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Space Use and Social Structure of Long-Tailed Singing Mice (*Scotinomys xerampelinus*)

SPACE USE AND SOCIAL STRUCTURE OF LONG-TAILED SINGING MICE (*SCOTINOMYS XERAMPELINUS*)

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Scotinomys xerampelinus, the long-tailed singing mouse, is diurnal and insectivorous, and exhibits a complex and unique calling behavior that is audible to humans. Little is known about the social structure of this species. We used livetrapping and radiotracking to investigate the spatial organization of a wild Panamanian population of long-tailed singing mice. We observed exclusive space use among females but not among males. For both males and females, individual home ranges (85% minimum convex polygons) typically overlapped with >1 animal of the opposite sex. No significant differences in body mass, hind-foot length, or home-range size (area) were found between males and females. Most individuals in the population nested alone. Patterns of space use and sexual dimorphism are frequently used to infer species' mating systems. Our results, in particular the tendency for individual home ranges to overlap with multiple potential reproductive partners, are most consistent with a promiscuous mating system.

Key words: home range, mating system, *Scotinomys*, social behavior, space use

The spatial distribution of individuals may be strongly influenced by social processes and thus patterns of space use are often used to infer the mating and social systems of a population (Gaulin and Fitzgerald 1988; Shier and Randall 2004; Steinmann et al. 2005). In particular, sex-specific differences in home-range use can yield insights into the mating system and can improve understanding of the behavior of little-studied species (reviewed in Clutton-Brock 1989, 1991; Gaulin and Fitzgerald 1988; Heske and Ostfeld 1990; Ostfeld 1985; Reichard 2003; Schradin and Pillay 2005; Shier and Randall 2004; Steinmann et al. 2005). For example, in polygynous mating systems, home ranges of males tend to overlap less than those of females, and a given female typically overlaps with only 1 male. In contrast, in promiscuous mating systems, home-range use by males and females is expected to be more equitable, with each individual's home range overlapping those of several members of the opposite sex. Finally, socially monogamous systems should be characterized by exclusive (nonoverlapping) home ranges, each of which is shared by a male–female pair (Clutton-Brock 1989; Ophir et al. 2008; Ostfeld 1985; Shier and Randall 2004).

Sexual size dimorphism is another attribute that is commonly used to infer animal mating systems (Heske and

Ostfeld 1990; Kleiman 1977). Polygynous mammals frequently display sexual size dimorphism, which is thought to result from intense reproductive competition among males. In contrast, males in monogamous or promiscuous species may be subject to less-intense competition, resulting in reduced selection for sexual size dimorphism (Darwin 1871; Heske and Ostfeld 1990; Orians 1969; Trivers 1972). At the same time, increased territoriality among females in promiscuous or socially monogamous systems also may contribute to the reduced sexual dimorphism observed in these species (Heske and Ostfeld 1990).

The long-tailed singing mouse (*Scotinomys xerampelinus*) occupies high-elevation cloud forests and grasslands in Panama and Costa Rica (Hooper and Carleton 1976). Currently, *Scotinomys* is placed in the superfamily Muroidea, the family Cricetidae, and the subfamily Neotominae (Musser and Carleton 2005; Steppan et al. 2004). Singing mice are named for their intriguing calls that span both ultrasonic and human-audible frequencies. The behavior and ecology of singing mice are largely undescribed, particularly with respect to their social behavior in the wild. The goal of this study was to characterize the spatial organization of a free-living population of *S. xerampelinus* in order draw inferences regarding the mating and social system of this species. We compared patterns of space use in *S. xerampelinus* to those expected under the various mating systems known to occur in rodents; the most common of these are promiscuity and polygyny (Ostfeld 1985; Waterman 2007), although social monogamy also is known to occur in ~5% of mammalian

species (Kleiman 1977). We predicted that, if the study population was polygynous, both space use and body size should be sexually dimorphic, with home ranges for males being larger and overlapping less than those of females; home ranges of females should overlap with only 1 male. In contrast, if the study population was promiscuous, sexual dimorphism should be less pronounced and home ranges for both males and females should overlap with those for multiple members of the other sex. Finally, if the study population was socially monogamous, there should be distinct home ranges shared by male–female pairs and little or no sexual size dimorphism. Our findings yield new insights into relationships between space use, sexual dimorphism, and the mating systems of small mammals.

