, rice granaries represent the natural habitat of the house mouse in Taiwan. The subspecies occurring in Taiwan is one of 4 subspecies under the rubric of *M. musculus* (see Boursot et al. 1996). *Mus m. musculus* occurs in eastern Europe, and its range spans the Eurasian continent to the north of the Yangtze River in China. *Mus m. domesticus* occurs in western Europe and the Mediterranean region and eastward into Iran and Afghanistan; its range abuts that of *M. m. musculus* in central Europe where a hybrid zone between the 2 subspecies exists (Sage et al. 1993). *Mus m. domesticus* has expanded its range to every continent, including America, Africa, and Australia, due to human maritime activities over the last 500 yrs. *Mus m. bactrianus* is distributed in central Asia and the Indian subcontinent where *M. musculus* supposedly originated (Boursot et al. 1996, Din et al. 1996). The last entity, *M. m. castaneus*, occurs in Southeast Asia, southern China, and Taiwan. An additional subspecies *M. m. molossinus* in Japan was shown to be a hybrid between *M. m. musculus* and *M. m. castaneus* (Yonekawa et al. 1994).

House mice in general have been a model and motor for ecological and evolutionary under-

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standing from early Darwinian days (Berry and Scriven 2005). They are renowned for their opportunistic and sturdy adaptability to variable environments (Berry and Jakobson 1975, Newsome et al. 1976, Bronson 1979 1984, Berry 1981a). However, the subspecies, *M. m. castaneus*, unlike *M. m. musculus* and *M. m. domesticus*, has been much less studied (Guo et al. 1994, Hong et al. 1992). Yu and Peng (2002) investigated the effects of historical human settlement on the genetic differentiation of *M. m. castaneus* on a regional scale. Little is known about the demographic responses of this unique subspecies to environmental factors (but see Chou et al. 1998), much less the physiological and behavioral mechanisms that mediate those responses. The natural habitat, i.e., rice granaries, of *M. m. castaneus* are unstable and experience frequent disturbances such as grain removal and poisoning. Thus, studies on the population responses of *M. m. castaneus* to such events should provide insights into population evolution and management of the species. In this study, we employed capture-recapture procedures to investigate the population ecology of *M. m. castaneus* inhabiting rice granaries in northeastern Taiwan.

MATERIALS AND METHODS

Study areas

The study was conducted in 2 granaries located in Ilan City and Chiao-Shi Township, ca. 10 km from each other in Ilan County, northeastern Taiwan. The granary in Ilan City (granary 1, hereafter) is a concrete building divided into 8 storage rooms (Fig. 1), each of which is 30 m long, 12 m wide, and 10 m high. Grain was stored in plastic sacks stacked up in six of the 8 rooms (Fig. 1). Crevices among the sacks made perfect nesting habitats for the mice. The empty rooms remained empty throughout the sampling period. The granary in Chiao-Shi Township (granary 2, hereafter) was similar but smaller (6 rooms, 27.6 m long, 10.8 m wide, and 7 m high each). Grains were stored in all 6 rooms, but we were only allowed to trap mice in two of the 6 rooms.

