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A Population Study of House Mice (*Mus musculus castaneus*) Inhabiting Rice Granaries in Taiwan

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Chih-Wen Chou, Pei-Fen Lee, Kao-Hong Lu and Hon-Tsen Yu (1998) A population study of house mice (*Mus musculus castaneus*) inhabiting rice granaries in Taiwan. *Zoological Studies* **37**(3): 201-212. Samples of house mice (*Mus musculus castaneus*) were collected from rice granaries in 5 townships in Taiwan to study the population biology of the species, including population dynamics, reproductive biology, sex ratio, and age structures. The population sizes among granaries were highly variable and this is assumed to result from changes of rice storage. House mice can breed year round, as expected by the species commensal habits. Two methods for age determination, i.e., tooth wear patterns and body weight criteria, were established and compared. Age structure of the populations seemed to have remained stable as a result of continuous breeding activities. Sex ratio of the populations were 1:1, but fewer males were represented among old mice than among young mice. Finally, we report on high rates of tapeworm infection and missing teeth in these mouse populations.

Key words: Age structure, Tooth wear, Population size, Sex ratio, Tapeworm.

Laboratory mice, derived from a few individuals of wild house mice (*Mus musculus domesticus* and *M. m. musculus*), have long served as model animals for many disciplines of biological studies (Festing and Lovell 1981, Morse 1981, Sage et al. 1993, Silver 1995). However, it is of ultimate importance to remember that wild populations of the species still harbor a vast amount of genetic variability that is not included in their laboratory counterparts. The phenotypic manifestation of this genetic variability can potentially offer biologists even more avenues to resolve questions being studied. It is therefore imperative to study wild populations of house mice to explore the full range of their biology.

Systematics of the house mouse is still an unresolved debate (Marshall 1981, Boursot et al. 1993, Sage et al. 1993); however, the general consensus is that there are 4 major entities (treated as either species or subspecies by various authors) under the rubric of *Mus musculus*, according to their geographical ranges. *M. m. musculus* occurs in eastern Europe, and its range spans the Eurasian continent to the north of the Yangtze River in China. *M. 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 exists between them (Sage et al. 1993). *M. m. domesticus* has expanded its range to other areas of the world due to human maritime activities during the last 500 years. *M. 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. The last 2 subspecies, unlike *M. m. musculus* and *M. m. domesticus*, have been much less studied. An additional subspecies *M. m. molossinus* in Japan has been shown to be a hybrid between *M. m. musculus* and *M. m. castaneus* (Yonekawa et al. 1988).

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Understanding age determination, age-related phenomena, sex ratio, reproduction, genetic variability, etc., is essential for studies of natural populations of an organism. A large body of such information is available for wild house mice (*M. m. domesticus*) in Europe (e.g., Berry 1981a, Pelikan 1981, Nachman et al. 1994), North America (e.g., Breakey 1963, Lidicker 1966 1976, DeLong 1967, Petras 1967, Selander 1970, Petras and Tooping 1981), the Pacific (Berry et al. 1981), and Australia (e.g., Newsome 1969, Singleton 1983 1989). In addition, some comprehensive information on the biology of the wild mice is available in *Biology of the House Mouse* (Berry 1981b), *The Wild Mouse in Immunology* (Potter et al. 1986), *Genetics in Wild Mice* (Moriwaki et al. 1994), and a chapter on wild mice (Sage 1981) in *The Mouse in Biomedical Research* (Foster et al. 1981). While some of the information can no doubt be extrapolated to Taiwanese house mice (*M. m. castaneus*), certain peculiar characteristics of this local subspecies surely remains to be discovered, for house mice are renowned for their opportunistic adaptability to variable environments (Berry and Jakobson 1975, Bronson 1979 1984, Berry 1981a). Furthermore, the subspecies *M. m. castaneus* represents a unique genetic entity, but until now we know very little about it. There is a current need to further explore the biology of this subspecies.

In this paper, we aim to gather information on the population biology of Taiwanese house mice (*M. m. castaneus*). First, we report on variation in population size among rice granaries. Second, we establish and contrast 2 methods for age determination, i.e., body weight criterion and tooth wear criterion. Third, we present data on the reproduction and demography of several geographic populations. Finally, we note high rates of tapeworm infection and missing teeth in these populations.

MATERIALS AND METHODS

Mouse populations and sampling methods

In Taiwan the occurrence of feral house mice in the wild is rare (Hseun et al. 1978), and most house mice are found in dwellings, outbuildings, and rice granaries. Rice is the major staple food crop in Taiwan, and therefore almost every township in the rice-producing lowlands has its own centralized rice granaries. In most cases, rice grains are stored in plastic sacks and are piled up in the granaries. Most of the granaries have been rebuilt as concrete buildings in the last 2 decades, leaving only a few old brick granaries with wooden beams and shingle roofs.