MATERIALS AND METHODS

Study site and study population.—The study site was located in Parque Internacional La Amistad in the Cerro Punta region of western Panama (8°53.718N, 82°37.123W; elevation 2,270 m). The study extended over 2 field seasons: August–September 2003 and May–June 2004. All data collection was performed in an abandoned pasture, which is reportedly a preferred habitat of *S. xerampelinus* (Hooper and Carleton 1976; Van den Bergh and Kappelle 1998). The study site was bordered on 2 sides by montane forest, on the 3rd side by a stream, and on the 4th side by a deep gully caused by a landslide. Vegetation at the site consisted mostly of grass but was dotted with elephant ears (*Colocasia*), oak trees (*Quercus*), shrubs (*Alnus* and *Wercklea*), tree stumps, and decomposing logs. In 2003, the grass at the site was ungrazed and was approximately 1 m tall. In 2004, the grass was initially much shorter due to grazing by horses before our arrival. Because this change in conditions between field seasons may have influenced key ecological parameters such as resource distributions and predator protection, it is possible that it affected the patterns of space use documented here.

During the 1st field season, both livetrapping ("trapping localities") and radiotracking ("fixes") data were used to characterize individual home ranges. These data were collected over a period of 18 days, from 19 August to 5 September 2003. Because of technical problems, including receiver failure, we were unable to collect telemetry data during the 2nd field season, which continued over a period of 35 days, from 24 May to 27 June 2004. Thus, only livetrapping data were used for the 2nd field season. This difference in data sets should not have affected our statistical comparisons of home-range attributes, because our method of overlap analysis generated both expected and observed values from the same data set (2003: livetrapping and radiotelemetry; 2004: livetrapping only). Although our data collection was limited to May, June, August, and September, the mountainous regions of western Panama have consistently wet weather throughout the year and *Scotinomys* reproduces aseasonally (Hooper and Carleton 1976), suggesting that space use by members of the study population should not vary greatly over the course of the year.

Livetrapping.—Animals were captured using Sherman live traps (5 × 6 × 16 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida). In 2003, a 40 × 40-m grid (10-m^2 cell size) containing 50 traps was established in the pasture about 30 m from the forest edge. In 2004, a 60 × 70-m grid containing 96 traps was established in the same location. A larger grid size was used to increase the number of animals captured, although the effective size of this grid was somewhat smaller (approximately 3,500 m^2) than the actual size because of patches of unused habitat (see "*Exclusivity of space use*" for details). Two traps were placed as close as possible to the corner of each grid cell, in the nearest suitable trapping microhabitat. We defined "suitable trapping microhabitat" as those places where a rodent would be likely to travel, that is, in or next to logs or within tall vegetation. The location of each animal captured was recorded to the nearest 0.5 m. Approximately midway through the 2004 field season (day 14), the traps were shifted 5 m in 1 direction along each axis of the grid, with the result that the traps were now in the middle of each grid square, rather than at the corners. This allowed for greater coverage of the microhabitats contained in the grid, thereby potentially increasing trapping success.

The mice were most active between 0700 and 1100 h (Hooper and Carleton 1976), so live traps were set between 0600 and 0700 h. To avoid biases associated with consistently trapping at the same time of day, we varied the order in which we set and checked traps and varied the time in the afternoon when traps were checked. Upon 1st capture, each individual was weighed, its sex was determined, and the length of its right hind foot was measured to provide data on sexual dimorphism in body size. Age (juvenile, subadult, or adult) and reproductive state (females: imperforate, perforate, lactating, or pregnant; males: nonscrotal or scrotal) also were recorded. Age was determined by body weight and reproductive condition (Hooper and Carleton 1976). Individuals weighing <8 g were classified as juveniles. Individuals between 8 g and 11.5 g and that were not yet sexually mature (imperforate for females and nonscrotal for males) were classified as subadults. Individuals > 11.5 g and all individuals that were sexually mature were classified as adults. Each animal was uniquely marked by clipping a unique combination of toes (Murray and Fuller 2000); previous studies of the closely related *S. teguina* (Langtimm 1992) have revealed that ear tags are typically torn out of the pinnae, thereby necessitating an alternative means of marking the animals. Toe-clipping was performed with a pair of clean, sharp dissecting scissors; no more than 2 toes per animal were clipped. Lidocaine cream (a topical anesthetic) was applied before clipping to minimize the animal's discomfort and, when necessary, a styptic swab was used to stop any bleeding. After completion of these procedures, the animal was released at the point of capture.

