Age, Reproduction, and Demography of the Spiny Rat (Muridae: *Niviventer coxingi*) in Subtropical Central Taiwan

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Hon-Tsen Yu and Yao-Sung Lin (1999) Age, reproduction, and demography of the spiny rat (Muridae: *Niviventer coxingi*) in subtropical central Taiwan. *Zoological Studies* **38**(2): 153-163. Annual reproductive cycles and demographic changes in a wild population of the spiny rat (*Niviventer coxingi*) in central Taiwan were studied. Reproductive status of the rat was investigated by autopsy and histological examination of the testes and ovaries. Age of each animal was categorized into one of 5 age classes by examining wear patterns of the upper molars. Using the 5 age classes as a priori groupings, a discriminant function analysis on 4 body and 23 cranial measurements was used to crosscheck the reliability of the age criteria by tooth wear. The rat shows sexual dimorphism in body weight and timing of sexual maturity. However, the dimorphism is age dependent: only males of age class III or older become heavier than females, and yet females gain sexual maturity at a younger age than males. Despite climatic seasonality in its natural habitats, the rat does not have a limited breeding season. Males remain potent after sexual maturity and large proportions of males in the population breed in every season. Females breed in all seasons. Nonetheless, fewer breeding females were present in the coldest months of the year. Demographic analysis across 15 mo indicates that young rats are recruited in all seasons, supporting the conclusion that the spiny rat can breed year round. Finally, we compare features of life histories and ecological characteristics between *N. coxingi* and *Apodemus semotus*.

Key words: Tooth wear, Sexual dimorphism, Sex ratio, Life history, Breeding season.

Life history evolution concerns phenotypic variation consists of demographic traits, including birth, age and size at maturity, number and size of offspring, growth and reproductive investment, lifespan, death, etc. (Stearns 1992). These traits provide the basis for analysis of what causes differences in fitness among particular life history features under investigation. Many rodents are well suited for such studies because of their short lifespan.

Rats of the genus *Niviventer* are murid rodents that are widely distributed in China, northern India, and Southeast Asia (Musser 1981). Two species of *Niviventer*, both endemic, occur in Taiwan and they have distinct elevational distributions; *N. coxingi* occurs from sea level to 1500 m, and *N. culturatus* from 1500 to 3700 m (Yu 1992 1994 1995). Both species of *Niviventer* primarily inhabit forests and are good tree climbers (Lin and Yu 1987, Yu 1993). Despite the broad distribution of *Niviventer*, there is little in-

formation on the biology of the genus (Harrison 1955 1961, Lin and Yu 1987).

In Taiwan, few other species of murid rodents have been studied in detail except the Formosan wood mouse, *Apodemus semotus* (Lin and Shiraishi 1992a,b,c,d, Lin et al. 1993, Yu 1993, Huang et al. 1997). It is interesting to compare some features of life history traits and ecological parameters between *N. coxingi* and *A. semotus* because they both occur in montane forests, occupying similar habitats, and both are thereby subjected to similar evolutionary forces shaping their life histories.

During 1981-1982 we studied a wild population of *N. coxingi* in central Taiwan (Yu 1983). Here we report the methods of age determination, and such features as growth pattern, sexual dimorphism, reproduction, and demography, etc. Finally, we compare and discuss the life histories between *N. coxingi* and *A. semotus*.

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MATERIALS AND METHODS

Study site

The study site is located at Chitou (23°40'N, 120°47'E; elevation 1150-1350 m) in central Taiwan, where forests are managed for research and teaching by National Taiwan Univ. The climate, which is divided into wet and dry seasons, is typical of montane areas in central Taiwan (Fig. 1; also see Yu 1993). The average annual rainfall is about 2600 mm. Most rainfall (85%) occurs during the wet season, from April through September. The copious precipitation is largely from local thunderstorms and typhoons. The dry season lasts from October through February. The average annual temperature is 16.6 °C. The highest monthly temperature occurs in July (20.8 °C) and the lowest in January (10.9 °C). The average monthly day length (Fig. 1) varies from 10.7 (December) to 13.6 h (June). Furthermore, fog, which rises from the valley bottom in the afternoon, is common year round. The monthly relative humidity is always greater than 85%.

