

Spatial Organization of a Forest-Dwelling Murid Rodent, *Niviventer coxingi*, in Subtropical Central Taiwan

Hai-Yin Wu^{1,*}, Hon-Tsen Yu²

¹Institute of Natural Resources, National Dong Hwa University, Hualien, Taiwan 974, R.O.C.

²Graduate Institute of Zoology and Department of Life Science, National Taiwan University, Taipei, Taiwan 106, R.O.C.

(Accepted May 28, 2004)

Hai-Yin Wu and Hon-Tsen Yu (2004) Spatial organization of a forest-dwelling murid rodent, *Niviventer coxingi*, in subtropical central Taiwan. *Zoological Studies* 43(3): 612-621. Hypotheses have been proposed that, for rodents, food type determines the spacing pattern of females, while the availability of potential mates determines the spacing pattern of males. For a frugivorous-omnivorous species such as *Niviventer coxingi*, females are hypothesized to be territorial or widely dispersed, while males should be non-territorial and widely ranging. The peculiar life history traits of female *N. coxingi* should further strengthen the constraints they exert on male spacing behavior. In this study, we attempted to examine sexual differences and seasonal variations in the spacing patterns of *N. coxingi*. A population was studied for 17 mo from Jan. 1982 through May 1983 by the mark-recapture method in a 9-ha grid at the Experimental Forest of National Taiwan University at Chitou, central Taiwan. Home range areas were larger in males than in females. Seasonal home range areas of the 2 sexes significantly differed in autumn 1982. Compared with adult females, adult males had greater mean and maximal inter-capture distances, and greater shifts in seasonal activity centers. Correlations between body weights and indices of spacing behavior (inter-capture distances and home range areas) were positive in males and negative in females. Inter-male home range overlap indices were higher than inter-female and inter-sexual overlap indices, especially in autumn 1982. The results suggest that the spacing pattern of *N. coxingi* is characterized by smaller and widely dispersed home ranges for females, larger home ranges for males, and a higher degree of intra- and inter-sexual home range overlap for males in the breeding season. The mating system is most likely promiscuous. The male-biased population structure, low reproductive intensity of the already scarce females, and the availability of food and suitable habitat may be responsible for the sexual differences and seasonal variations of the spacing behavior. <http://www.sinica.edu.tw/zool/zoolstud/43.3/612.pdf>

Key words: Home range, Mating system, Population density, Spacing pattern, Territoriality.

Spatial organization and mating systems of animals are among the central themes in behavioral ecology and are believed to be determined by spatiotemporal availability of resources. For mammals in general, and many rodents in particular, females spend considerable energy and time bearing and nursing offspring, while males try to increase their chances of inseminating females. Given these intersexual differences in parental investment, it is hypothesized that the reproductive success of females should be resource-limited, whereas that of males should be female-limited (Trivers 1972, Ostfeld 1985, Ostfeld et al. 1985, Tew and Macdonald 1994).

Various hypotheses on spacing patterns and mating systems of rodents have been proposed. Ostfeld (1985) suggested that food types (differing in abundance, distribution, and rate of renewal) determine the spacing pattern of female rodents (food defense hypothesis), which in turn determines the territoriality of male rodents (female in space model; Ostfeld 1990). Ims (1988) modified Ostfeld's model by taking into account temporal variations in availability of receptive females (female in time and space model; Ostfeld 1990). Although field studies and experiments have revealed considerable interspecific differences and intraspecific flexibility in territorial systems of small

*To whom correspondence and reprint requests should be sent. Fax: 886-3-8633260. E-mail: hywu@mail.ndhu.edu.tw

mammals, most studies give supportive evidence to the above hypotheses (e.g., Madison and McShea 1987, Lambin and Krebs 1991, Pusenius and Viitala 1993). Wolff (1993) questioned the above hypotheses by asserting that the ultimate function of female aggression and territoriality is for pup defense. Notwithstanding, he agreed that “the species-specific food habits do result in different spacing patterns based on the distribution of particular food types” (Wolff 1993: p. 367).

Although most discussions on this topic have been focused on Holarctic microtines, modal social systems are believed to exist in other rodent species as well. However, the realized pattern for a species should be modified by species-specific life history traits and habitat-specific ecological constraints. For a better understanding of the extent of phenotypic plasticity in the spatial organization of small mammals, Ostfeld (1990) and Batzli and Henttonen (1993) urged researchers to conduct additional studies to test the existing hypotheses.

Niviventer coxingi is an endemic species in Taiwan. It is the only murid species inhabiting forest habitats from low to middle elevations in Taiwan (Yu 1994). Population dynamics of the species have been studied in Yangmingshan, northern Taiwan (Chang-Chien 1989, Chang 1991), and in the Experimental Forest of National Taiwan University at Chitou, central Taiwan (Wu and Yu 2000). Both populations produce 2 cohorts of young a year. The major breeding season is in late summer and autumn (Wu and Yu 2000). The species preferred fruits, seeds, and insects in *ad libitum* feeding tests (Liu 1990, Wu pers. observ.). It therefore falls into the seeds, fruits, and forbs (SFF) diet group (Ostfeld, 1990). In forest habitats, SFF diets are sparsely and patchily distributed, and are slowly renewed. Females of the SFF-diet species are supposedly territorial or widely dispersed, while males are expected to employ a wide searching strategy to access females (Ostfeld 1990). Moreover, *N. coxingi* females exhibit some peculiar life history traits, such as low breeding intensity, prolonged maternal care, and high over-winter mortality (Wu and Yu 2000). These attributes make the temporal availability of females unpredictable to males and may strengthen the constraints of female distribution on the spacing behavior of males. Therefore, males are expected to range more widely in the breeding season. In this study, we analyzed field data collected by the mark-recapture method to examine the movement and ranging patterns of *N. coxingi*.