Radiotelemetry.—In 2003, all adults caught on the grid were outfitted with radiocollars at the time of 1st capture. Holohil transmitters (model BD-2NC; Holohil Systems Ltd., Carp, Ontario, Canada) were affixed to individuals using a plastic

cable-tie collar threaded through flexible Tygon tubing (Saint-Gobain Performance Plastics, Akron, Ohio). The transmitters weighed 0.60 g, which is <5% of the mean body mass of adults on the study grid (14.2 g $\pm$ 0.2 SE, n = 44 animals). Each collared animal was placed in a small cage for a period of 2–3 h so that we could monitor the fit of the collar before the animal was released. Collars were removed at the end of the study. A Telonics receiver and a 3-element yagi antenna (Telonics Inc., Mesa, Arizona) were used to locate the animals following the homing and triangulation techniques of Mech (1983) and White and Garrott (1990); locations were recorded using our grid cell markers. Collared animals were located once per day; the resulting interval between radiofixes was long enough to ensure that consecutive data points were likely statistically independent (Kenward 2001). To minimize potential biases associated with only taking fixes at certain times of the day (Kenward 2001), we spread radiotracking efforts across all daylight hours (when *Scotinomys* is active); we also conducted some sampling at night to identify nest sites.

All procedures were reviewed and approved by the University of Florida Institutional Animal Care and Use Committee, and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Research and collecting permits were obtained from the government of Panama.

Analyses of home ranges.—To characterize home ranges, we 1st defined grid residents as those animals that were caught or located via radiotelemetry on the grid ≥ 4 times during the study. This allowed us to exclude nonresidents that were passing through the grid. Requiring ≥ 4 data points would have severely limited the number of animals included in our analyses. Although 4 was the minimum number of records required, the majority of animals identified as grid residents (18 of 20) were characterized by ≥ 4 data points. Our number of data points (both minimum and average) was comparable to those of published studies estimating rodent home ranges (Adler et al. 1997; Batzli and Henttonen 1993; Bergallo and Magnusson 2004; Priotto et al. 2002; Ribble et al. 2002; Seamon and Adler 1999; Tchabovsky et al. 2004). Because individuals were collared upon 1st capture, some of these animals were later determined to not be resident on the grid. Density of grid residents was determined by dividing the number of residents by the grid area, and extrapolating to hectares. Only adults were included in these analyses.

Sample sizes from 2003 were too small to compare directly home ranges generated from radiotracking and trapping data and thus we combined the 2 data sets. We confirmed that there was no correlation between number of data points and home-range area. This was checked for each field season separately and with data for both field seasons combined (2003: r^2 = 0.050, P = 0.533, n = 10; 2004: r^2 = 0.103, P = 0.367, n = 10; pooled seasons: r^2 = 0.094, P = 0.188, n = 20). We plotted cumulative total animals trapped during the study versus total trapping time; this relationship reached a plateau, suggesting that we successfully trapped all animals in the study grid.

Home-range sizes and degree of overlap were estimated using minimum convex polygons (MCPs—Mohr 1947) generated by the Ranges 6 software program (Kenward et al. 2003). We chose this method of home-range estimation because our analyses include both livetrapping and radio-tracking data, and MCPs can be compared across different data collection methods. MCPs also are comparable across studies that use differing grid cell numbers and sizes, making our analyses suitable for comparisons with other home-range studies (Jones and Sherman 1983; Oakwood 2002; Ribble et al. 2002; Seamon and Adler 1999). Initially, 85% MCPs (recalculated with the arithmetic mean—Kenward et al. 2003) were generated for each grid resident; 85% MCPs were chosen because they exclude infrequent forays outside of the home range, thereby providing a potentially more accurate estimator of home-range area and overlap than 100% MCPs (Kenward 2001; Wauters et al. 2005, 2007). Because some individuals in our sample were characterized by only a few data points, we also examined 100% MCPs in order to ensure that estimates of home-range size and overlap were not unduly altered by the exclusion of some locations. Estimates of home-range area included radiofixes that were located outside of the grid. We compared sizes of home ranges of males and females both between and within years using the Mann–Whitney U-test.