From June 1995 through February 1996, we collected a large number of house mice from rice granaries in 12 townships (Chou 1996) to embark on a study of the population genetic of the species in Taiwan. In 4 particular townships, we trapped as many mice as we could in a period of 9 consecutive days to investigate the age structure and features of the reproductive biology of the respective mouse populations. These townships are: (1) Shijou, (2) Tsztung, (3) Linnei, and (4) Ershuei. The 4 townships are located close together on a flood plain west of the central mountain ranges of the island (Fig. 1). Two granaries in each township were sampled. In each granary, we deployed 25 foldable Sherman traps (either 5.1 × 6.4 × 22.9 or 7.6 × 9.5 × 30.5 cm) baited with peanut butter and oats. Traps were checked every morning and re-baited whenever necessary. In Tsztung and Ershuei townships, trapping was discontinued after 4 days since the numbers of captures were very

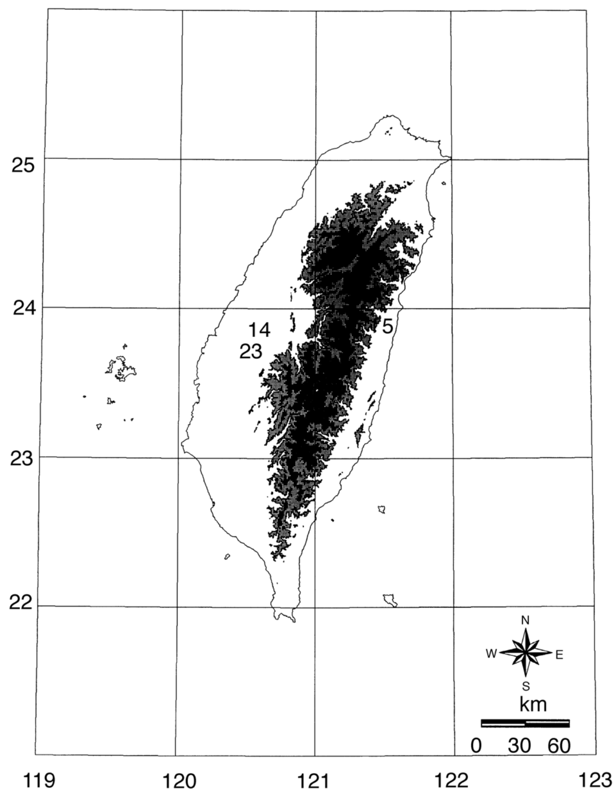

Fig. 1. Map of Taiwan showing townships where house mice were collected. 1. Shijou, 2. Tsztung, 3. Linnei, 4. Ershuei, and 5. Shoufeng. Light gray areas, 1000-2000 m; dark gray areas, 2000-3000 m; dark areas, above 3000 m elevation.

low (also see Results). The mice caught were kept alive in cages until the end of the trapping session and were brought back to the lab for further processing. We also collected a large sample of mice from a 5th township (Shoufeng; Fig. 1) in eastern Taiwan.

Autopsy and specimen preparation

When the mice were sacrificed the following measurements were taken at autopsy: body weight (BW), head and body length (HB), tail length (TL), hind foot length (HF), and ear length (Ear). Standard stuffed study-skin or flat-skin specimens were prepared as vouchers. Tissue samples of heart, liver, spleen, kidney, and muscle were placed in cryogenic tubes for storage in liquid nitrogen tanks.

To determine reproductive status, the following items were recorded: for males, position of testes (scrotal or not), the length and width of 1 testis, the length of the seminal vesicle, and the visibility of tubules in the caudal epididymis (being visible indicates sperm storage); for females, perforation of the vagina, swollen teats and a naked ring around the nipple (indicating lactation), and the condition of the uteri. Marshall (1981) categorized the uteri into 4 stages according to their appearance: thread, string, cord, and embryo. The mice of the thread and string stages are treated as sexually immature and those of the cord and embryo stages as mature. Embryos were counted to estimate litter sizes.

To prepare the skeleton specimens, the eviscerated carcasses were left to dry underneath a light bulb and cleaned by a colony of dermestid beetles (*Dermestes maculatus*) in an aquarium (60 $\times$ 30 $\times$ 45 cm) at room temperature. Cleaned skeletons were then left in 5% ammonia water for 3-4 days, transferred to liquid detergent for another 3-4 days, followed by several brief changes of distilled water, and were air-dried. For each individual, catalog numbers were written in permanent ink on the skull, mandible, and a few parts in the post-cranial skeleton.

After a few autopsies, we noticed a high incidence of tapeworms (*Hymenolepis nana*) in the digestive tracts of the mice, normally 1 worm in each mouse that was infected. Although no special efforts were made to search for the worm, we routinely recorded its presence whenever observed.

Sexual dimorphism

Sexual dimorphisms in body weight and size were examined by Student *t*-test (Sokal and Rohlf 1981). Three measurements were chosen to represent the size of the mice: head and body length (HB), condylo-incisive length (CIL), and mandibular length (m3). The last 2 measurements were chosen because they have the highest loadings in a principal component analysis (PCA) of a series of cranial measurements, thereby being good indicators of skull size in the house mouse (Chou 1996).

Age determination

Two methods were employed to estimate the age of the mice, by body weight (BW) and by tooth wear (TW) pattern.

Body weight

Since a sample of house mice can comprise more than 1 cohort (age class), the frequency distribution of body weights in the sample is usually complicated by the representation of different cohorts, thereby creating a polymodal distribution. Consequently, the underlying modes in a body weight distribution are determined as different age classes, and cut-off points are chosen by looking for the inflection points on probability plots of body weight. See Cassie (1954) and Harding (1949) for examples of this method in detail and Yu (1993) for its application in studies of small mammals. The PPLOT procedure in the PC-version of SYSTAT (1990) was used to generate probability plots of body weight.