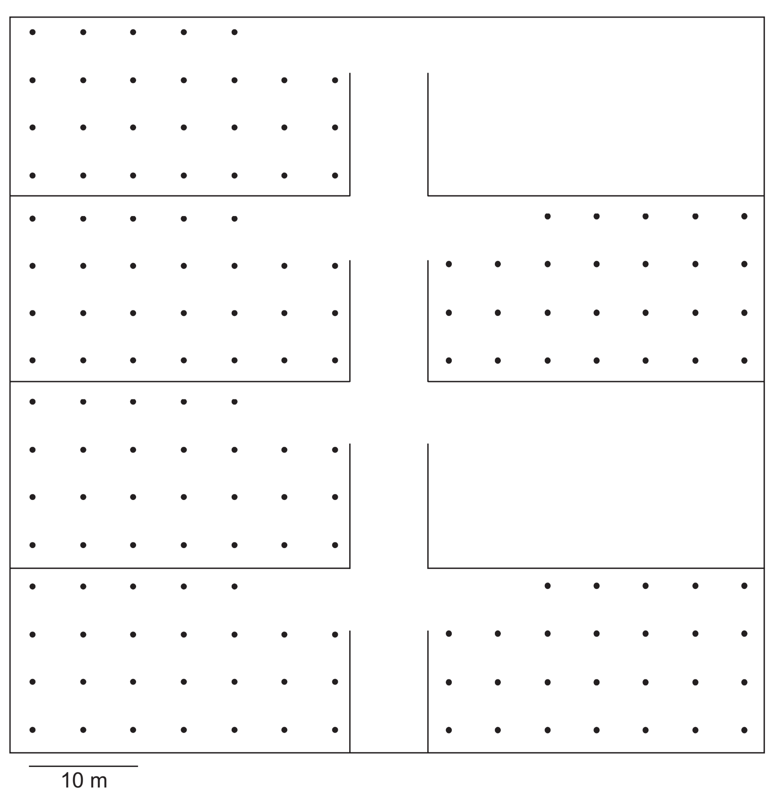

Fig. 1. Layout of granary 1 (in Ilan City). Each room is 30 m long, 12 m wide, and 10 m high. Grain was stored in 6 of the 8 rooms. Granary 2 (in Chiao-Shi Township) is similar but smaller (6 rooms each 27.6 m long, 10.8 m wide and 7 m high). The dots in each room indicate trapping stations.

Trapping protocol

A mark-recapture program was continued for 13 mo, from July 1999 through July 2000, except in Sept. 1999, when a devastating earthquake prevented us from sampling granary 2. Trapping was carried out for 2 nights in granary 1 and 1 or 2 nights in granary 2 every month. During this period, 26 Sherman live traps were set on a 4 by 7 grid in each room (6 rooms storing grains at the beginning of the study in granary 1, and 2 rooms in granary 2) (Fig. 1). The traps were laid on the top of the grain sacks. In several rooms, grain sacks were removed during different months (Fig. 2), after which the rooms remained empty until the end of the study. One room was emptied approximately every 3 mo in granary 1, and all rooms were emptied in early Mar. in granary 2. Trapping continued even when the grain sacks had been removed.

In an attempt to collect tissues from all individuals for genetic analysis (Wu 2001), we trapped for 9 nights in granary 1 and 3 nights in granary 2 on the very 1st trapping session in July 1999. Traps were baited with rolled oats mixed with peanut butter. Each mouse was marked by toe-clipping upon the 1st capture. The clipped toes were stored in 95% ethanol. Sex, weight, reproductive status, and location on a grid were recorded at each capture. All mice captured were released at the exact spot of capture afterwards.

A rodent control program was enforced in early Aug. 1999 (Fig. 2) at both granaries. A single dispenser of liquid poison was placed in each room and left without being refilled. The liquid poison remained until Oct., when the poison was either consumed or had evaporated.

Trappability and population size

We calculated the maximum trappability since there were few recaptured animals (Krebs and Boonstra 1984). We used a direct enumeration method (Slade and Blair 2000) to estimate population sizes. Since the mouse population in granary 2 was trapped for 1 or 2 nights every month, we only used the trapping record from the 1st night for the population size estimation of granary 2. Similarly, although we trapped for 9 nights during the 1st trapping session in July 1999, we only used the trapping record from the first 2 nights for population size enumeration of granary 1. Furthermore, the capture number per night (for the respective instances of 9 and 3 trapping nights) did not show a declining trend, rendering it impossible to estimate the population size by extrapolation. All trapping records were used in the analyses of sex ratio, age structure, and spatial distribution.

Reproductive status and age structure

The reproductive status was determined for each mouse when captured. A female was considered to be in a breeding condition if it was pregnant (detected by palpation) and/or lactating (with swollen nipples). A male was considered to be in a breeding condition when its testes had descended into the scrotum.