Natural vegetation is typical of middle elevations in central Taiwan, comprising evergreen broadleaf forests which are dominated by trees of the families Lauraceae and Fagaceae (also see Yu 1993). However, large pr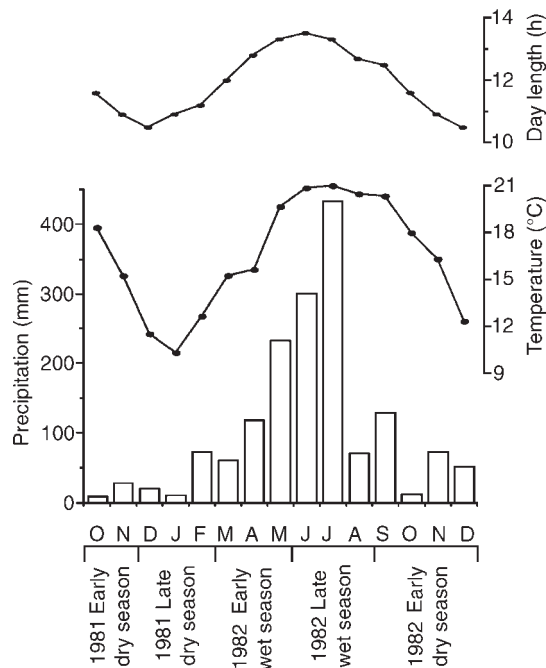oportions of the virgin forests are re-placed by Japanese fir (*Cryptomeria japonica*) plantations, underneath which some broadleaf trees (e.g., *Ficus erecta beecheyana* and *Phoebe formosana*) flourish. Ground cover is dominated by several herbaceous plants (*Elatostema edule*, *E. lineolatum major*, *Alocasia macrorrhiza*, *Parachampionella flexicaulis*, *Pilea funkikensis*) and ferns (*Diplazium pseudo-doederleinii* and *Monachosorum henryi*).

In addition to *N. coxingi*, there are 13 species of mammals recorded from Chitou, including 3 flying squirrels (*Petaurista alborufus*, *P. petaurista*, and *Belomys pearsoni*), 2 tree squirrels (*Callosciurus erythraeus* and *Dremomys pernyi*), 3 shrews (*Crocidura attenuata*, *Crocidura kurodai*, and *Anourosorex squamipes*), 3 species of Viverridae (*Viverricula indica*, *Paguma larvata*, and *Herpestes urva*), 2 species of Mustelidae (*Mustela sibirica* and *Melogale moschata*), and the Formosan macaque (*Macaca cyclopis*). Among these, the weasel (*M. sibirica*) is supposed to be a major predator to *N. coxingi*.

Specimens and autopsy

Totally 204 rats were collected from October 1981 through December 1982, mostly from plantation forests. The rats were captured by use of snap traps with banana or sweet potato as bait. Most specimens were autopsied fresh, but some were stored in a freezer until autopsy was performed. Before freezing, each rat was put in a plastic bag to minimize loss of weight due to dehydration (Banks 1965). Frozen specimens were autopsied within 2 wk of their capture.

At autopsy, body weight and 4 body measurements, head and body length (HB), tail length (TL), hind foot length (HF), and ear length (EAR), were first recorded. Reproductive status was then evaluated. For the male, (1) position of testes (scrotal or abdominal); (2) length and width of left testis, and pair weight of testes; (3) pair weight of epididymis and visibility of tubules in cauda epididymis; and (4) length and pair weight of seminal vesicle were noted. For the female, we recorded (1) lactation (milk in nipples when squeezed); (2) vaginal perforation; (3) numbers of normal and reabsorbed embryos in uteri; and (4) presence of placental scars in uteri. The left testis and epididymis, or both ovaries were removed and fixed in Bouin's solution. The organs were embedded in paraffin, sectioned at 10 µm thick, and stained with Harris hematoxylin and eosin. The stage of spermatogenesis and spermatozoa storage in the cauda epididymis, and presence

Fig. 1. Monthly precipitation (vertical bars), temperature, and photoperiod at Chitou, Taiwan. Seasons are indicated at the bottom of the figure.

of corpora lutea and preovulatory follicles (Peters and McNatty 1980) in ovaries were examined under a microscope.

A male is here considered sexually mature when the tubules in the cauda epididymis are visible to the naked eye and spermatozoa are found in its histological sections. A female is considered sexually mature when preovulatory follicles or corpora lutea are seen in sections of the ovaries.

Skulls of rats were extracted and cleaned for use in determining age. All skulls are deposited as voucher specimens in the Museum of Vertebrate Zoology, Univ. of California, Berkeley.

Age determination

Age classes are determined based on the sequence of tooth eruption and wear patterns of occlusal surfaces as follows (Fig. 2): Age I—M^3 not fully erupted; no wear on occlusal surface on M^1 and M^2; Age II—M^3 fully erupted; little wear on occlusal surfaces on M^1 and M^2; Age III—occlusal surface of upper molars worn; protocone-paracone and hypocone-metacone connected in M^3, forming a single enamel lake; Age IV—mure of M^3 lacking or anterocone-paracone and hypocone-metacone connection complete on M^2; Age V—mure of M^2 and M^3 lacking, cusps of both molars each forming a single enamel lake; protocone-paracone and hypocone-metacone connected in M^1.

Pair weight of dry lens was initially recorded for potential use in determining age. However, the lack of animals of known age makes it difficult to use this criterion. Relationship between lens weight and age classes is presented for reference. Preparation of lens weight follows procedures in Morris (1972).