Tooth wear pattern

Chewing food causes continual attrition of the molars of the house mouse, so that the degree of tooth wear can be assumed to be proportional to age (Morris 1972). Skulls of mice were examined under a dissecting microscope and qualitative features on dental eruption and wear patterns of occlusal surface of upper molars were used in determining age classes.

Discriminant function analysis

In order to cross-examine the reliability of the age criteria by the 2 age-determining methods, we took 17 cranial measurements to employ in discriminant function analyses (DFA) using the respective age classes as *a priori* groupings. The analyses offer an opportunity to determine if the age classes indeed fall into natural groups correlated with cranial dimensions The cranial measurements include (see Fig. 2A in Chou 1996): (1)

condylo-incisive length (CIL); (2) length of diastema (LD); (3) length of maxillary molars (LM); (4) length of 1 incisive foramen (LIF); (5) breadth across incisive foramen (BIF); (6) breadth of incisor tips (BIT); (7) breadth of palatal bridge (BPB); (8) length of orbital fossa (LOF); (9) breadth of nasals (BN); (10) least interorbital breadth (LIB); (11) zygomatic breadth (ZB); (12) breadth of braincase (BB); (13) breadth of zygomatic plate (BZP); (14) breadth of 1st maxillary molar (BM1); (15) depth of incisor (DI); (16) breadth across exoccipital condyles (BOC); (17) length of auditory bulla (LAB). Definition and illustrations of the measurements are also given by Carleton and Musser (1995), Voss (1988), and Voss et al. (1990). The analyses were done with SAS programs (SAS Inst. Inc. 1990) on a Pentium personal computer.

Age structure and seasonal variation of reproduction

Age structures were constructed based on BW age classes for samples from each granary. Since we sampled the 4 western townships in the summer (August 1995) and a single eastern township (Shoufeng) in the winter (February 1996), we can compare reproductive intensity in the 2 seasons. Nonetheless, it is noteworthy that the results of this comparison could be confounded by spatial variation since seasonal samples were not collected from the same locations.

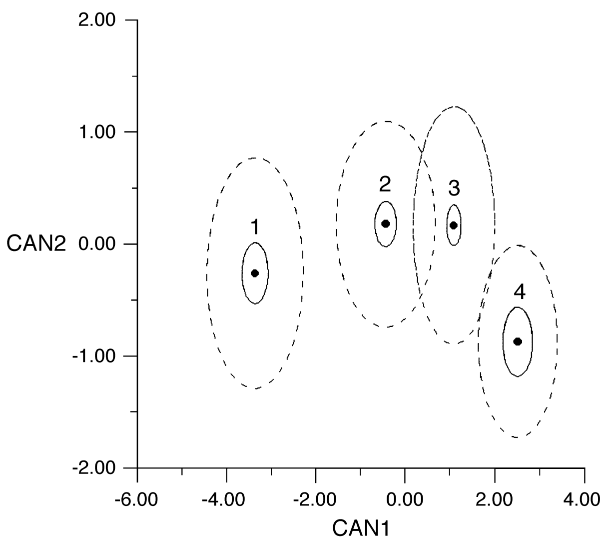

Fig. 2. Plots of the first 2 canonical variables in the discriminant function analysis using 17 skull measurements. Numbers indicate the *a priori* age groupings by body weight. Dots show the centroids of each age class with ellipses of standard deviation (broken line) and 95% confidence interval (solid line). The variables most closely associated with the first 2 canonical variables are CIL, DI, BZP, BIT, ZB, LAB, BOC, and LIB.

RESULTS

Trapping results

Trapping records show that population sizes of house mice can vary a great deal in different granaries (also see Appendix 2 in Chou 1996). In Shijou township, 2 granaries (nos. 7 and 8) were trapped and yielded captures of 112 and 115 mice (50 mice/100 trap nights and 52 mice/100 trap nights), respectively. Furthermore, the daily capture (ranging from 9 to 15) for the 9 consecutive days did not decline as one would expect, implying that there were large numbers of mice yet to be trapped. Trapping in 2 granaries (nos. 3 and 9) from Linnei township yielded a total of 108 mice (37 mice/100 trap nights and 11 mice/100 trap nights from each granary). In sharp contrast, only 8 mice were caught in Ershuei township (4 mice/100 trap nights) and 1 mouse in Tsztung township (0.5 mice/100 trap nights), resulting from 4 days of trapping. In addition, daily captures in the last 2 townships never exceeded 2 mice. A different trapping regime was used in Shoufeng (20 Sherman traps in 1 granary for 2 days) and 35 mice (88 mice/100 trap nights) were caught. As a result, 379 mice were captured from the 5 townships. These mice were used for various studies (Chou 1996) and only 269 mice from 3 townships (Shijou, Linnei, and Shoufeng) were included in the study of reproduction and demography.

Sexual dimorphism

Females exceed males in both body weight and size (Table 1). Two sets of tests were performed: first, mice of each TW age were tested separately; second, all age groups combined were tested. Although young animals do not differ between the 2 sexes, mice of older age groups are significantly different (detailed results are available in Chou 1996). To provide general trends, only results of all ages are presented.