We assigned each mouse to one of 3 age classes based on body weight (BW): age class 1 (BW < 9 g), age class 2 (9 g ≤ BW < 12 g), and age class 3 (BW ≥ 12 g), according to (Chou et al. 1998). Individuals with BWs of ≥ 15 g were included in age class 3, since we captured a few heavy mice and some among those were pregnant females.

To analyze temporal variations in the sex ratio, age structure, and spatial distribution patterns, we arbitrarily divided the sample into 6 time periods largely according to sample sizes. For

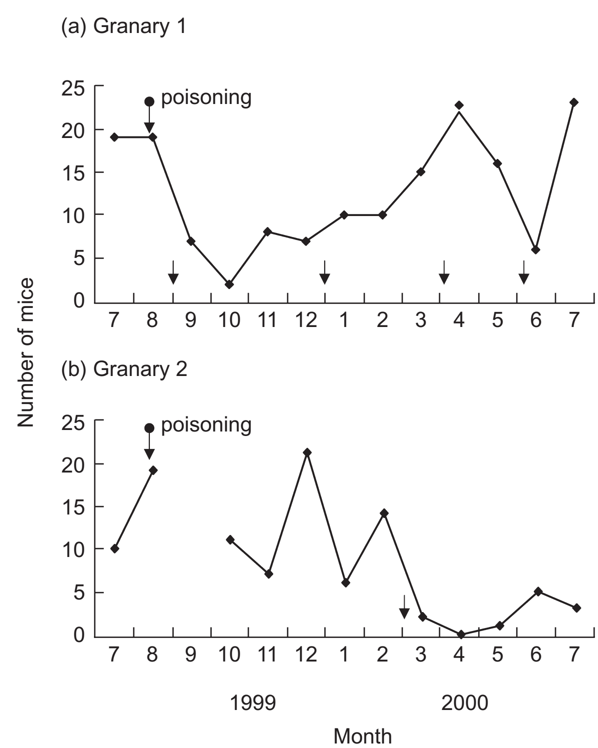

Fig. 2. Numbers of house mice caught during each trapping session in granaries 1 (based on 2 nights) and 2 (based on 1 night). Arrows on the x-axis indicate the time of grain removal, and the filled arrow indicates when poisoning treatment began.

granary 1, the 6 periods were (1) July 1999, (2) Aug. 1999, (3) Sept.-Dec. 1999, (4) Jan.-Feb. 2000, (5) Mar.-May 2000, and (6) June-July 2000. For granary 2, the 6 periods were (1) July 1999, (2) Aug. 1999, (3) Oct.-Nov. 1999, (4) Dec. 1999, (5) Jan.-Feb. 2000, and (6) Mar.-July 2000.

Spatial distribution

The spatial distribution patterns of house mice within the granaries were examined by comparing the number of mice captured in traps laid along the edge of the wall (peripheral traps) and those away from the wall (interior traps). Since the numbers of peripheral traps and interior traps differed (16: 10; see Fig. 1), we adjusted the expected values accordingly when performing the Chi-square test.

RESULTS

Recapture rate and trappability

In granary 1, 110 males and 112 females were trapped a total of 248 times during 13 mo of sampling. Only 10.8% of all individuals (24/222) were caught more than once. In granary 2, 71 males and 61 females were trapped a total of 174 times during 7 mo of sampling. Only 25.8% (34/132) of mice were caught more than once. Among the total multiple captures of 58 mice, 1 was caught 4 times, 8 were caught 3 times, and the rest were caught twice. The maximum trappability values (Krebs and Boonstra 1984) were 40.5% and 60.4% for granaries 1 and 2, respectively.

All of the time during the study, the traps were far from saturated. We used 26 traps in each room; however, on average, we caught fewer than 3 mice per night in any given room in granary 1 (6 rooms), and fewer than 11 mice per night in granary 2 (2 rooms).