In order to evaluate the reliability of the age criteria by tooth wear, 4 body measurements and 23 cranial measurements were employed in discriminant function analyses using the 5 age classes as a priori groupings. The cranial measurements include: (1) length of skull (SKL); (2) length of nasal (NL); (3) breadth of nasal (NB); (4) length of rostrum (RL); (5) breadth of rostrum (RB); (6) interorbital breadth (IOB); (7) zygomatic breadth (ZB); (8) breadth of braincase (BBRNC); (9) height of braincase (HBRNC); (10) breadth of zygomatic plate (BZPL); (11) length of diastema (LDIAST); (12) palatilar length (PAL1); (13) palatal length (PAL2); (14) length of incisive foramina (LINCF); (15) breadth of incisive foramina (BINCF); (16) length of palatal bridge (LPALB); (17) breadth of palatal bridge (BPALB); (18) breadth of mesopterigoid fossa (BMESO); (19) length of bulla (LBUL); (20) breadth of bulla (BBUL); (21) height of bulla (HBUL); (22) breadth of incisive tip (BINCT); and (23) length of tooth row (LTR). These measurements were taken as described by Musser (1970). Analyses were done with SAS programs (SAS Institute Inc. 1986) in a mainframe computer on the Univ. of California, Berkeley campus.

Seasonal variation

Seasonal changes in reproduction and demography (age structure) are analyzed after dividing the entire sampling period into 5 seasons which span 1981 and 1982 (Fig. 1). The division is primarily based on climatic seasonality. As a result, the early dry season signals the annual decrease in rainfall and temperature, and the late dry season encompasses the coldest months of the year. By contrast, the early wet season indicates the annual increase in rainfall and temperature, and the late wet season represents the warmest months of the year.

RESULTS

Age determination

Table 1 gives Mahalanobis distances calculated using 7 measurements (SKL, HF, HB, BINCT,
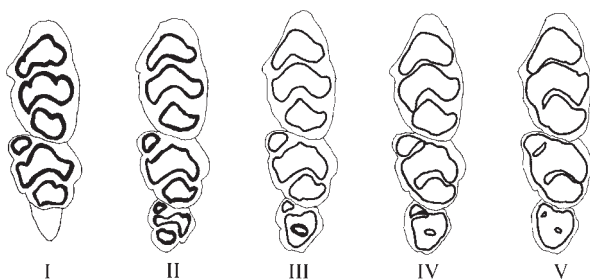

Fig. 2. Tooth eruption and wear patterns in left maxillary molars of *Niviventer coxingi* for 5 age classes. See text for detailed descriptions of each age class.

Table 1. Mahalanobis distances (above) between age classes in *Niviventer coxingi* and the probability testing the distance between pairs of age classes which equals 0

Age class	II	III	IV	V
I	4.10***	6.05***	7.38***	7.94***
II		2.57***	4.37***	4.90***
III			2.03*	2.44***
IV				0.86^{ns}

***$p < 0.001$, *$p < 0.05$, $^{ns}p > 0.05$.

BMESO, BZPL, and RL) which were chosen by stepwise selection in the discriminant function analysis. Pairwise comparisons of distances between age classes indicate that, except that between age IV and V, all are significantly different from 0. Fig. 3 visually displays distances among the 5 age classes. Age classes I, II, and III each forms a distinct group of its own, but age classes IV and V are virtually a group by themselves. The centroids of age classes IV and V are rather close to each other and their ellipses of both standard deviation and 95% confidence interval overlap. Therefore the results justify the use of tooth wear criteria to determine age classes in *N. coxingi*, and 4 age classes can be distinguished.