We tested the hypothesis that *N. coxingi* males move farther and have larger home ranges than females. We also examined seasonal variations in the ranging patterns of the species.

MATERIALS AND METHODS

The fieldwork was conducted at the Experimental Forest of National Taiwan University at Chitou in central Taiwan (23°40'N, 120°47'E; elevation 1100~1400 m) from Jan. 1982 to May 1983. The climate and the vegetation of the study area were described by Yu and Lin (1999). The climate in Chitou is cool and humid. Average monthly temperatures range from 11 to 22°C. Annual precipitation is 3000 mm, with a rainy season extending from Mar. to Sept. during which 80% of the precipitation occurs. Relative humidity is about 90% year-round.

Most of the vegetation in Chitou is a combination of conifer and bamboo plantations. The original broadleaf forest can only be found along a steep slope on the west side of Mt. Phoenix where the study was conducted. The broadleaf forest is dominated by trees of the families Lauraceae and Fagaceae, which is similar to natural forests at mid-elevations elsewhere in Taiwan (also see Yu 1993, Yu and Lin 1999).

A grid system of 9 ha was established. The entire grid covered 2 types of vegetation, the eastern part (higher elevation) was situated in a broadleaf forest and the western part (lower elevation) in a 20-year-old Japanese fir (*Cryptomeria japonica*) plantation (Wu and Yu 2000). The area was divided into 218 squares of 400 m² each, and a trapping station (dots in Fig. 1) was set in the center of each square whenever possible. In total, 220 mesh-wire rodent traps (24 x 15 x 11 cm) baited with sweet potatoes were set; 2 traps were placed at each trapping station in the Japanese fir plantation and 1 trap at each station in the natural forest.

The length of the monthly trapping sessions lasted for 3~5 nights: 5 nights for the first 2 mo (Jan.~Feb. 1982), 4 nights from Mar. 1982 through Feb. 1983, and 3 nights for the last 3 mo (Mar.~May 1983). Rats were marked with numbered ear tags, weighed, and examined for reproductive condition (position of the testes in males; vaginal perforation, pregnancy, and lactation in females). Each rat was assigned as being a juvenile or adult based on body weight (< 110 g for juveniles and ≥ 110 g for adults) at each capture.

Detailed accounts of using body weight as an age criterion are given elsewhere (Yu and Lin 1999, Wu and Yu 2000).

Three indices of spacing behavior, (1) mean and (2) maximal inter-capture distances (IDs) (expressed as mean ID and max. ID), and (3) home range areas, were analyzed on a seasonal basis. We divided the entire study period into 6 seasons: (1) winter 1981, Jan.~Feb. 1982; (2) spring 1982, Mar.~May 1982; (3) summer 1982,

June~Aug. 1982; (4) autumn 1982, Sept.~Nov. 1982; (5) winter 1982, Dec. 1982~Feb. 1983; and (6) spring 1983, Mar.~May 1983. Rats that were captured for 3 mo or longer were assumed to be residents. The minimum unweighted trappability (Krebs and Boonstra 1984) was high for both sexes, which reduced the likelihood of mistaking transients for residents. Only adult residents that were captured at least 5 times in a single season were included in the analysis. Rats that were