Age determination

Body weight (BW) age

Probability plots were first created separately by sex; however, the results do not differ substantially despite the sexual dimorphism. Data for both sexes are analyzed together; 3 inflection points and thus 4 modes in the distribution (age classes) were found: BW age 1 (< 9 g); BW age 2 (≥ 9 and < 12 g); BW age 3 (≥ 12 and < 15 g); and BW age 4 (≥ 15 g).

Fig. 2 visually displays the first 2 canonical variables of DFA using 17 cranial measurements among the 4 BW age classes. All age classes appear to form distinct natural groups of their own; none of the centroids or their ellipses of 95% confidence interval overlap. The ellipses of standard deviation show the degree of dispersion of the 2 canonical values, and they indicate some overlap between BW ages 2 and 3, a slight overlap between BW ages 3 and 4, and no overlap between BW ages 1 and 2. Furthermore, pairwise comparisons of Mahalanobis' distances between age classes indicate that all distances differ significantly from 0 (Table 2).

Table 1. Comparison of body weight (BW), head and body length (HB), condylo-incisive length (CIL), and mandibular length (m3) between 2 sexes of *Mus musculus castaneus* in Taiwan

Variable	Sex	N^a	Mean	SD	*t*-value
BW (g)	F	156	12.12	2.97	2.73**
	M	144	11.23	2.63	
HB (mm)	F	156	73.96	7.31	3.65***
	M	144	71.08	6.36	
CIL (mm)	F	155	18.99	1.11	4.88***
	M	145	18.40	1.00	
m3 (mm)	F	156	10.52	0.62	5.60***
	M	144	10.17	0.48	

[a] Including samples collected all over Taiwan, see Chou (1996).
**$p < 0.01$, ***$p < 0.001$.

Tooth wear (TW) age

Six age classes can be distinguished by the dental eruption and wear pattern as follows (Fig. 3):

TW age 1: M^3 incompletely erupted and unworn.

TW age 2: M^3 fully erupted and slightly worn, but occlusal surface not flat, still tubercular; M^1 and M^2 with little wear on occlusal surface.

TW age 3: M^3 well worn and occlusal surface flat or concave; M^1 protocone and paracone fused, and anterolingual and anterolabial conules fused; M^2 protocone and paracone, and hypocone and metacone fused.

TW age 4: M^3 flat or concave; M^1 occlusal

Table 2. Mahalanobis' distance matrix among 4 age classes by body weight. Distances are calculated based on 17 skull measurements. Statistics (MANOVA) are used to test the null hypothesis that distances between pairs of age classes are equal to 0

Age class	2	3	4
1	3.00***	4.48***	5.94***
2		1.60***	3.15***
3			1.80***

***$p < 0.001$.

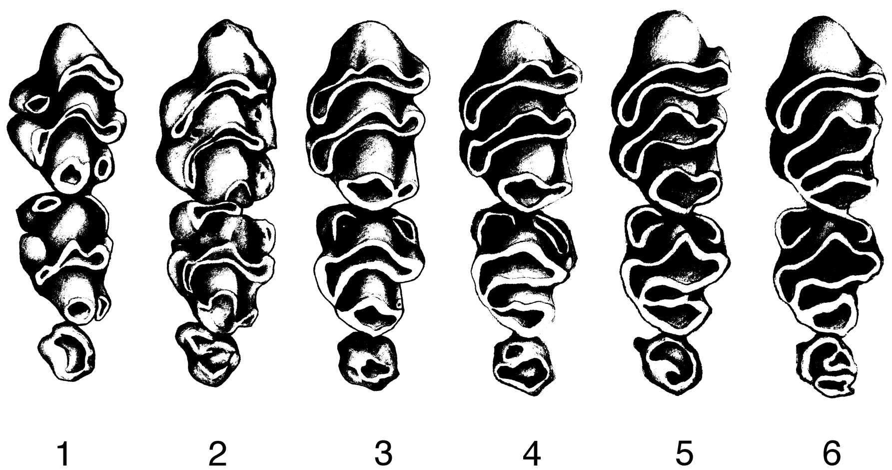

Fig. 3. Tooth wear patterns of upper left molars indicating 6 age classes in *Mus musculus castaneus*.

surface well worn, and hypocone and metacone becoming fused; M^2 anterolingual and anterolabial conules much reduced.

TW age 5: M^3 flat or concave; all cusps of M^1 further reduced; M^2 protocone-paracone and hypocone-metacone connections complete, and anteroloph and anteroconule much reduced.

TW age 6: M^3 concave; M^1 protocone-paracone and hypocone-metacone becoming connected; all cusps of M^2 much reduced.

Fig. 4 illustrates the plots of the first 2 canonical variables of DFA using 17 cranial measurements among the 6 TW age classes. Although the centroids and the 95% confidence ellipses of all 6 TW age classes do not overlap, the ellipses of standard deviation show various degrees of overlap among TW ages 2, 3, 4, and 5. Comparisons of Mahalanobis' distances between TW age classes (Table 3) indicate that the distance between the following pairs are not different from 0: TW ages 3 and 6, TW ages 4 and 5, TW ages 4 and 6, and TW ages 5 and 6. However, the power of the statistical test between TW ages 3 and 6 is hindered by the small sample size of TW age 6. In summary, TW age classes also provide a good means to determine the age in house mice except in TW ages 4, 5, and 6. The last 3 TW age classes probably represent a single age group.