Growth and sexual dimorphism

Growth profiles of 5 measurements (BW, HB, TL, HF, and EAR) and dry lens weight are depicted by plotting means of 5 age classes (Fig. 4). When all age classes are pooled for a *t*-test comparison, 3 measurements show overall sexual dimorphism, BW ($t = 2.52$, DF = 200, $p < 0.05$), HB ($t = 2.45$, DF = 199, $p < 0.05$), and HF ($t = 6.03$, DF = 199, $p < 0.001$). However, while the difference for HF is consistent throughout all age classes, this is not true for BW and HB (Fig. 4). BW and HB do not differ much between the 2 sexes until after age III. Males are heavier than females at ages IV and V and only grow larger than females at age V, as means and 95% confidence intervals do not overlap (Fig. 4).
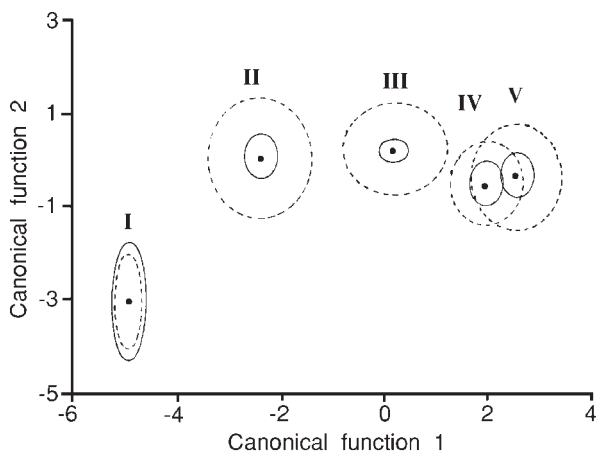
Relatively speaking, all measurements and dry lens weight increase faster before age III than after. Yet males seem to be able to add weight continuously through all age classes.
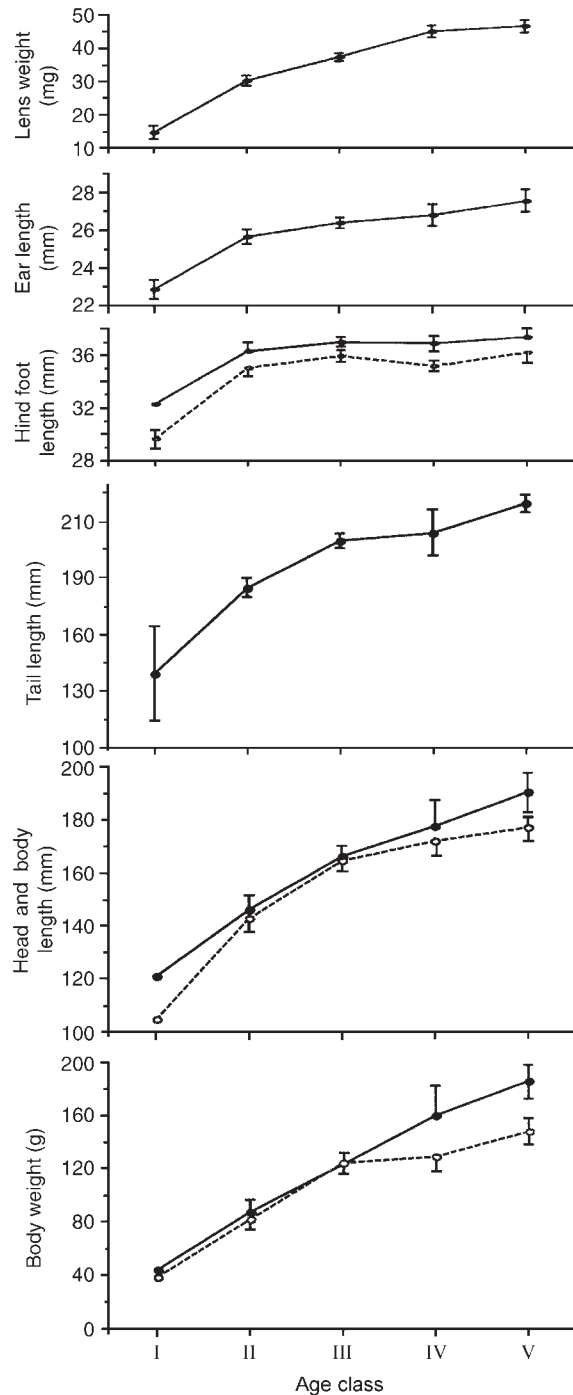

Fig. 3. Plots of the first 2 canonical variables in the discriminant function analysis using skull and body measurements. Roman numbers indicate the a priori groupings by tooth wear criteria. Dots show the centroids of each age class with ellipses of standard deviation (broken lines) and 95% confidence intervals (solid lines).

Fig. 4. Growth profiles of lens weight, 4 external measurements, and body weight in *Niviventer coxingi*. Vertical bars represent 95% confidence intervals. When sexual dimorphism exists, dashed lines represent profiles in the female.

Age at sexual maturity and sex ratio

The percentage of individuals that reach sexual maturity was computed according to sex and age classes (Fig. 5). The sex ratio for each age class is indicated by sample sizes given in Fig. 5. The interactions among age, sex ratios, and maturity rate are analyzed by a contingency analysis (Table 2). For both sexes the percentage of sexually mature individuals increases progressively by age (significant interaction between age and maturity; Table 2), from age classes I (0%) to V (100%). Yet, the rates of increase from age classes II through IV are quite different in the 2 sexes as reflected by significant interaction between sex and maturity rate (Table 2). Males tend to attain sexual maturity more slowly than do females. The trend is epitomized by the situation in age class III. While only 47% of males produce sperm, 80% of the females are ready to ovulate (presence of preovulatory follicles) or have already ovulated (presence of corpora lutea). Moreover, significant interaction between age and sex (Table 2) marks inconsistent sex ratios across age classes. There are more females than males in age class II, but the reverse is true in age class III. Sex ratios in age classes I, IV, and V are about the same. However, differences in sex ratios might have been an artifact of the unequal catchabilities of different age and sex groups.

Male reproduction

Based primarily on histological examination, males are assigned to one of 3 reproductive categories: pre-breeding, breeding, and post-breeding individuals. Table 3 gives the average lengths and/or weights of reproductive organs for animals of the 3 categories.

Pre-breeding: Testes small, average length 11.96 mm and weight 0.46 g; seminiferous tubules 50-165 µm in diameter, with spermatogonia, primary spermatocytes, and trace numbers of early spermatids. Cauda epididymis small, average weight 0.07 g; tubules not discernible to the naked eye, and there are no spermatozoa therein. Seminal vesicle
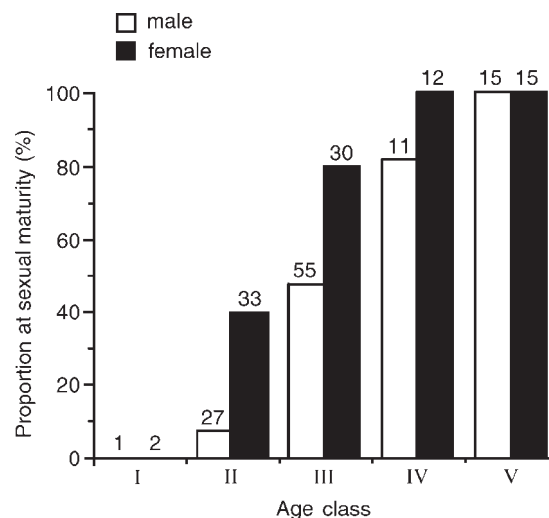

Fig. 5. Percentage of animals at sexual maturity for 5 age classes in both sexes of *Niviventer coxingi*. Numbers are sample sizes for each category.