Population size

Temporal variations in population size were examined by direct enumeration (Fig. 2). We caught 94 and 47 different individuals during the 1st trapping session (with 9 and 3 d of trapping) in granaries 1 and 2, respectively. The mouse population in granary 1 plummeted to single digits within a month after the poisoning treatment began (early Aug. 1999). However, the population immediately rebounded, and grew steadily until the following spring (Fig. 2a). The population size increased 10-fold between Oct. 1999 and Apr. 2000.

The mouse population in granary 2 demonstrated a different trend. It was not clear, however, if the population size crashed after the poisoning because a devastating earthquake prevented us from sampling in Sept. 1999 (Fig. 2b). The population sizes in granaries 1 and 2 are not directly comparable because population estimates for granary 2 were based on 1 instead of 2 nights of trapping. Nevertheless, the temporal dynamics based on 1 night of trapping in granary 1 closely resemble those based on 2 nights of trapping. The population size estimated based on 2 nights of trapping was about 1.7 times (164 total animals for all months) of that based on 1 night (94 total animals for all months) of trapping. Yet the population size of granary 2 sharply declined after Feb. 2000 when the grain sacks in all 6 rooms (including the 2 rooms in which we were allowed to trap) had been completely removed (Fig. 2b), thus devastating the habitat.

Sex ratio, age structure, and reproduction

The sex ratios significantly deviated from 1 in only 1 case (Jan.-Feb. 2000 in granary 2; Table 1). The age structure changed after the poisoning treatment began (Fig. 3a, b). The proportion of adults (in age classes 2 and 3) increased after poisoning (Aug. 1999), from 61% ± 14% during July-Aug. to 87% ± 6% during Oct.-Dec., turning into an inverted triangle. The strongly inverted triangular age structure was evident until Feb. in both granaries.

Females entered a breeding condition only in age classes 2 and 3, and none of the age class 1 females was found to be either pregnant or lactating. In contrast, the majority of males in age class 1 had already entered sexual maturity (Fig. 3a, b). In addition, breeding activities were continuous throughout the year for both sexes.

Growth in body weight

Growth patterns of mice are evident from the change in body weight for mice caught more than once during the study (Fig. 4). Two situations may have confounded the estimates: (1) pregnancy in females might have accelerated growth; and (2) the intervals between recaptures were so long that the growth had reached an asymptote. After eliminating both situations from the analysis, we calculated a body growth rate of 0.92 ± 0.40 g/mo for males (n = 7, mean ± SD), and 0.83 ± 0.60 g/mo for females (n = 8). Moreover, adult females (BW ≥ 9 g, including age classes 2 and 3) grew slightly more slowly than young females (BW < 9 g, i.e., age class 1): adults grew at 0.5 ± 0.41 g/mo while the young grew at 0.96 ± 0.55 g/mo. Growth rate in males did not differ with age. The mean body weight of all males at 1st capture was 12.04 ± 2.82 g (n = 62) and that of all females was 14.35 ± 2.91 g (n = 98).

Spatial distribution

We examined the spatial distributions of mice in granary 1. The probability that a trap would catch a mouse was not random. Overall, a greater proportion of mice than expected was caught along the walls (82%), and a smaller proportion of mice than expected was caught away from the walls (18%; χ^2 = 40.40, p < 0.0001). Both males (χ^2 = 15.65, p < 0.0001) and females (χ^2 = 25.28, p < 0.0001) showed similar trends.

DISCUSSION

Most studies on the population ecology of the house mouse were conducted on feral (e.g., Singleton et al. 2005) or enclosed populations (e.g., Drickmer and Brown 1998). Our study is a rare case that focuses on populations living in rice granaries, i.e., the natural habitats of the house mouse in Taiwan, and offers a unique opportunity to understand the ecology of the house mouse, particularly for the less-studied subspecies, *M. m. castaneus*.

Low trappability has been observed in numerous studies of house mouse populations inhabiting natural and semi-natural habitats (see Krebs et al.