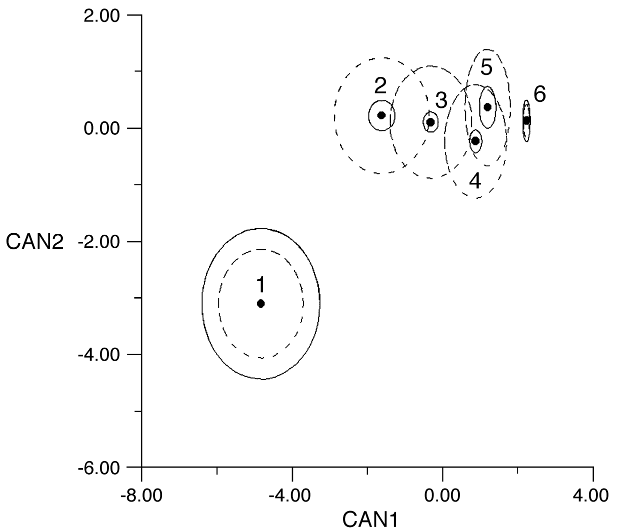

Fig. 4. Plots of the first 2 canonical variables in the discriminant function analysis using 17 skull measurements. Numbers indicate the *a priori* age groupings by tooth wear criteria. Dots show the centroids of each age class with ellipses of standard deviation (broken line) and 95% confidence interval (solid line). The variables most closely associated with the first 2 canonical variables are CIL, DI, BZP, BIT, BL, LIB, LAB, and BOC.

Comparison between the 2 methods

To further compare the results of the 2 age-determining methods, we analyzed each TW age class by plotting its BW age-class distribution frequency (Fig. 5). A heterogeneity *G*-test (Sokal and Rohlf 1981) shows that frequencies among the 6 TW age classes are different ($G_{adj.} = 54.60$, $d.f. = 15$, $p < 0.001$). In addition, the frequencies of TW age classes are compared in a pairwise fashion, except those with small cell samples (TW ages 1, 5, and 6; Fig. 5). The results indicate that TW ages 2, 3, and 4 are different from one another in BW age frequencies: between TW ages 2 and 3 ($G_{adj.} = 19.52$, $d.f. = 3$, $p < 0.001$); between TW ages 2 and 4 ($G_{adj.} = 72.02$, $d.f. = 3$, $p < 0.001$); and between TW ages 3 and 4 ($G_{adj.} = 32.72$, $d.f. = 3$, $p < 0.001$). TW age 1 includes only mice of BW age 1, but the frequencies of TW ages 5 and 6 do not seem to be different from TW age 4 (Fig. 5). The results corroborate the conclusion of the multivariate analysis that there are 4 main age classes.

Demography and reproduction

We analyzed the age structures and reproduction of the mouse populations based on the BW age criterion. Here populations are defined as the mice inhabiting a single granary in any township. Therefore, we present data for 5 populations: 2 from Shijou township (Fig. 6), 2 from Linnei township (Fig. 7), and 1 from Shoufeng township (Fig. 8).

Shijou township

Mouse populations in the 2 granaries have rather similar age structures for both sexes (Fig. 6). The 2 populations are dominated by mice of BW

Table 3. Mahalanobis' distance matrix among 6 age classes by tooth wear pattern. Distances are calculated based on 17 skull measurements. Statistics(MANOVA) are used to test the null hypothesis the distances between pairs of age classes are equal to 0

Age class	2	3	4	5	6
1	4.89**	5.74***	6.61***	7.03***	8.08⁻
2		1.45***	2.55***	2.90***	4.49*
3			1.32***	1.70***	3.53 ns
4				1.00 ns	2.82 ns
5					2.53 ns

* $p < 0.05$,** $p < 0.01$,*** $p < 0.001$,ns $p > 0.05$, - not tested due to small sample size.

age classes 2 and 3, comprising 70% or more of the populations. The youngest (BW age 1) and the oldest mice (BW age 4) comprise the remainder (less than 30%) of the populations.

The majority of males were in breeding condition (86% in granary no. 7, and 66% in granary no. 8, respectively, Fig. 6). In contrast, only 3 females were pregnant from the 2 granaries (Fig. 6), although more than half of the females were sexually mature (65% in granary number 7 and 51% in granary number 8).