Table 2. Results of multiway contingency analysis of sexual maturity rate and sex ratio in 5 age classes of *Niviventer coxingi*

Interaction	DF	G-value
Age × Sex × Maturity	4	1.63[ns]
Age × Maturity	8	76.39***
Age × Sex	8	16.25*
Sex × Maturity	5	18.85**

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, [ns]$p > 0.05$.

Table 3. Reproductive characteristics[a] of non-breeding, breeding, and post-breeding males of *Niviventer coxingi*

| Status | Testis | | Seminal vesicle | | Epididymis |
	length (mm)	weight (g)	length (mm)	weight (g)	weight (g)
Pre-breeding	11.96 ± 3.99 (57)	0.46 ± 0.62 (58)	6.51 ± 2.19 (56)	0.03 ± 0.05 (56)	0.07 ± 0.08 (57)
Breeding	25.78 ± 2.53 (46)	4.77 ± 1.01 (46)	18.65 ± 3.85 (46)	1.25 ± 0.69 (45)	1.07 ± 0.35 (44)
Post-breeding	22.06 ± 2.59 (5)	1.75 ± 0.85 (5)	14.18 ± 4.00 (5)	0.34 ± 0.12 (5)	0.45 ± 0.07 (5)

[a]Mean ± SD (sample size).

not swollen, average length 6.51 mm and weight 0.03 g.

Breeding: Testes enlarged, average length 25.78 mm and weight 4.77 g; seminiferous tubules 175-280 μm in diameter, containing numerous late spermatids and spermatozoa. Cauda epididymis swollen, average weight 1.07 g; tubules discernible, their walls consisting of a single layer of epithelial cells, and full of spermatozoa. Seminal vesicle enlarged, average length 18.65 mm and weight 1.25 g.

Post-breeding: Testes still enlarged, average length 22.06 mm nearly as long as those of breeding males; but few or no spermatozoa present in semiferous tubules, average weight 1.75 g, or 36% of breeding males'. Cauda epididymis reduced in weight, average 0.45 g or ca. 40% of breeding males'; tubules still discernible, yet clogged by cell debris with no spermatozoa. Seminal vesicles reduced slightly in length, averaging 14.18 mm but reduced much in weight, averaging 0.34 g, or 27% of breeding males'.

Among 109 males autopsied, 58 (53%) were pre-breeding, 46 (41%) breeding, and 5 (6%) post-breeding. The age of pre-breeding males spans age classes I to IV, predominately age classes II and III, with 95% altogether. One (2%) belongs to age class I, and two (3%) to age class IV. Forty-six breeding males comprise age classes as follows: 2 (4%) age II, 26 (57%) age III, 6 (13%) age IV, and 12 (26%) age V. Finally, 5 males were post-breeding, 2 (40%) age class III and 3 (60%) age class V. Consequently, it appears that the majority of males remains sexually competent once they reach sexual maturity. Only few males may go into seasonal reproductive decline (i.e., 2 post-breeding males of Age III) and few may enter reproductive senescence (i.e., 3 post-breeding males of Age V).

Female reproduction

Parallel to males, females are categorized into 3 groups: pre-breeding, breeding, and post-breeding individuals. The categories are determined on the basis of results of autopsy.

Pre-breeding: Uteri pale and thread-like, without embryos or placental scars. Nipples not swollen and often not noticeable.

Breeding: Pregnant (embryos in uteri), or lactating.

Post-breeding: Presence of placental scars in the uteri but not currently pregnant or lactating.

Ninety-two females were autopsied, including 34 (37%) pre-breeding, 33 (36%) breeding, and 25 (27%) post-breeding. Ages of pre-breeding females ranged from age classes I to IV, mostly in ages class I and II, totally 80%; 6 (18%) in age class III, and 1 (2%) in age class IV. For breeding females, the largest group was in age class III with 14 (42%), followed by both age classes IV and V (7 or 21% each), and age class II with 5 (16%). Post-breeding females comprised 10 (40%) in age class III, 8 (32%) in age class V, 4 (16%) in age class IV, and 3 (12%) in age class II. However, for post-breeding females it is difficult to tell whether a female is in reproductive senescence or in temporary reproductive depression due to seasonal effects.