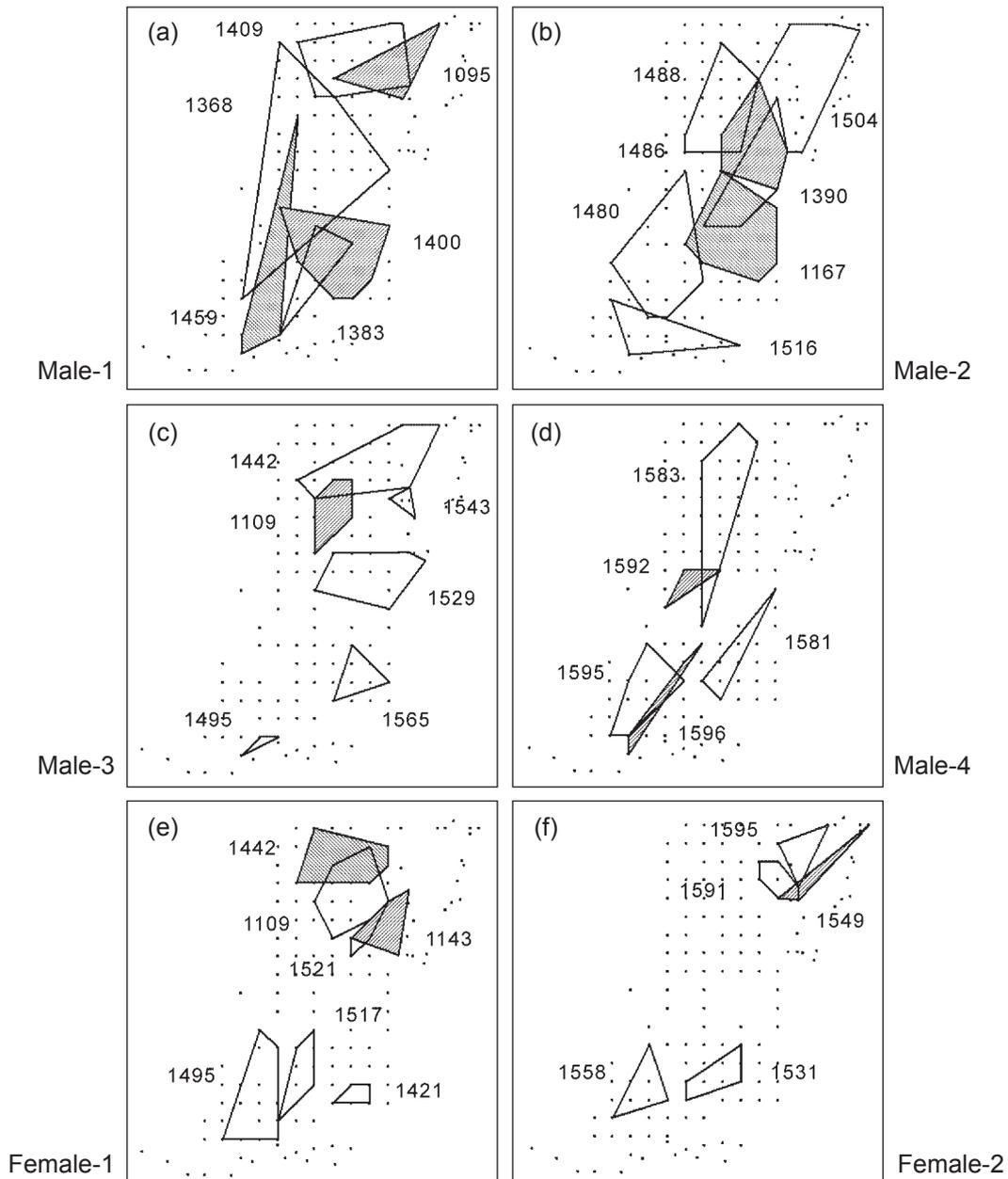


Fig. 1. Spatial distribution of the home ranges of *Niviventer coxingi* in the study area at Chitou, central Taiwan. Adult residents that were captured at least 5 times during the study period (winter 1981~spring 1983) were included. For a better visual effect, home ranges are drawn in multiple panels (a-d, males; e and f, females) and in shaded areas. Dots indicate trapping stations. Numbers are the tag numbers of the rats.

trapped more often ($> 1/2$ captures) in traps along the border of the trapping grid were excluded. Since there were only 2 mo of field work in the 1st season (winter 1981), data on spacing patterns in that season were excluded to maintain equal trapping efforts in each season. All home range estimates were constructed as minimum convex polygons using the program CALHOME (Kie et al. 1994). We also estimated the overall home range areas for adult residents that were captured at least 5 times during the entire study period. Nonparametric Wilcoxon-Mann-Whitney and Krustal-Wallis tests were employed for sexual and seasonal comparisons of spacing indices. Relationships between body weights and spacing indices were examined by Spearman's rank correlation coefficients.

We assessed inter- and intra-sexual spatial

dispersion patterns by comparing the distances between the seasonal activity centers of all possible male-male, male-female, and female-female pairs. A seasonal activity center was calculated as the arithmetic mean of the coordinates of the trapping stations where a rat was captured in 1 season, weighted by the frequency of captures at each station (Hayne 1949). We calculated the distance between the activity centers in successive seasons for each rat.

We used a home range overlap index and a square overlap index to assess intra- and inter-sexual range overlaps of adult rats. The home range overlap index was calculated for each adult and is expressed as the number of adults of the same or opposite sex whose home ranges overlapped with the focal individual. The square overlap index is expressed as the proportion of the

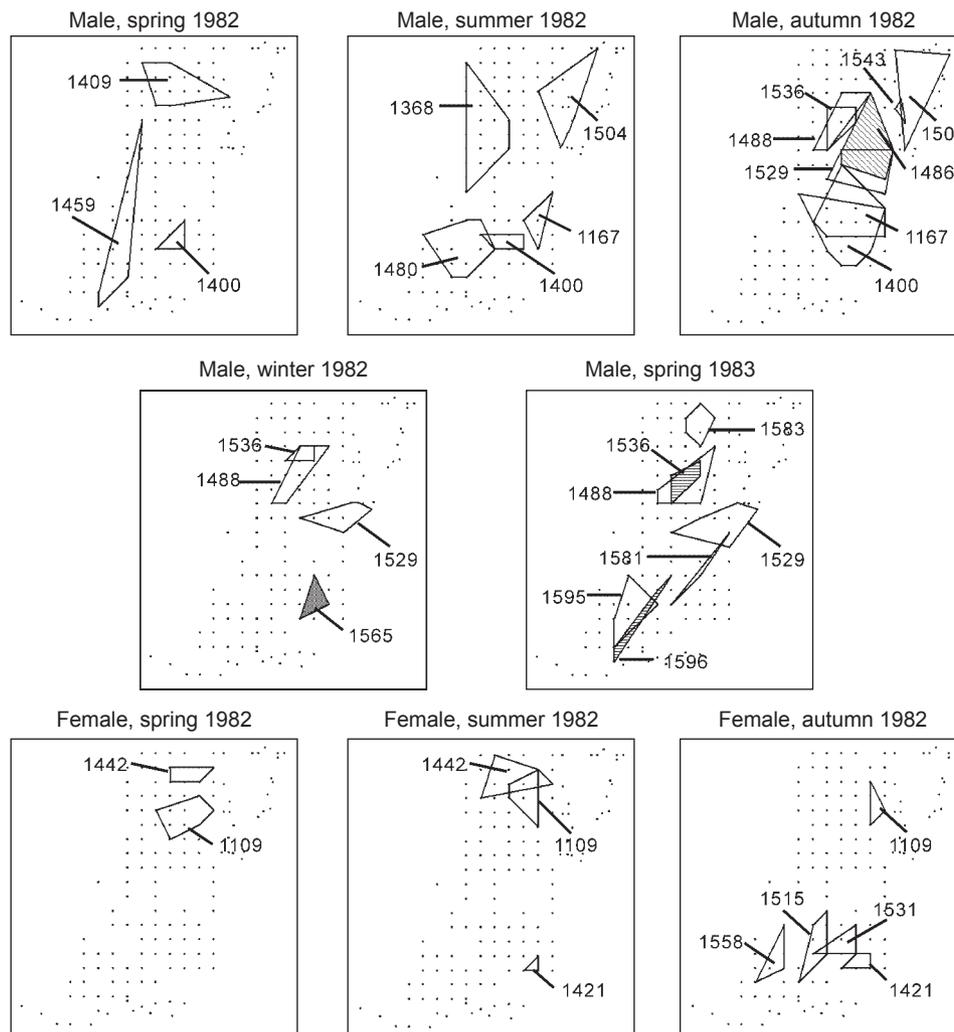


Fig. 2. Home ranges of *Niviventer coxingi* in the 5 seasons from spring 1982 to spring 1983. Adult residents that were captured at least 5 times in a season were included. Dots indicate trapping stations.