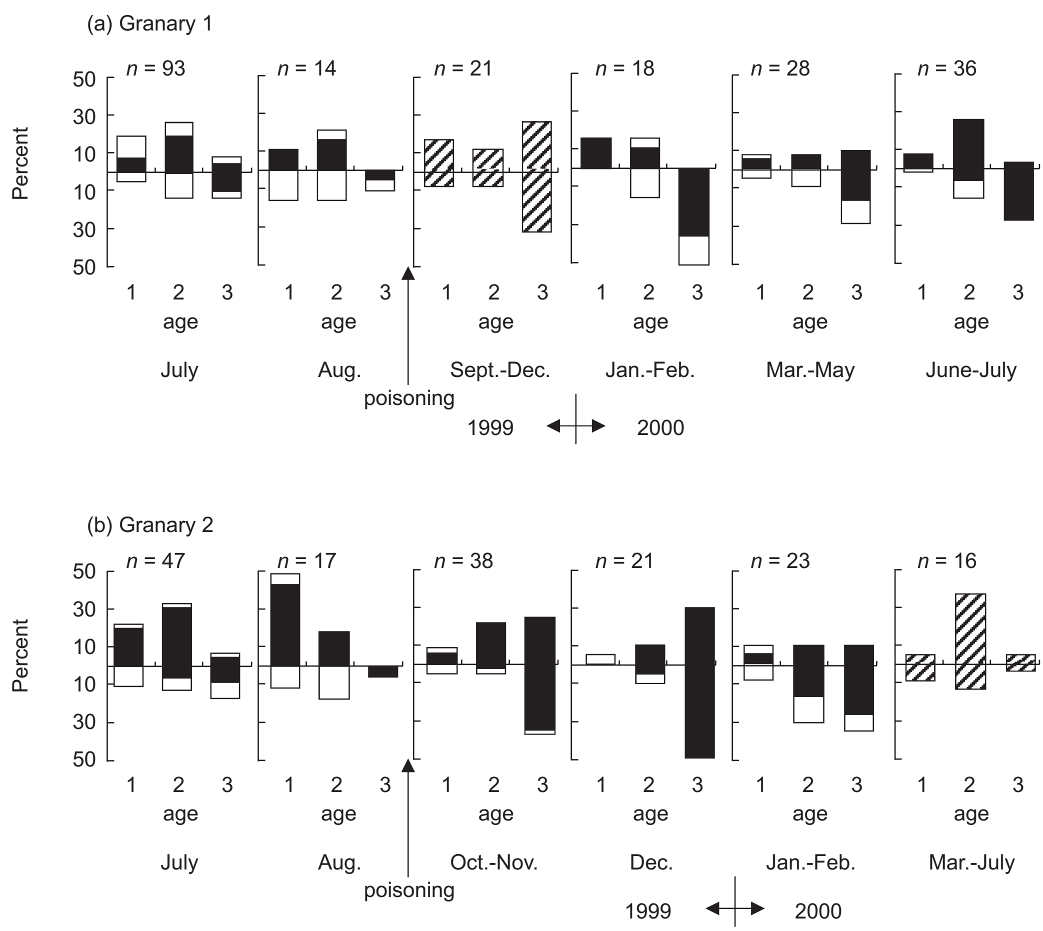

Fig. 3. The proportion of each age group (age groups 1, 2, and 3, see main text for explanation) in each gender category. The proportions of males and females are given above and below the horizontal line, respectively. The black filling within the bars indicates the proportion of individuals in a reproductive condition. The hatched-line filling within the bars indicates missing data on the reproductive condition.