Exclusivity of space use.—We examined exclusivity of space use by employing a variation of the method described by Batzli and Henttonen (1993). Specifically, we used a null hypothesis of random placement of home ranges throughout the grid. Observed home-range overlap that was significantly less than expected under the null (random) model suggests that conspecifics were demonstrating spatial exclusion, thus meeting 1 criterion for territorial behavior (Batzli and Henttonen 1993; Priotto and Steinmann 1999). In contrast, observed home-range overlap that did not differ from expected or that was greater than expected would be interpreted, respectively, as evidence of nonexclusion or affiliation.

For the overlap analyses, we excluded any radiotracking fixes that were located outside of the trapping grid; home-range boundaries were then recalculated using this modified data set. The method of Batzli and Henttonen (1993) for assessing overlap requires estimation of the proportion of the grid used by each animal and thus only points from within the grid were appropriate for this analysis. Our null hypothesis assumes that each home range has an equal probability of occurring at any location on the grid (Batzli and Henttonen 1993). Thus, each grid cell must represent usable habitat. We defined usable habitat as each grid cell that contained a trap in which ≥ 1 animal was captured. In 2003, every grid cell contained successful traps; in 2004, 7 grid cells did not contain successful traps; when these cells were excluded, the area of the grid was reduced from 4,200 m^2 to 3,500 m^2.

Mean values for expected overlap were generated by 1st calculating the expected overlap for each pair of animals resident on the grid during the same season (Batzli and Henttonen 1993). Mean values for observed overlap were generated from the observed overlap for each pair of animals

(Ranges 6—Kenward et al. 2003). We used the same method to compute expected and observed values for overlap between same-sex and opposite-sex pairs. A key attribute of this method is that it calculates expected values using only observed home-range and grid size and is therefore robust to variation in the methods used to estimate home-range size. For example, if radiotracking gives larger home-range estimates than livetrapping, it will produce larger observed overlaps, but it also will yield correspondingly larger expected overlaps. The result is a powerful method for comparing overlap estimated from disparate data sets, including data sets that combine trapping and radiotracking data.

Expected and observed data values were compared using the Wilcoxon signed rank test. Data were analyzed within each season (2003 and 2004 separately) and also across years (2003 and 2004 combined). All results are reported $\pm$ 1SE, and an alpha level of 0.05 was used for all statistical tests.

RESULTS

Study population attributes.—In 2003, 24 adults (9 males and 15 females, sex ratio = 0.6:1) were trapped on the study grid. In 2004, 20 adults (9 males and 11 females, sex ratio = 0.8:1) were trapped on the study grid. The density of residents (i.e., animals captured $\geq$4 times on the study grid) in 2003, when vegetation was overgrown, was 62 mice/ha; in 2004, when vegetation was grazed, density was 28 mice/ha. Females were found to be pregnant or lactating or both from June to September 2003 and May to August 2004; this represents the entire study period as well as some pre- and poststudy trapping of animals on the site. This finding is consistent with the data of Hooper and Carleton's (1976) indicating that reproduction by *Scotinomys* is aseasonal. The ratio of scrotal males to perforate, pregnant, or lactating females was 9 to 13 (0.7:1) in 2003 and 8 to 10 (0.8:1) in 2004.

For body weights and hind-foot lengths we included animals livetrapped on the study grid as well as some individuals captured in the area surrounding the study grid. Mean body weights for males and nonpregnant females were not significantly different (males, 14.4 $\pm$ 0.3 g, n = 43; females, 13.9 $\pm$ 0.3 g, n = 37; Student's t-test, t = −1.291, $d.f.$ = 78, P = 0.201). Similarly, mean hind-foot lengths for males and females were not significantly different (males, 18.3 $\pm$ 0.1 mm, n = 41; females, 18.3 $\pm$ 0.1 mm, n = 37; t = −0.169, $d.f.$ = 76, P = 0.867). Thus, we found no evidence of sexual size dimorphism among members of the study population.