number of squares (1 square = 400 m²) shared by at least 2 adults of the same or opposite sex to the total number of squares occupied by all adult males or females. Both indices were calculated on a seasonal basis. Inter- and intra-sexual overlap indices were compared using the Friedman test (Siegel and Castellan 1988). Throughout the paper, all means are reported with \pm standard error (SE).

RESULTS

Captures and population numbers

In a total of 14,520 trap-nights during the period from Jan. 1982 through May 1983, 84 males and 62 females were trapped 485 and 343 times, respectively. Numbers of *Niviventer coxingi* captured in each season varied from 23 to 57. The population density was lowest in spring 1982; it increased to the highest level in autumn 1982, and thereafter declined again. Despite the seasonal variation in population size, there were always more adult males than females. A full account of population dynamics and demography is given in Wu and Yu (2000).

Sexual and seasonal differences in spacing behavior

The overall home range areas were determined for 24 males (captured 11.2 ± 2.1 times in

5.5 ± 0.9 mo) and 12 females (captured 11.9 ± 1.6 times in 6.4 ± 0.6 mo). The distributions of their home ranges in the study area are shown in Fig. 1. The mean size of overall home ranges for males was 4824.7 ± 859.1 m², which is more than twice that for females (2213.5 ± 440.5 m²). The difference in overall home range areas between the 2 sexes was significant ($U = 80$, $p = 0.03$). The correlation between overall home range areas and the numbers of capture records was significant for males ($r_s = 0.528$, $p = 0.008$) but not for females ($r_s = 0.188$, $p = 0.559$). This result implies that the tendency to underestimate overall home range areas was greater in males than in females. It is also possible that home ranges in males shift over time, whereas female ranges are more stable, but there were too few data to examine that possibility.

In total, 27 males from 5 seasons and 10 females from 3 seasons met the criteria for inclusion into the analysis of seasonal spacing behavior (Fig. 2). No females captured in the last 2 seasons were included. Among those individuals, males in summer and autumn 1982 were significantly heavier than those in the other seasons, while females in the 3 seasons were of similar weight (Table 1).

The mean and max. IDs were significantly greater in males than in females (mean ID, $U = 69$, $p = 0.024$; max. ID, $U = 75$, $p = 0.04$) (Table 1). The difference in the home range areas of the 2 sexes did not reach a significant level ($U = 79$, $p = 0.55$). However, the frequency distribution patterns of the home range areas in males and

Table 1. Indices of spacing behavior (mean and maximal inter-capture distances and home range areas) and body weights of adult resident *Niviventer coxingi* in the 5 seasons from spring 1982 to spring 1983. Values are presented as the mean \pm SE

	Spring 1982	Summer 1982	Autumn 1982	Winter 1982	Spring 1983	Five seasons combined
Mean inter-capture distance (m)						
Male	53.8 \pm 21.1	58.9 \pm 12.7	57.0 \pm 7.1	38.5 \pm 7.6	47.7 \pm 5.4	51.8 \pm 4.1
Female	39.9 \pm 3.6	40.3 \pm 11.2	33.8 \pm 6.3	---	---	37.0 \pm 4.3
Maximal inter-capture distance (m)						
Male	126.9 \pm 48.9	98.6 \pm 20.6	94.3 \pm 10.7	66.2 \pm 8.4	85.5 \pm 12.2	92.3 \pm 7.8
Female	52.4 \pm 7.6	60.3 \pm 17.7	64.7 \pm 10.6	---	---	60.9 \pm 7.1
Home range areas (m ²)						
Male	3230 \pm 1218	3653 \pm 1100	3963 \pm 846	1456 \pm 389	1938 \pm 465	2928 \pm 398
Female	1800 \pm 800	1800 \pm 872	1080 \pm 225	1456 \pm 389	1938 \pm 465	1440 \pm 301
Body weight (g)						
Male	140.4 \pm 14.4	189.3 \pm 7.9	168.7 \pm 13.1	137.4 \pm 21.1	139.1 \pm 11.4	157.1 \pm 7.0
Female	140.1 \pm 7.2	146.6 \pm 7.0	138.5 \pm 13.9	---	---	141.3 \pm 7.0
Sample size (male, female)	(3, 2)	(5, 3)	(8, 5)	(4, -)	(7, -)	(27, 10)

females were dissimilar. While the range areas of nine of 10 females were smaller than 3000 m², the areas of 12 of 27 males were larger than 3000 m². Moreover, spatial shifts in seasonal activity centers were greater in males than in females ($U = 15, p = 0.019$).

Correlations between body weights and the 3 spacing indices differed in the 2 sexes. Males showed a significant positive correlation between body weights and spacing indices (Table 2), i.e., larger males tended to move farther or have larger ranges than smaller males. Negative correlations were found in adult females, but only the correlation between body weights and mean inter-capture distances was significant (Table 2).

Seasonal variations in the 3 spacing indices were not statistically significant for either sex. Yet for males, there was an apparent reduction in space use in winter 1982. In the 3 seasons when sexual comparisons were possible, males tended to move farther or have larger ranges (Table 1). But only the male ranges in autumn 1982 were statistically larger than those of females ($U = 6, p = 0.04$).