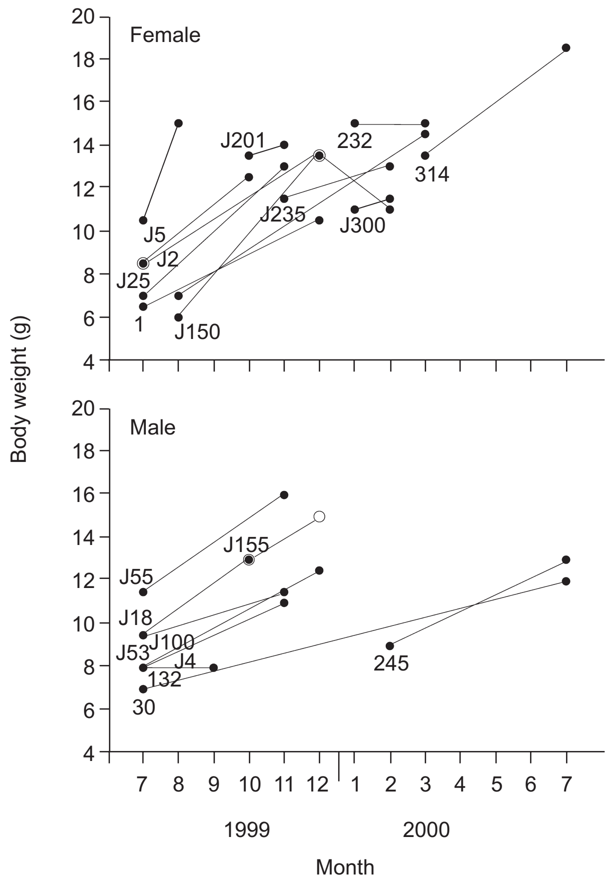

Fig. 4. Changes in body weights for female and male house mice. The numbers are individual identifiers. Open circles were used for J2 and J155 to differentiate the overlapping data points.

1994 for a review) and commensal habitats (Pocock et al. 2004). Similarly, the trappability of the 2 populations in our study was relatively low. Only 10.8% and 25.8% of mice in granaries 1 and 2, respectively, were caught more than once. Low trappability may have resulted from the frequent disturbances that are inherent on modern agricultural lands and in anthropogenic structures (Chambers et al. 2000). In our case, the periodic removal of grain and the practice of mouse poisoning were major disturbances that imposed strong environmental stresses and caused major losses (mortality and/or emigration) and low trappability. Another possible cause of low trappability would be the social interactions of mice, since the tendency of a mouse to enter a trap might be influenced by the odor left from a mouse caught previously in the same trap (Sokolov et al. 1984, Drickamer 1997, Drickamer and Brown 1998). We did not clean the traps after each capture. However, we collected and cleaned the traps, when a trapping session was over. Moreover, the traps were re-laid randomly between trapping sessions. This practice reduced the effects of individual odors.

With an abundant food supply and the protection afforded by a concrete structure, the mouse population should remain relatively stable throughout the year as suggested by the continuous breeding activity. However, the populations fluctuated 10 fold in both granaries over the year. The decline in population size in granary 1 during fall

Table 1. Sex ratios of house mouse populations. *p* Values are for χ^2 tests against a 1: 1 sex ratio

Month	Sample size	Sex ratio (male: female)	*p* Value
Ilan city			
July 1999	93	1.45: 1	0.08
Aug. 1999	14	0.75: 1	0.59
Sept.-Dec. 1999	21	0.91: 1	0.83
Jan.-Feb. 2000	19	0.46: 1	0.11
Mar.-May 2000	28	0.56: 1	0.13
June-July 2000	36	0.8: 1	0.50
Chiao-Shi Township			
July 1999	47	1.47: 1	0.19
Aug. 1999	17	1.83: 1	0.23
Oct.-Nov. 1999	38	1.11: 1	0.75
Dec. 1999	21	0.75: 1	0.51
Jan.-Feb. 2000	23	0.35: 1	0.02
Mar.-July 2000	16	1.67: 1	0.35

1999 was clearly a result of poisoning. The liquid poison was present from Aug. to Oct., which corresponded with population lows during the late fall. Nevertheless, the mouse population immediately rebounded, and grew 10 fold from Oct. 1999 to Apr. 2000. The dip in June 2000 was probably due to chance since the population size was high in July. The removal of grains in granary 1 did not seem to affect population sizes, although intensive interactions between residents in intact rooms and immigrants from emptied rooms must have existed in this granary. Because social interactions can be a major force driving the dynamics of small mammals (e.g., Krebs 1979 1996, Heske 1987), the complex behavioral processes associated with social disbandment, dispersal, and colonization are aspects of house mouse ecology that warrant further studies.