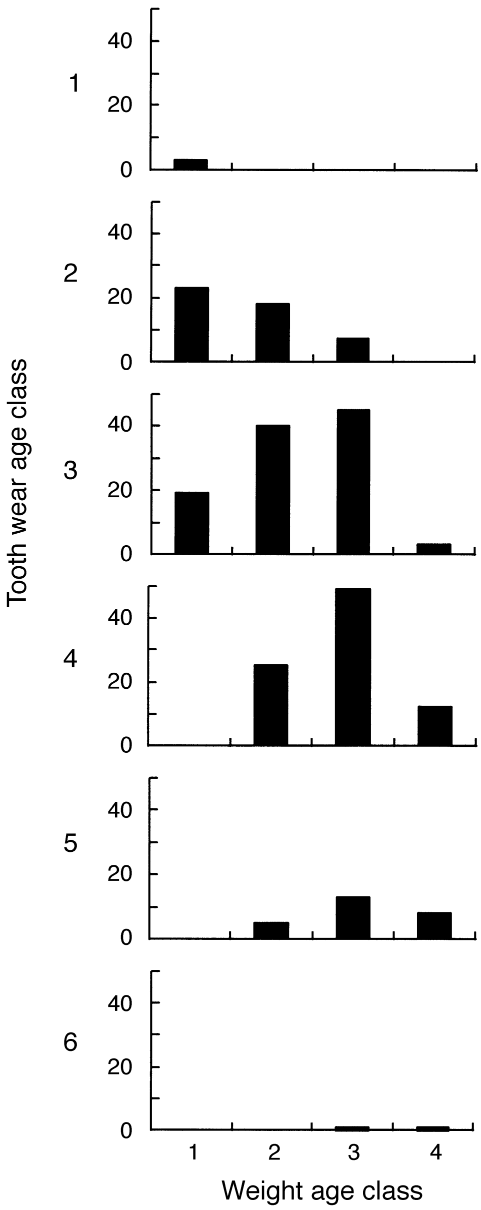

Fig. 5. Distributions of tooth wear age classes against body weight age in *Mus musculus castaneus*.

Linnei township

Age structures in the 2 granaries are different from each other (Fig. 7). Similar to those in Shijou

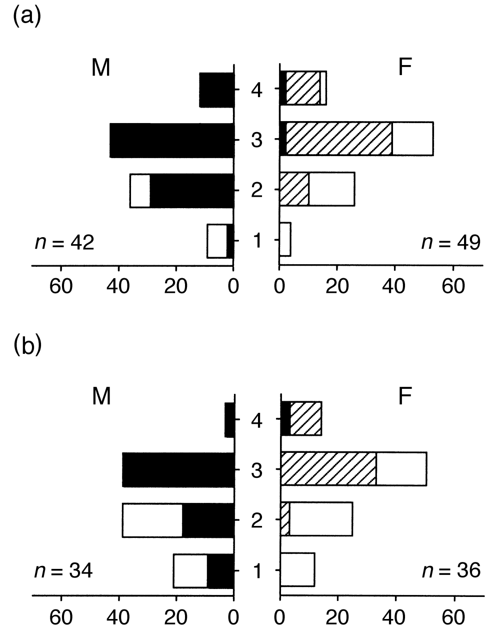

Fig. 6. Age structure and reproductive status of *Mus musculus castaneus* from granaries in Shijou township. (a) Granary 7; (b) Granary 8. Male: solid block, breeding (sperm in cauda epididymis); empty block, immature. Female: solid block, pregnant; hatched block, sexually mature but not pregnant; empty block, immature.

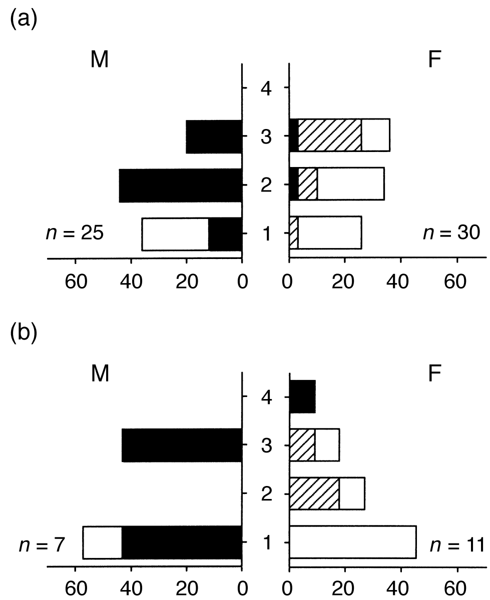

Fig. 7. Age structure and reproductive status of *Mus musculus castaneus* from granaries in Linnei township. (a) Granary 3; (b) Granary 9. The reproductive status is described in Fig. 6.

township, BW ages 2 and 3 are most abundant in granary no. 3 (64% in the males and 71% in the females), while the population of granary no. 9 has distinct age structures for both sexes, with young mice of BW age 1 being the dominant group (Fig. 7).

As in Shijou township, the majority (75% or more) of males were in breeding condition, yet fewer females than in Shijou township were sexually mature (38% in granary number 3 and 36% in granary number 9). Three females were pregnant.

Shoufeng township

Age structures and reproduction were analyzed for just 1 granary in Shoufeng township (Fig. 8). Here, BW age 3 alone comprises half of the samples for both males (51%) and females (63%), making them the most conspicuous age class.

Again, the majority (73%) of males were in breeding condition. In contrast, both the proportion of mature (67%) and number of pregnant females (6 mice) were higher than for the other populations sampled.

Seasonal variation

No obvious demographic shift was found between seasons. Except for granary no. 9 in Linnei township, the dominant age classes were BW age 2 and/or 3 in both summer and winter (Figs. 6, 7, 8). There is also no conspicuous variation in reproductive intensities between the 2 seasons. Most males remain sexually active in both seasons; 6 of the 12 pregnant females were caught in winter.

Other remarks on reproduction

Male

The testis length is related to BW age class; the mean values increase from BW age 1 to BW age 4 (Table 4). The trend holds for the length of the seminal vesicles (Table 4). These trends indicate that the reproductive capacity increases progressively in males as they grow older. Moreover, males seem to be able to breed continuously throughout their life once they reach sexual maturity, as all except 1 male (Shoufeng township) of BW ages 3 and 4 (Figs. 6, 7, 8) had sperm in the epididymis.