Spatial dispersion patterns among male-male, male-female, and female-female pairs did not significantly differ ($H_{2, 152} = 0.906, p = 0.636$) (Table 3). However, the 3 groups had different frequency distribution patterns for distances between activity centers. In the female-female and male-female groups, the distances were bimodally distributed, whereas in the male-male group, the distribution was unimodal (Fig. 3).

Overlap in home ranges

Home range overlap indices are presented in Table 4 where a series of numbers is shown for each season. Each number in the series represents the number of adult rats whose home ranges overlap with each focal individual. Among the 4 categories of comparison, more 0 (indicating no

overlap) values were found in intra-sexual groups, except for male-male overlap in autumn 1982. The seasonal variation in the inter-male home range overlap index was significant ($H_{4, 27} = 16.75, p = 0.0022$), which was influenced by the high degree of overlap in autumn 1982. In autumn 1982, all 8 focal males overlapped with from 1 to 4 other males. In addition, the home ranges of four of the focal males in that season overlapped with at least that of 1 female, while the others overlapped with none (Table 4). The 4 males with

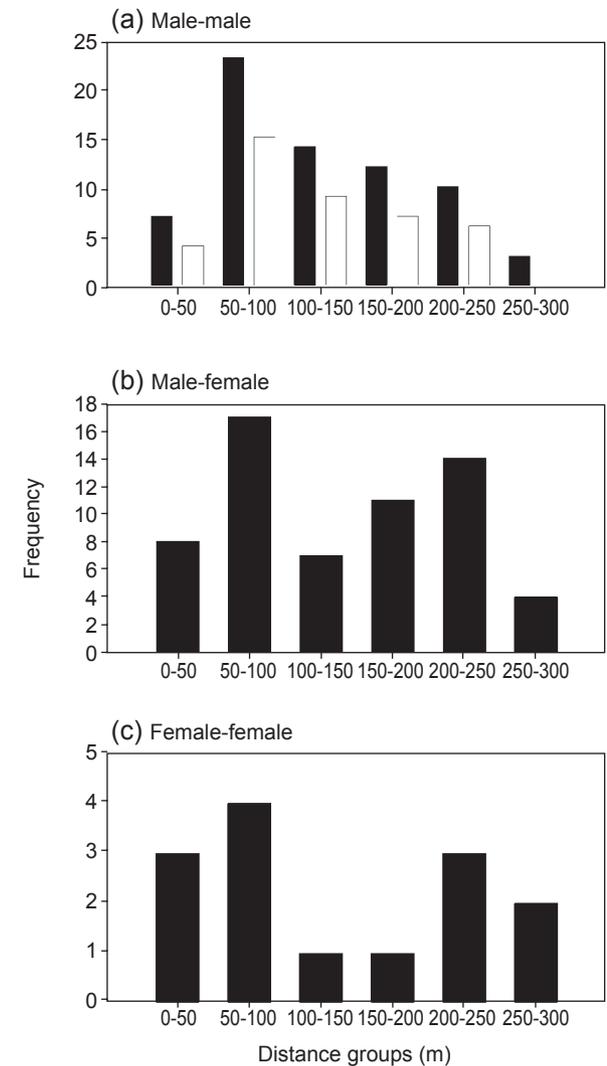


Fig. 3. Frequency distributions of distances between the seasonal activity centers of all possible male-male (a), male-female (b), and female-female (c) pairs. Male-male comparisons were possible in 5 seasons, while the other comparisons were not possible in the last 2 seasons. Therefore, the distributions of male-female and female-female comparisons are based on data from 3 seasons. Male-male comparisons in 3 seasons (closed bar) as well as in 5 seasons (open bar) were separately constructed.

Table 2. Spearman's rank correlation coefficients between body weights and the 3 indices of spacing behavior in male and female *Niviventer coxingi*

	Mean inter-capture distance	Maximal inter-capture distance	Home range area
Male	0.575 ***	0.434 *	0.543 ***
Female	-0.685 *	-0.506	-0.152

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.005$.

female neighbors were all old residents that had been marked before autumn 1982, while the others were recruits of the season.

Positive correlations were found between the number of total squares occupied by adults and the number of adults of either sex in each season. Yet, the correlation was significant in females but not in males (Fig. 4a). In addition, numbers of adult males significantly correlated with seasonal inter-male overlap indices (Fig. 4b). Significant differences were found among the 4 categories of overlap indices (Friedman test statistics = 15.8, $p < 0.005$), and in particular, the overlap for female-male pairs was among the greatest (Fig. 4b). Taken together, the results imply that males and females responded differently to an increase in the adult population size. As the number of adults increased, the total range occupied by either sex expanded. Range expansion was more obvious in females. Whereas adult females tended not to overlap with other adult females, males showed a greater magnitude of overlap with either males or females.

DISCUSSION

Spacing patterns of *Niviventer coxingi* support the prediction for frugivorous-omnivorous rodents (Ostfeld 1985); namely, smaller and more-widely dispersed home ranges for females and larger home ranges for males. The mating system for species with such spacing patterns is likely to be polygynous or promiscuous (Madison 1980, Bubela and Happold 1993), which can be differentiated by the degree of intra- and inter-sexual overlap (Topping and Millar 1996). The low inter-female overlap, high inter-male overlap, and the wide-ranging spacing behavior of males suggest that promiscuity is the most likely system for this species. Consequently, females restrict their movements within small home ranges, while males range over extensive areas to search for potential mates.