On the other hand, fluctuations in population sizes demonstrated in granary 2 drastically differed from those in granary 1. Since the 2 granaries were only 10 km apart, and were situated in similar commensal surroundings, conditions outside the granaries, e.g., weather, should have had minimal effects on the 2 populations. The schedule of grain removal seemed to be the only discrepancy between the 2 granaries that could have contributed to the different dynamic patterns. In contrast to the pulsed removal of grains in granary 1, the removal of grains in granary 2 occurred only once in Feb. 2000, during which all rooms in the granary were emptied. Not surprisingly, the mouse population plummeted, and remained low until the end of the study. Although poisoning was also carried out during Aug.-Oct. 1999, it was not clear if poisoning had any effect on the population size since if a crash occurred, the population recovered quickly.

Regardless of disturbances imposed by poisoning and grain removal, the sex ratio of the *Mus* populations remained close to 1: 1. The sex ratio is thought to reflect an animal's ability to respond to natural selection. An equal sex ratio is favored in polygynous species when resources are plentiful (Wright et al. 1988). Our observations of the sex ratio of house mouse populations inhabiting rice granaries support Wright's hypothesis. In contrast, the age structure seemed to be considerably affected by poisoning. The age structures in both granaries before the poisoning treatment began were biased toward younger age groups, whereas older age groups became dominant after poisoning began. Because the population, at least in granary 1, was growing after poisoning, we expected an age structure dominated by young age groups. However, a reverse trend was observed, and remained so until the following spring, suggesting that the poisoning event disproportionately targeted the youngest age class. Since poisoning did not disrupt breeding activities, it seems that poisoning prevented births and/or hindered the survival of young mice.

House mice are opportunistic breeders, and can breed continuously under commensal situations (Bronson 1989, Bronson and Heideman 1994). As expected, mice in both granaries appeared capable of breeding year-round. Most mice in breeding condition were in age class 2 or 3 (BW ≥ 9 g). However, a large proportion of male mice in age class 1 (BW < 9 g) were also in a breeding condition. This implies that the house mouse becomes sexually mature and participates in breeding activities at a young age, particularly for males.

The average monthly body growth rates of males and females were 0.92 and 0.83 g/mo, respectively. The data offer an opportunity to estimate the time required to advance from 1 age class to the next. The increment in body weight between 2 age classes was 3 g, which implies 3.3 (males) and 3.6 mo (females) were required to advance from 1 age class to the next. We could not determine the age of the youngest age class since the growth rate of body weight from neonates to 9 g is unknown. Nonetheless, the typical house mouse reproductive schedule is known: they mature at 4-6 wk of age with a 19-21 d gestation period, and a 21 d lactation period (Berry 1981b). Using the growth rate as an indicator of generation turnover, we estimated that it would take about 6 mo for a mouse to grow from age class 1 to age class 3. A 3 mo generation time seems typical for the house mouse (Berry 1981b).

In summary, the house mouse (*Mus musculus castaneus*) inhabiting rice granaries appeared to show adaptations to the opportunities and demands of this commensal environment, which offers both benefits (stable weather conditions and rich food resources) and costs (poisoning). The living environment, however, fluctuated both spatially and temporally due to the pulsed removal of grain sacks and the practice of poisoning. Although both types of disturbances affected the size and structure of the house mouse populations, the continuous breeding activity and rapid reproductive rates apparently allow *M. m. castaneus* to persist successfully in rice granaries.

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