Most grid residents appeared to nest solitarily. Of the 10 animals radiotracked during 2003, 4 males and 4 females consistently nested alone. However, the remaining 2 animals (1 male and 1 female) shared a nest for several nights.

Home-range areas.—Our calculations of home-range area were not restricted to data points recorded on the grid. As a result, for 2003, we were able to include an additional 2 males and 2 females, resulting in a total of 14 animals included in analyses of home-range area. The average number of data points per individual was 9.8 $\pm$ 1.4. No additional animals

were included in analyses for 2004 and, thus, the average number of data points per individual remained 8.5 $\pm$ 1.0. Home-range areas based on 85% MCPs did not differ between males and females in either year (Figs. 1 and 2a; Mann–Whitney U-tests; 2003: z = −0.192, $n1$ = 7, $n2$ = 7, P = 0.85; 2004: z = −0.94, $n1$ = 5, $n2$ = 5, P = 0.35). Home-range areas (85% MCPs) for each sex did not differ significantly between years (Fig. 2a; Mann–Whitney U-test; females: z = −1.056, $n1$ = 7, $n2$ = 5, P = 0.29; males: z = −0.893, $n1$ = 7, $n2$ = 5, P = 0.37). Similarly, home-range areas based on 100% MCPs did not differ significantly between males and females (Fig. 2b; Mann–Whitney U-tests; 2003: z = 0, $n1$ = 7, $n2$ = 7, P > 0.999; 2004: z = −1.358, $n1$ = 5, $n2$ = 5, P = 0.17) nor did home-range areas (100% MCPs) for each sex differ significantly between years (Fig. 2b; Mann–Whitney U-tests; females: z = −1.705, $n1$ = 7, $n2$ = 5, P = 0.09; males: z = −0.244, $n1$ = 7, $n2$ = 5, P = 0.81). In both years, home-range areas based on 100% MCPs were significantly larger than those based on 85% MCPs, with an average difference of 345 $\pm$ 117 m^2 in 2003 and 255 $\pm$ 86 m^2 in 2004 (Wilcoxon signed rank tests; 2003: z = −3.180, n = 14, P = 0.002; 2004: z = −2.803, n = 10, P = 0.005).

Home-range overlap.—For the home-range overlap analyses, we were only able to use fixes that were within the study grid. During 2003, 24 of the animals captured were also radiotracked over 18 days (total n = 158 data points). Ten of these animals were located $\geq$4 times within the grid and were classified as grid residents (average number of data points per animal, fixes and trapping localities combined: 6.9 $\pm$ 0.8; radiofixes per animal: 3.5 $\pm$ 0.3; trapping localities per animal: 3.2 $\pm$ 1.0). During 2004, 20 animals were trapped over 35 days (total n = 104 data points). Ten of these animals had $\geq$4 capture localities on the grid (average trapping localities per animal: 8.5 $\pm$ 1.0). Despite the difference in grid size between the 2 field seasons, we had identical sample sizes (5 males and 5 females) in each field season. None of the animals marked in 2003 was recaptured in 2004 and, thus, the 2 seasons represent independent samples. The mean number of data points per animal did not differ significantly between seasons (Mann–Whitney U-test: z = −0.983, $n1$ = 10, $n2$ = 10, P = 0.318) and thus we pooled data from both seasons for some analyses. The mean number of data points per animal in the pooled data set was 7.7 $\pm$ 0.7.

In 2003 (Figs. 1a and 1b), none of the observed home-range overlaps were significantly different from expected for either 85% or 100% MCPs (Table 1; Wilcoxon signed rank tests, P > 0.05). In 2004 (Figs. 1c and 1d), female–female home-range overlap was significantly less than expected for both 85% and 100% MCPs (Table 1; Wilcoxon signed rank tests; 85% MCP: z = −1.753, n = 5, P = 0.080; z = −2.023, n = 5, P = 0.043). All other comparisons of home-range overlap in 2004 (85% and 100% MCPs) were not significantly different from expected (Table 1; P > 0.05).