Female territoriality is another prediction from Ostfeld's (1985) model on spacing patterns of rodents with an SFF diet. In this study, the exclusiveness of adult home ranges could not be determined by live trapping. However, adult males and

Table 3. Distances between seasonal activity centers (m) of male-male, male-female, and female-female pairs

	Spring 1982	Summer 1982	Autumn 1982	Winter 1982	Spring 1983
Male-male	179.0 ± 53.1 <i>n</i> = 3	143.2 ± 19.6 <i>n</i> = 10	102.0 ± 10.5 <i>n</i> = 28	123.8 ± 28.4 <i>n</i> = 6	138.2 ± 16.3 <i>n</i> = 21
Male-female	167.3 ± 42.9 <i>n</i> = 6	154.3 ± 20.3 <i>n</i> = 15	128.3 ± 11.7 <i>n</i> = 40	---	---
Female-female	59.3 <i>n</i> = 1	176.5 ± 71.2 <i>n</i> = 3	132.4 ± 26.8 <i>n</i> = 10	---	---

Table 4. Inter- and intra- sexual home range overlap indices¹ for all adult males or females in the 5 seasons from spring 1982 to spring 1983

	Spring 1982	Summer 1982	Autumn 1982	Winter 1982	Spring 1983
Male-male	0, 0, 0	0, 0, 0, 1, 1	1, 1, 1, 2, 2, 2, 3, 4	1, 1, 2, 2	0, 1, 1, 1, 1, 1, 1
Male-female	0, 2, 0	0, 0, 1, 1, 1	0, 0, 0, 0, 1, 1, 2, 3	---	---
Female-male	1, 1	1, 1, 1	0, 1, 2, 2, 2	---	---
Female-female	0, 0	0, 1, 1	0, 0, 1, 1, 2	---	---

¹The index indicates the number of rats of the same or opposite sex whose home ranges overlapped with each adult individual.

females differed in the degree of range overlap with individuals of the same or opposite sex. Our results indicated that as the number of adults increased, the number of squares visited collectively by either sex increased more in females, whereas the increase in intra-sexual overlap index was more pronounced in males (Fig. 4). In addition, we also found that males had larger home range areas and overlapped with a greater number of individuals in autumn than in other seasons

(Tables 1, 4). Therefore, we conclude that in autumn when the population size was high, males ranged over large areas, which brought them into greater contact with others. On the contrary, females remained dispersed in autumn as well as in other seasons, which limited their contacts with other females. Nevertheless, the study area was far from saturated with resident females (see Figs. 1, 2). Females may be “facultatively territorial” due to their lack of opportunity to encounter other females at such a low female density.

In spite of being widely dispersed, *N. coxingi* females in the study area were found in 2 clusters, as observed in Figs. 1 and 2, or from the bimodal distribution of the distances between activity centers of females. Two non-exclusive explanations are proposed. Females with overlapping ranges might be mother-daughter pairs or young siblings that establish home ranges near their natal ranges. Topping and Millar (1996) proposed that the degree of genetic relatedness in a rodent population will determine the degree of inter-female overlap. It is also possible that neighboring females are attracted to certain spots by specific resources or habitat features as reported in Ostfeld et al. (1985). Considering the lack of other murid species in *N. coxingi*'s range and the low population density of the species, we reiterate our speculation that numbers of *N. coxingi* are limited by habitat- or resource-related extrinsic factors (Wu and Yu 2000). *Niviventer* species are known to be forest-dwelling rodents (Nowak 1991), with some members of the genus being more dominant in forests than in other habitats (Wu and Yu 2000). Adler (1996) showed that *N. culturatus*, a congener allopatric to *N. coxingi*, prefers large logs. The higher capture rate of *N. coxingi* in the mast year of Fagaceae trees than in years of crop failure as reported elsewhere (Wu 1999) suggests that food might be a limiting resource in some populations. These observations reveal the possibility that *N. coxingi*, especially females, is limited by habitat- or resource-related factors. The negative correlation between female body weight and movement parameters found in this study suggests that larger females might occupy better ranges which might accord them greater fitness.

Trivers (1972) proposed that the general mode for the spacing pattern of male mammals is limited by access to females. This pattern should be dynamic in response to spatial and temporal variations in female availability (Ims 1987, Ostfeld 1990). Intra-sexual overlap of male rodents has been shown to increase as the number of adult

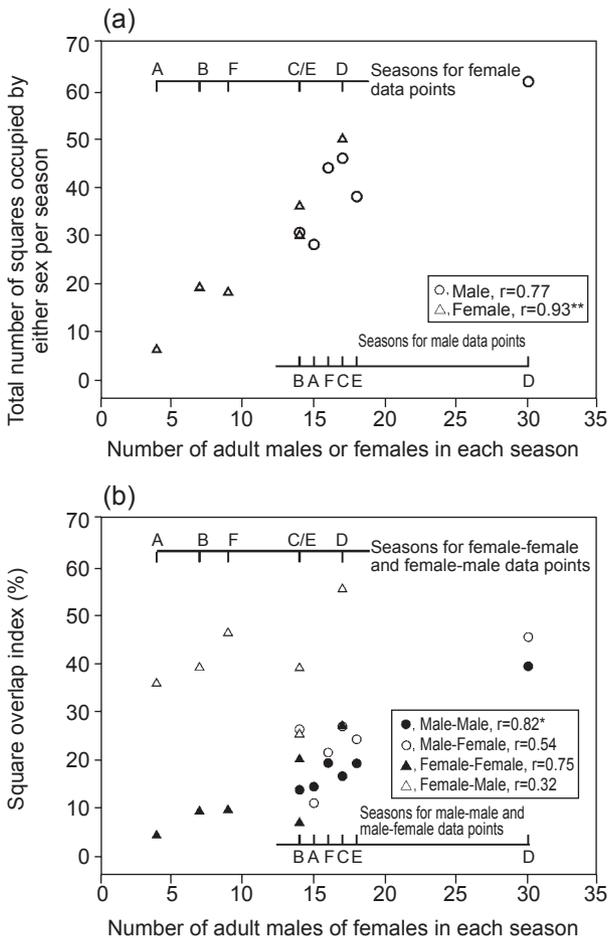


Fig. 4. Scatter-plots of the number of adult *Niviventer coxingi* known to be present and the total numbers of squares occupied by both sexes (a) and the inter- or intra-sexual square overlap indices (b) in the 6 seasons from winter 1981 to spring 1983. The corresponding seasons for data points of females and males are indicated by the tick-marks (A-F) in the upper and lower horizontal lines in each plot, respectively. A, winter 1981; B, spring 1982; C, summer 1982; D, autumn 1982; E, winter 1982; and F, spring 1983. Since the numbers of adults are presented in increasing order, seasons do not appear in chronological order. Spearman's rank correlation coefficients between the numbers of adult males or females and total numbers of squares occupied by either sex and the square overlap indices in the 6 seasons are shown in the legend boxes.