Litter size and pregnancy: Embryos were found in 12 females. Litter sizes ranged 2-5 and averaged (mean ± SD) 3.8 ± 1.1. The numbers of corpora lutea averaged 4.3 ± 0.8. Among pregnant females, 5 had embryos and placental scars, thus they were multiparous; the remaining 7 were primiparous. Mean litter size of primiparous females was 4.1 ± 0.9 and that of multiparous females 3.6 ± 1.1. The difference is not significant (*t*-test, *p* > 0.05), but this may have resulted from small sample sizes for the test. For the 12 pregnant females, pre-implantation mortality rate was estimated to be 7.8% ([no. of copora lutea - no. of embedded embryos]/no. of copora lutea) and post-implantation mortality rate 4.3% (no. of reabsorbed embryos/no. of total embryos).

Placental scars were observed in 50 non-pregnant females, 27 had 1 set, and 23 had 2 sets. This suggests that females can give birth to at least 2 litters during a lifetime.

Seasonal variation of reproduction and demography

Seasonal changes of reproductive intensity and demography were judged by plotting age structure and reproductive status of each age group (Fig. 6). Since only 2 rats of age class I appeared in the entire sample, they are combined into age class II. Age classes IV and V are also combined because they are essentially similar. Age structures are thereby constituted of 3 age groups, which can be reckoned as juveniles (age classes I+II), subadults (age class III), and adults (age classes IV+V) in the populations. In addition, interactions among age structure, reproductive status, and season were tested by contingency analysis (Table 4).

Male: The interrelation between season and reproduction was tested to see whether or not reproduction in males depends on the season. The interaction was not significant (Table 4), suggesting that males do not have definite breeding seasons. In fact, there were always good proportions of breeding

males in the populations in all seasons (Fig. 6), further confirming that males breed continuously across all seasons. Nonetheless, 5 post-breeding males were captured, four in the early dry season of 1981 and one in the late dry season of 1981, the cooler seasons of the year (Fig. 6). Yet, since three of 5 post-breeding males belong to age V, the reproductive regression may have more likely resulted from senility than seasonal cycling.

Males of all age groups were constantly present and the test does not support a significant change in age structures across seasons (Table 4). However, shifts in age distribution between seasons can be noticed (Fig. 6). In particular, some populational trends are noteworthy. First, throughout all seasons, recruitment rates of juveniles are consistently > 20% (Fig. 6) except in the early wet season of 1982 when juveniles made-up < 10%. The result suggests con-
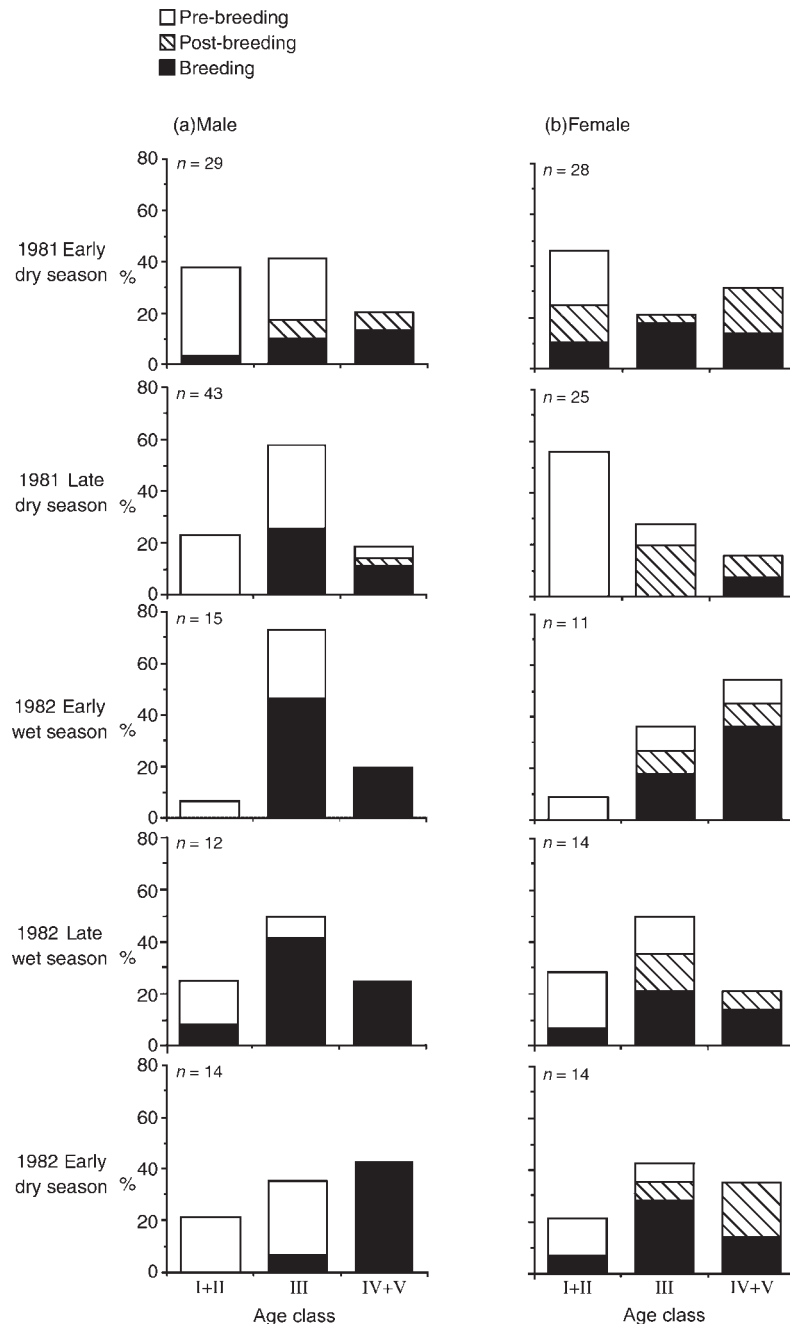