Although the 2003 comparison of female–female home-range overlap (85% MCPs) was not significant (P = 0.080), the pattern was the same as the 2004 female–female home-
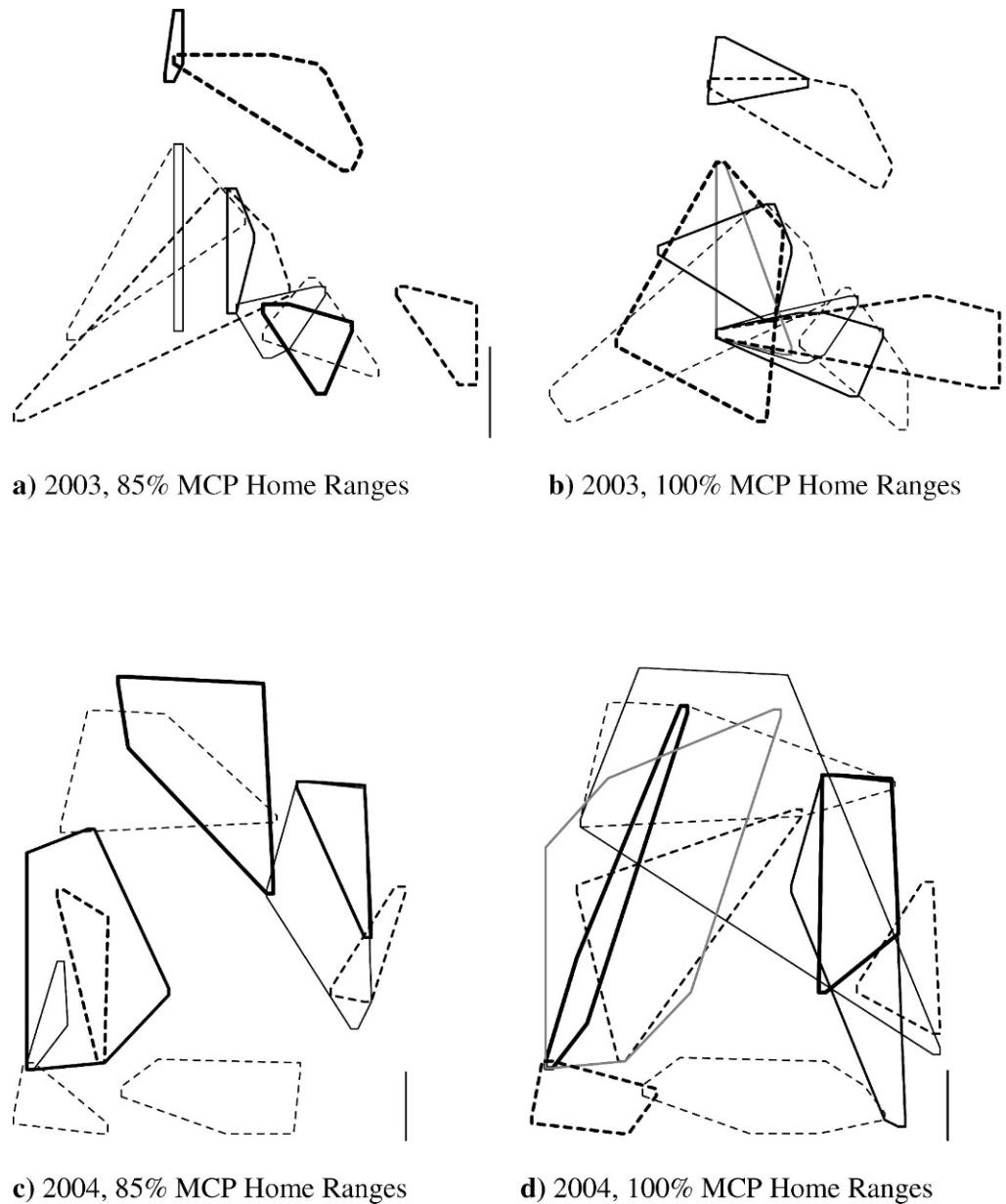
a) 2003, 85% MCP Home Ranges   b) 2003, 100% MCP Home Ranges