* $p < 0.05$; ** $p < 0.01$.

males increases (Ims 1987, Nelson 1995a). In *N. coxingi*, the level of male-male overlap was higher in autumn (the main breeding season) than in other seasons. Priotto et al. (2002) reported a similar situation in *Calomys venustus*. But they proposed that the degree of home range overlap was dependent on breeding season instead of on population density. In this study, the population peaked in the breeding season. Therefore, it was not possible to differentiate the effects of breeding season and population density on the degree of home range overlap. Studies of multiple populations (e.g., Adler et al. 1997) or for multiple years (e.g., Priotto and Steinmann 1999, Priotto et al. 2002) are needed.

The higher male-male overlap in the breeding season might be explained by the widely accepted view that territory is economically indefensible for males when inter-male competition is high or when females are widely dispersed and briefly receptive (Tew and Macdonald 1994). Zwicker (1989) thought that the high degree of intra-sexual interactions of *Microtus breweri* in the breeding season was symptomatic of an intensification of the likely reproductive strategies of each sex. Adler et al. (1997) found a high degree of range overlap in some populations of the forest-dwelling *Proechimys semispinosus*. They suggested that resources in tropical forests might be randomly or too patchily distributed or ephemeral to permit maintenance of territories. However, Salvioni and Lidicker (1995) warned that large home range overlap should not be interpreted as a lack of territoriality. Males may be intra-sexually territorial on one hand and make long-distance excursions on the other which would give them a home range larger than the defended territory. In *N. coxingi*, males are larger than females (Yu and Lin 1999). Sexual size dimorphism is often thought to be the result of sexual selection by contest competition in males over females, territories, or other resources needed to gain mates (Andersson 1994). We cannot rule out the possibility of male-male competition and territoriality in *N. coxingi*. Intensive radio tracking studies, behavioral experiments (e.g., Ims 1987, Korytko and Vessey 1991), experimental manipulation of food availability, and information on spatial distribution and density of either sex (Ims 1987, Nelson 1995a 1995b, Bond and Wolff 1999, Jonsson et al. 2002) may help to reveal fine-scale spacing patterns and the degree of home range exclusiveness of *N. coxingi*.

The reproductive success of a promiscuous male is related to the number of mates it can

inseminate. It is not easy for *N. coxingi* males to achieve such a goal because receptive females are widely dispersed in space and unpredictable in time (Wu and Yu 2000). Under such constraints, males are required to be vigorous or big enough to maintain large home ranges or to make long daily excursions, which can be revealed by a correlation of home range areas with movement parameters (Tew and Macdonald 1994) or with body weights (Gliwicz 1997). *Niviventer coxingi* seems to choose the latter strategy; home range areas and mean and maximal inter-capture distances of males were positively correlated with body weight. If a large body size in males permits occupation of large home ranges that in turn improves reproductive success as suggested by Gliwicz (1997), selection would push males to channel more energy into growth in body weight than into early reproduction. This coincides with Yu and Lin's (1999) interpretation of sexual dimorphism (adult males larger than adult females) and pubertal strategies (males mature later than females) in *N. coxingi*. Furthermore, detailed inspection of Table 4 reveals a dichotomy in the inter-sexual overlap indices of males; only residents showed range overlap with females. This suggests that resident males might also have some advantages over recruits in finding potential mates.

In summary, based on our previous findings (Wu and Yu 2000) and the present results, we propose that the mating system of *N. coxingi* is most likely to be promiscuous. Sexual differences and seasonal variations in their spacing behavior may be accounted for by the male-biased population structure, low reproductive intensity of the already scarce females, and the availability of food and suitable habitat of the species.

Acknowledgments: We would like to thank the following people and institutes for their assistance in various phases of the study. C. L. Luo, Y. S. Lin, S. P. Yo, J. G. Kie, and the Experimental Forest Station at Chitou kindly offered labor, computer programs, facilities, etc. Yi-Huey Chen read a later version of the manuscript, resulting in significant improvements. The fieldwork was supported in part by the National Science Council of the R.O.C.

REFERENCES

- Adler GH. 1996. Habitat relations of two endemic species of highland forest rodents in Taiwan. *Zool. Stud.* 35: 105-