Fig. 6. Seasonal variation in demography and reproductive status for *Niviventer coxingi*.

tinuous breeding. Second, except in the early dry season of 1982, adults sustained the same fraction of the population (ca. 20%). Lastly, proportions of breeding subadults were lower in the dry seasons than wet seasons, whereas the majority of adults retained breeding capability across all seasons (Fig. 6). Therefore, seasonal effects more greatly influence slowing maturation of subadults than suppression of breeding capacity of adults.

Female: Breeding females occurred in all seasons, and the interaction between season and reproduction was not significant (Table 4). The evidence, therefore, supports non-seasonal breeding in females. Nonetheless, the *p* value (0.051) of this test is rather marginal. A careful perusal at Fig. 6 reveals that, even though females were breeding in every season, the reproductive activity appears reduced in the late dry season of 1981, the coldest season of the year.

Similar to males, changes of age structures in females were noticeable, even though the test of interaction between season and age was not significant (Table 4). Females show the same recruitment pattern of juveniles as do males. Juveniles always accounted for more than 20% (Fig. 6), except in the early wet season of 1982 when juveniles constituted just under 10%. The result further corroborates the conclusion that *N. coxingi* can breed year-round. A major demographic transition occurred between the late dry season of 1981 and early wet season of 1982 (Fig. 6). In the former season, juveniles made-up the largest age group followed by subadults and adults. In the latter season, however, the trend is reversed. In general, certain female juveniles had begun to breed, yet none of the juveniles in the late dry season of 1981 were breeding (Fig. 6), although they constituted more than 50% of the population. As in males, the evidence indicates that female juveniles also mature more slowly in this coldest season.

DISCUSSION

Reproduction and seasonality

Seasonal breeding in mammals is primarily shaped by 3 environmental forces: physical, dietary, and social (Bronson 1989, Bronson and Heideman 1994). Among these 3, dietary factors are by far the most important. The physical factors in Chitou are strikingly seasonal (dry and wet seasons; Fig. 1), and the seasonality in temperature and rainfall, no doubt, would affect the growth of plants, and thus food availability. The phenology of vegetation and food

availability in similar habitats have been described elsewhere (Yu 1993), and we do not expect those of Chitou to be much different. Basically, there are 2 sets of food sources available: (1) the peak of vegetative growth and fungal production in the wet season and (2) abundant fruits and seed crops in the dry season. As a result, food for the omnivorous *N. coxingi* appears plentiful throughout the year. Therefore, it may be expected that *N. coxingi* does not have pronounced breeding seasons.

Notwithstanding, since lactation and maternal dependence of young in *N. coxingi* (Lin and Yu 1987) are energetically demanding, female rats seem to somewhat reduce their reproductive activities (Fig. 6) in the coldest months (late dry season; Fig. 1) of the year, during which time energy needs for thermoregulation are also high. Yet, energetically speaking, males are less susceptible to food restriction than are females and, thereby, do not show seasonally reduced reproductive activities as do females.

Social cues could play an important role in reproduction, particularly for animals that have an intricate social organization. Evidence suggests that this is the case for *N. coxingi*, for the rats have a characteristic spatial distribution in the forests (unpubl. data). The females have more static and well-defined home ranges than do males. In contrast, males appear to wander more than females.

Sexual dimorphism and pubertal development

In terms of pubertal strategies, the 2 sexes can be differentiated because evolutionary forces appear to act differently on pubertal rats of the 2 sexes (Bronson 1989). While females compete for resources necessary to sustain energy demands of pregnancy and lactation, males compete with each other for breeding territories or mates. In this regard, 2 phenomena in *N. coxingi* are of particular interest. First, males reach sexual maturity later than females (at age III); puberty occurs at age III in 80% of fe-

Table 4. Results of multiway contingency analysis of seasonal variation in age structure and reproduction of *Niviventer coxingi*

Interaction	DF	*G*-value	
		male	female
Season × Age × Reproduction	8	8.29[ns]	10.81[ns]
Season × Reproduction	12	19.87[ns]	20.94[a,ns]
Season × age	16	17.69[ns]	

[ns]$p > 0.05$. [a]$p = 0.051$.

males but in fewer than 50% of males (Fig. 5). Second, sexual dimorphism of body weight is age dependent: this difference does not occur until after age III (Fig. 4). It appears that males delay maturity and divert energy to growth in size, i.e., body weight. If delaying maturity allows further growth in body weight and fecundity increases with size, then delayed maturity leads to higher initial fecundity. However, it is not immediately clear whether or not an increase in body weight ensures increased fecundity in male *N. coxingi*. Supposedly, heavier body weight allows a male rat to gain easier access to potential mates. Therefore, it would be advantageous for a male to place priority in growth of body weight as long as the effects outweigh the advantages of early sexual maturation.