c) 2004, 85% MCP Home Ranges   d) 2004, 100% MCP Home Ranges

FIG. 1.—Home ranges for individual *Scotinomys xerampelinus* located (captured or fixed via telemetry) on the study grid $\geq$4 times for (a) 2003, 85% MCP Home Ranges, (b) 2003, 100% MCP Home Ranges, (c) 2004, 85% MCP Home Ranges, and (d) 2004, 100% MCP Home Ranges. Home ranges are calculated using the arithmetic mean method. Home ranges for males (solid lines) and females (dashed lines) are shown; 10-m scale lines are indicated.

range overlap, with observed overlap being less than expected (Table 1). Therefore, we pooled the data to assess the strength of the shared pattern across years. Pooling both years, the female–female home-range overlap was significantly less than expected for 85% but not for 100% MCPs (Fig. 3; Wilcoxon signed rank tests; 85% MCPs: $z = -2.701$, $n = 10$, $P = 0.007$; 100% MCPs: $z = -1.886$, $n = 10$, $P = 0.059$). Male–male 100% MCP home-range overlap was significantly greater than expected in the pooled data (Wilcoxon signed rank test; $z = -1.988$, $n = 10$, $P = 0.047$). All other pooled overlap comparisons were not significantly different from expected.

For the pooled data set (85% MCPs), each home range was overlapped on average by the home ranges of 2.2 $\pm$ 0.3 other animals (Figs. 1a and 1c); when an individual was overlapped by another individual, the area of overlap was on average 19.5% $\pm$ 5.7% of the focal animal's home range. Males overlapped on average with 1.0 $\pm$ 0.2 other males; when a male was overlapped by another male, the area of overlap was on average 22.5% $\pm$ 12.6%. Females overlapped on average with 0.2 $\pm$ 0.1 other females; when a female was overlapped by another female, the area of overlap was on average 3.0% $\pm$ 6.4% of the focal animal's home range. Mice of each sex overlapped with similar numbers of opposite-sexed animals (males: 1.6 $\pm$ 0.2; females: 1.6 $\pm$ 0.4). When a male was overlapped by a female, the area of overlap was on average 12.0% $\pm$ 5.8% of the male's home range. When a female was
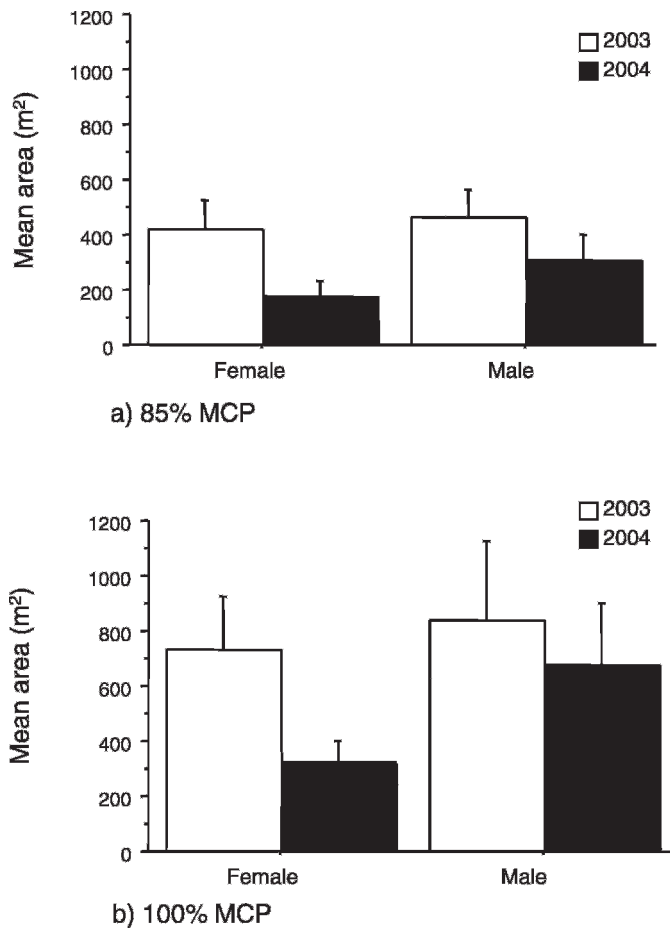
Fig. 2.—Comparisons of mean home-range sizes of *Scotinomys xerampelinus* across seasons for a, c) 85% minimum convex polygon and b, d) 100% minimum convex polygon. Data shown are means ± 1 *SE*. All comparisons are not statistically significant (*P* > 0.05).
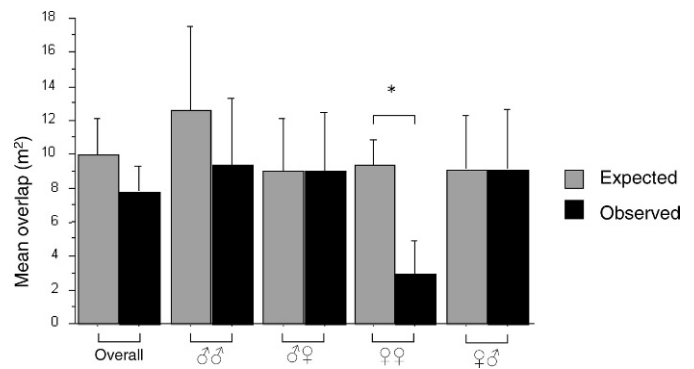