- 110.
- Adler GH, M Endries, S Protter. 1997. Spacing patterns within populations of a tropical forest rodent, *Proechimys semispinosus*, on five Panamanian islands. *J. Zool.* **241**: 43-53.
- Andersson M. 1994. Sexual selection. Princeton, NJ: Princeton Univ. Press.
- Batzli GO, H Henttonen. 1993. Home range and social organization of the singing vole (*Microtus miurus*). *J. Mammal.* **74**: 868-878.
- Bond ML, JO Wolff. 1999. Does access to females or competition among males limit male home-range size in a promiscuous rodent? *J. Mammal.* **80**: 1243-1250.
- Bubela TM, DCD Happold. 1993. The social organisation and mating system of an Australian subalpine rodent, the broad-toothed rat, *Mastacomys fuscus* Thomas. *Wildlife Res.* **20**: 405-417.
- Chang SW. 1991. The population ecology of *Niviventer coxingi* in the Miantianshan area. Master's thesis, National Taiwan University, Taipei, Taiwan. (in Chinese)
- Chang-Chien LW. 1989. The ecology of rodents in the Miantianshan area of Yangmingshan National Park. Master's thesis, National Taiwan University, Taipei, Taiwan. (in Chinese)
- Gliwicz J. 1997. Space use in the root vole: basic patterns and variability. *Ecography* **20**: 383-389.
- Hayne DW. 1949. Calculation of size of home range. *J. Mammal.* **30**: 1-18.
- Ims RA. 1987. Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *J. Anim. Ecol.* **56**: 585-596.
- Ims RA. 1988. Spatial clumping of sexually receptive females induces space sharing among male voles. *Nature* **335**: 541-543.
- Jonsson P, T Hartikainen, E Koskela, T Mappes. 2002. Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. *Evol. Ecol.* **16**: 455-467.
- Kie JG, JA Baldwin, CJ Evans. 1994. CALHOME: home range analysis program. Fresno, CA: US Forest Service, Pacific Southwest Research Station.
- Korytko AI, SH Vessey. 1991. Agonistic and spacing behaviour in white-footed mice, *Peromyscus leucopus*. *Anim. Behav.* **42**: 913-919.
- Krebs CJ, R Boonstra. 1984. Trappability estimates for mark-recapture data. *Can. J. Zool.* **62**: 2440-2444.
- Lambin X, CJ Krebs. 1991. Spatial organization and mating system of *Microtus townsendii*. *Behav. Ecol. Sociobiol.* **28**: 353-363.
- Liu JS. 1990. Study on the relationships between rodents and vegetation in the Tsaikongkungshan area of Yangmingshan National Park. Master's thesis, National Taiwan University, Taipei Taiwan. (in Chinese)
- Madison DM. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behav. Ecol. Sociobiol.* **7**: 65-71.
- Madison DM, WJ McShea. 1987. Seasonal changes in reproductive tolerance, spacing, and social organization in meadow voles: a microtine model. *Am. Zool.* **27**: 899-908.
- Nelson J. 1995a. Intrasexual competition and spacing behaviour in male field voles, *Microtus agrestis*, under constant female density and spatial distribution. *Oikos* **73**: 9-14.
- Nelson J. 1995b. Determinants of male spacing behaviour in microtines: an experimental manipulation of female spatial distribution and density. *Behav. Ecol. Sociobiol.* **37**: 217-223.
- Nowak RM. 1991. Walker's mammals of the world. 5th ed. Baltimore, MD: The Johns Hopkins Univ. Press.
- Ostfeld RS. 1985. Limiting resources and territoriality in microtine rodents. *Am. Nat.* **126**: 1-15.
- Ostfeld RS, WZ Lidicker, EJ Heske Jr. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. *Oikos* **45**: 433-442.
- Ostfeld RS. 1990. The ecology of territoriality in small mammals. *TREE* **5**: 411-415.
- Priotto J, A Steinmann. 1999. Factors affecting home range size and overlap in *Akodon azarae* (Muridae: Signodontinae) in natural pasture of Argentina. *Acta Theriol.* **44**: 37-44.
- Priotto J, A Steinmann, J Polop. 2002. Factors affecting home range size and overlap in *Calomys venustus* (Muridae: Signodontinae) in Argentine agroecosystems. *Mamm. Biol.* **67**: 97-104.
- Pusenius J, J Viitala. 1993. Varying spacing behaviour of breeding field voles, *Microtus agrestis*. *Ann. Zool. Fenn.* **30**: 143-152.
- Salvioni M, WZ Lidicker Jr. 1995. Social organization and space use in California voles: seasonal, sexual, and age-specific strategies. *Oecologia* **101**: 426-438.
- Siegel S, NJ Castellan Jr. 1988. Nonparametric statistics. 2nd ed. New York: McGraw Hill.
- Tew TE, DW Macdonald. 1994. Dynamics of space use and male vigour amongst wood mice, *Apodemus sylvaticus*, in the cereal ecosystem. *Behav. Ecol. Sociobiol.* **34**: 337-345.
- Topping MG, JS Millar. 1996. Spatial distribution in the bushy-tailed wood rat (*Neotoma cinerea*) and its implications for the mating system. *Can. J. Zool.* **74**: 565-569.
- Trivers RL. 1972. Parental investment and sexual selection. In B Campbell, ed. *Sexual selection and the descent of man*. Chicago, IL: Aldine, pp. 136-179.
- Wolff JO. 1993. Why are female small mammals territorial? *Oikos* **68**: 364-370.
- Wu HY. 1999. Is there current competition between sympatric Siberian weasels (*Mustela sibirica*) and ferret badgers (*Melogale moschata*) in a subtropical forest ecosystem of Taiwan? *Zool. Stud.* **38**: 443-451.
- Wu HY, HT Yu. 2000. Population dynamics of spiny rat, *Niviventer coxingi*, in a subtropical montane forest at Chitou, central Taiwan. *J. Zool. Lond.* **250**: 339-346.
- Yu HT. 1993. Natural history of small mammals of subtropical montane areas in central Taiwan. *J. Zool. Lond.* **231**: 403-422.
- Yu HT. 1994. Distribution and abundance of small mammals along a subtropical elevational gradients in central Taiwan. *J. Zool. Lond.* **234**: 577-600.
- Yu HT, YS Lin. 1999. Age, reproduction and demography of the spiny rat (*Niviventer coxingi*; Muridae) in subtropical central Taiwan. *Zool. Stud.* **38**: 153-163.
- Zwicker K. 1989. Home range and spatial organization of the beach vole, *Microtus breweri*. *Behav. Ecol. Sociobiol.* **25**: 161-170.