Comparison between *N. coxingi* and *A. semotus*

In addition to *N. coxingi*, there is a 2nd species of murid rodent (*A. semotus*) in Taiwan which has been studied in sufficient detail to permit a comparison between the 2 species. *A. semotus* occurs in similar types of forests but at higher elevations (Lin and Shiraishi 1992a, Yu 1993 1994, Huang et al. 1997). Table 5 summarizes a few pertinent features of life history traits and ecological characteristics for *N. coxingi* and *A. semotus*.

One fundamental difference beyond phylogeny between the 2 species is size; *A. semotus* is smaller than *N. coxingi*, the former weighing just 1/5 of the latter. This difference alone affects various aspects of life histories and ecology among animal species (Reiss 1989), such as litter sizes, longevity, parental investment, reproductive cycles, energy demands, etc. While it may be predicted that smaller species tend to produce larger litters and more litters during their lifetimes, it appears not to be the case here. Both species have about the same litter size and produce 2-3 litters per lifetime. By contrast, the larger *N. coxingi* does live longer and reaches sexual maturity later than *A. semotus*. This is consistent with usual generalizations. Furthermore, the smaller *A. semotus* shows a conspicuous bimodal annual reproductive cycle whereas *N. coxingi* seems to breed year-round.

Finally, in *A. semotus* both sexes have similar sizes of home range. This is similar to the home range size of female *N. coxingi*, although *N. coxingi* males occupy almost twice as much area as females. Yet, more importantly, the population density of *A. semotus* (35.3 mice/ha) is much higher than that of *N. coxingi* (2-5 rats/ha). In consequence, this implies that the population of *A. semotus* consists of many individuals having overlapping home ranges, whereas that of *N. coxingi* shows the opposite.

Population density of *N. coxingi* is seemingly limited by its larger body size, which demands more total energy to support. The tree-climbing habit of *N. coxingi* may, somewhat, fulfill the energy demands, for this habit allows the rat to explore resources inac-

Table 5. Comparison of some features of life history traits and ecological parameters between 2 species of rodents from montane forests in central Taiwan

Trait/parameter	*Apodemus semotus*	*Niviventer coxingi*
Adult body weight (g)	26.9 (18.5-39.0)[a]	134.6 (55-228)
Litter size	3.83 (2-6)[b]	3.8 (2-5)
	3.49 (1-5)[c]	
Litters per lifetime	2-3[b]	2-3
Age at sexual maturity	2 mo[g]	5.5 mo[e,*]
		9 mo[e,#]
Lifespan	6 mo[b]	15 mo[e]
Annual breeding cycle	bimodal[b,c]	continuous
Activity mode	terrestrial	terrestrial/arboreal
Population density (no/ha)	35.3 (5.7-66.7)[d]	2-5[e]
Adult home range (m^2)		
Male	2282[d]	4948[f]
	(500-5000)	(200-20200)
Female	2547[d]	2305[f]
	(200-5100)	(600-4800)

[a]Yu 1993. [b]Huang et al. 1997. [c]Lin and Shiraishi 1992a. [d]Lin and Shiraishi 1992b. [e]Wu and Yu 1998a. *winter cohort, #summer cohort. [f]Wu and Yu 1998b. [g]Lin et al. 1993.

cessible to *A. semotus*. Interestingly, litter size and lifetime productivity of *A. semotus* are no larger than those of *N. coxingi*. Perhaps, the colder climate at higher elevations prevents *A. semotus* from being more prolific due to higher energy demands for thermal regulation. A highland *Niviventer* species, *N. culturatus*, sympatric with *A. semotus* shows a smaller litter size (2.44; Yu 1993) to *N. coxingi*. This contrast can further reflect that severe climatic conditions at higher elevations do limit the productivity of animals.

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臺灣中部亞熱帶山地森林刺鼠族群之年齡、生殖與人口統計研究

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我們研究臺灣中部山區一個刺鼠族群的生殖週期與人口統計變化。生殖活動係以觀察外生殖器官和性腺組織切片來判定。年齡則利用臼齒磨損程度來界定，共訂出五個年齡群；我們也利用判別分析檢定五個年齡群的可信度。刺鼠在體重和成熟年齡上兩性不同；年輕雄鼠（年齡 III 以前）體重和雌鼠並無差異，年長雄鼠（年齡 IV 和 V）則較雌鼠為重。雌鼠較雄鼠先達性成熟。雖然中部山區的氣候有顯著的季節性，但刺鼠並無明顯的生殖季節。雄鼠在性成熟後可持續生殖，而且在不同季節內，族群中有多數的雄鼠處於生殖狀態。雌鼠亦屬於終年生殖型。人口統計學的分析顯示，在不同季節內皆有幼鼠加入族群，此一結果亦顯示刺鼠終年可生殖。最後，我們比較刺鼠和森鼠的生活史特徵和生態特性。

關鍵詞：臼齒磨痕，雌雄二型，性比，生活史，生殖季節。

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