Female

In spite of large sample sizes, relatively few females were pregnant: 12 out of 147 (8%) had embryos in the uteri. Litter size ranged from 1 to 5 and averaged 3.5. Mice from Shoufeng township produced more offspring per litter (N = 6, mean = 4.2) than did either those of Linnei township (N = 3, mean = 3.3) or Shijou township (N = 3, mean = 2.3).

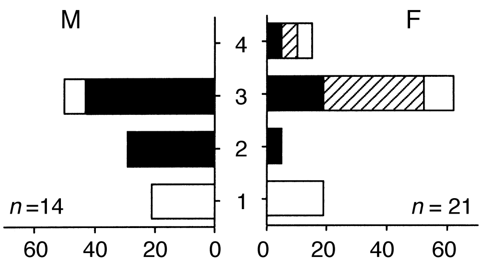

Fig. 8. Age structure and reproductive status of *Mus musculus castaneus* from 1 granary in Shijou township. The reproductive status is described in Fig. 6.

Sex ratio

With all age classes were combined, sex ratio (female/male) of the mouse populations varied among granaries (Table 5), although none of these

Table 4. Length (Mean ± SD mm) of male reproductive organs in 4 body weight age classes of *Mus musculus castaneus*. Sample size in parentheses

Body weight age class	Testis length	Seminal vesicle length
1	3.93 ± 1.07 (27)	2.67 ± 1.23 (15)
2	5.16 ± 1.07 (43)	5.12 ± 1.35 (41)
3	5.59 ± 1.02 (46)	6.16 ± 1.30 (45)
4	5.83 ± 1.47 (6)	6.50 ± 0.84 (6)

Table 5. Sex ratio (female:male) of *Mus musculus castaneus* from 5 granaries in 3 townships in Taiwan. Sample sizes are shown in parentheses

Township and granary	Age class[a]		All ages
	1 and 2	3 and 4	
Shijou 7	0.79 (34)	1.48 (57)	1.17 (91)
Shijou 8	0.65 (33)	1.64 (37)	1.06 (70)
Linnei 3	0.95 (39)	2.20 (16)	1.20 (55)
Linnei 9	2.00 (12)	1.00 (6)	1.57 (18)
Shoufeng	0.71 (12)	2.28 (23)	1.50 (35)

[a] By body weight, also see text; age classes 1 and 2 represent young mice and age classes 3 and 4 old mice.

deviates significantly from an equal sex ratio (χ^2-test, $p > 0.05$). When data were analyzed separately by age, except for granary 9 of Linnei township, all other granaries have more females than males in old mice (BW ages 3 and 4) but a slight excess of males in the young age classes (BW ages 1 and 2) (Table 5). Despite discrepancies in sex ratios between age groups, none of the ratios is different from 1 (χ^2-test, $p > 0.05$) and sex ratios of young and old age groups in each granary are not different from each other (*G*-test, $p > 0.05$).

Prevalence of tapeworm infection

During the autopsy, tapeworms (*Hymenolepis nana*) were often found in the digestive tract. The prevalence rate (the percentage of animals examined that were infected) was estimated to be 63% for males, 69% for females, and 66% for both sexes combined.

Missing molars

We also found a high frequency of missing molars in mice across all age classes. In most cases, the 3rd upper molar was missing and yet sometimes 2 molars, either 1 upper plus 1 lower 3rd molar or 2 upper 3rd molars, were missing. Moreover, there was no apparent trace of root holes in the cranium/mandible which means that the missing teeth had never erupted from the bony crest. Overall, 55% of the mice examined (N = 269), including all age classes, have at least 1 missing molar. Missing molars are not peculiar to any particular population from the 3 townships, and the occurrence ranged from 46% to 64% in all populations. Females (60%, N = 147) had a slightly more frequent occurrence of missing molars than did males (50%, N = 122), but the difference was not significant (*G*-test, $p > 0.05$).

DISCUSSION

Variation in population size

The mouse population in each granary resembles an independent population and, therefore, offers an opportunity to investigate the causes of variation in mouse population size in these granaries. Although our trapping regimes were not sufficiently prudent to allow estimates of mouse population size, numbers of mice inhabiting each granary vary a great deal. At least 2 extreme situations exist: granaries inhabited by very few mice (Ershuei township, 8 mice and Tsztung township, 1 mouse) and those with large numbers of mice (of which Shijou township and Shoufeng township are extraordinary examples). In Shijou township's 2 granaries, daily captures did not decrease during the trapping session. For instance, in Shijou granary no. 8, 15 mice were caught on the 1st day and 12 mice on the last; 10 or more mice were caught every day, resulting in a total capture of 115 mice. Quite a few mice could still be seen running in the granary on the last day of trapping. The causes of this discrepancy in mouse numbers in different granaries are not immediately clear but food is certainly not a limiting factor, as plenty of surplus grain was available in all granaries. However, the number of mice in a granary may be related to the history of grain storage. Two crops of rice are harvested each year and usually a single crop is stored in a granary up to 2-3 years during which the grain sacks are piled up and left alone. At the end of these 2-3 years, all sacks are removed to be processed, depleting the shelters and habitats of the mouse residents. The mice must disperse and find another suitable habitat, perhaps another granary containing a different crop. A complex cycle of dispersal, colonization, and population growth dynamics must exist in the granaries. As a result, the mouse population size in any granary may in part depend on the time phase in such a process.

Age determination

The 2 age determination methods are useful, although each has its own merits and limitations. The body weight method offers a quick and easy way to age an animal without sacrificing it, and it is thereby suitable for live-trapping studies. Tooth attrition is a slow process and, thus, it can potentially provide a method with finer resolution if animals of known ages are available as references. However, tooth wear criterion applies only to cleaned skulls, and some training is required before the criterion can be accurately used. However, by employing the 2 methods in combination, one can have much better resolution in determining age. For instance, mice that are classified as BW age 4 can be further separated by the tooth wear pattern (Fig. 5); mice categorized as TW ages 5 and 6 are likely older than those of TW ages 3 and 4.

Reproduction

The house mouse has evolved an opportunistic reproductive strategy (Bronson 1989, Bronson and Heideman 1994); in commensal situations, it can breed continuously. As expected, mice in rice granaries appear capable of breeding throughout the year. Pregnant females and a high proportion of competent males were found in both summer and winter. However, the female pregnancy rate remains low (8.2%) for the whole sample ($N = 147$). The low pregnancy rate may imply that the realized reproductive success in mice depends not only on physiological conditions but also on social organization. House mice are known to have definite breeding units or demes (Reimer and Petras 1967, Berry and Jakobson 1974, Sage 1981). Normally, such units comprise a territorially dominant male, several females, and some subordinate males, and the social structure, once established, remains stable for an extended period of time. Consequently, a newly-founded mouse population may grow rapidly initially and level off after reaching an "upper bound" (Reimer and Petras 1967). As most of our mice included in the reproductive studies came from granaries that were "crowded" with mice, reproductive outputs for the mouse populations were likely to be approaching the "upper bound" that 1 granary could support. The low pregnancy rate is a reflection of the "crowded" situation for the populations.

Sex ratio

Sex ratio has been implicated in an animal's ability to respond to natural selection. When food supply is plentiful, polygynous species favor an equal sex ratio (Wright et al. 1988), and that is what we found in the 5 mouse populations (Table 5). Notwithstanding, when age stratification is considered, a female-biased sex ratio seems to be favored in old mice rather than in the young in 4 out of 5 populations (excluding the population of Linnei 9; Table 5). The shift from male-biased to female-biased sex ratios appears to indicate fierce fighting among male mice to establish and maintain territories (Reimer and Petras 1967).

Parasites

The study of parasites in wild house mice has attracted some recent attention (Sage et al. 1986, Moulia et al. 1991, Tattersall et al. 1994) focusing on parasite loads in hybrid zones between *M. m. domesticus* and *M. m. musculus*. The occurrence of endoparasites is fairly common in the 2 subspecies. Although our estimate of the prevalence rate (66%) of the tapeworm (*H. nana*) in *M. m. castaneus* is conservative, it is much higher than that reported for various populations of *M. m. domesticus* (27.3% or less; Tattersall et al. 1994). It will be interesting to further investigate the parasite loads in *M. m. castaneus* and compare the results to those of other subspecies.

Missing teeth and nutrition requirements

It remains unclear why molars (especially M^3) are so often missing in the populations of studied mice, but it may likely be caused by a nutritional deficiency in the diet. Molar eruptions in young laboratory rats are retarded when rat dams are fed with a low (8%) protein diet as compared to a nutritionally adequate diet containing 25% protein (Navia and Narkates 1980). We do not know whether this is the case for our house mice since other nutritional elements such as vitamin D and calcium are also involved in tooth formation and development. The monotonous diet (rice grain) may likely cause nutritional deficiency in house mice living in granaries.

Conclusions

Four conclusions can be drawn from this study:

(1) Mouse population sizes in granaries can vary considerably, and this phenomenon is probably related to the history of grain storage. A complex cycle of dispersal, colonization, and population dynamics must exist in the granaries. Consequently, mouse population size in any granary may partially depend on the time phase of grain storage.

(2) Either the TW or BW age-determining methods can give satisfactory results. Age structure based on the BW age and the autopsy of reproductive organs indicate that house mice in the granaries are capable of breeding year round.

(3) Mouse populations tend to shift to a female-biased sex ratio at older ages, which may imply fierce fighting among male mice to establish and maintain territories.

(4) Heavy tapeworm loads and high rates of missing molars are found in the mouse populations. These may be related to genetic components and nutrition of the mouse populations.

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臺灣米倉內小家鼠之族群研究

周志文[1] 李培芬[1] 盧高宏[2] 于宏燦[1]

我們在臺灣五個鄉鎮的穀倉，採集小家鼠研究其族群生物學，包括族群量、生殖生物學、性比和年齡結構等。各地穀倉內的小家鼠族群量變化頗大，這可能和稻米儲存的時間有關。小家鼠可以終年生殖，和他們與人共居的習性相關。我們建立並比較兩種鑑定小家鼠年齡的方法：臼齒磨痕和體重。不同季節，穀倉內的老鼠族群年齡結構維持穩定，似乎是連續生殖的結果。多數族群的性比為1：1，但是在年長的老鼠中，公老鼠的數目似乎少於母老鼠。我們也發現小家鼠族群中有很高的蠹蟲感染率，而且有嚴重的缺齒情況。

關鍵詞：年齡結構，臼齒磨痕，族群量，性比，蠹蟲。

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