Fig. 3.—Mean ± 1 *SE* expected (random) and observed areas of home-range overlap of *Scotinomys xerampelinus*. Analyses are based on 85% minimum convex polygons; data from 2003 and 2004 were pooled. Observed = observed average area of home-range overlap on the study grid. Expected = average area of home-range overlap predicted from random placement of home ranges on the study grid. An asterisk (*) indicates *P* < 0.05, Wilcoxon sign rank comparisons of observed and expected areas of overlap. *n* = 10 males and 10 females. ♂♂ = males overlapped by males; ♂♀ = males overlapped by females; ♀♀ = females overlapped by females; ♀♂ = females overlapped by males.

overlapped by a male, the area of overlap was on average 20.3% ± 10.1% of the female's home range. Comparing intersexual with intrasexual overlap, we found that in 2003, the observed average home-range overlap (85% MCPs) of males by other males (1.7 ± 1.0 m^2) was significantly less

than that for males overlapped by females (5.2 ± 1.3 m^2; Wilcoxon signed rank test; $z = -2.023$, $n = 5$, $P = 0.043$). No other intersexual or intrasexual patterns of overlap were significantly different from expected.

For the pooled data set (100% MCPs), each home range was overlapped on average by the home ranges of 4.7 ± 0.4 other animals (Figs. 1b and 1d); when an individual was overlapped by another individual, the area of overlap was on average 18.1% ± 3.4% of the focal animal's range. Males overlapped on average with 2.4 ± 0.3 other males; when a male was overlapped by another male, the area of overlap was on average 27.3% ± 9.2% of the focal animal's home range. Females overlapped on average with 1.2 ± 0.3 other females; when a female was overlapped by another female, the area of overlap was on average 10.7% ± 5.6% of the focal animal's home range. Mice of each sex overlapped with similar

TABLE 1.—Comparison of expected versus observed areas of home-range overlap of *Scotinomys xerampelinus*. Analyses are based on 85% minimum convex polygons calculated with the arithmetic mean method. Comparisons of expected and observed values were according to Batzli and Henttonen (1993). Obs. overlap = observed home-range overlap on the study grid. Exp. overlap = expected area of home-range overlap based on random placement of home ranges on the study grid. Means are given ± 1 *SE*. ♂♂ = males overlapped by males; ♂♀ = males overlapped by females; ♀♀ = females overlapped by females; ♀♂ = females overlapped by males.

	Mean exp. overlap (m^2)	Mean obs. overlap (m^2)	*P*-value	*Z*-value
2003				
Overall	4.2 ± 1.1	4.6 ± 1.3	>0.1	−0.866
♂♂	0.6 ± 0.1	1.7 ± 1.0	>0.1	−0.405
♂♀	2.8 ± 0.7	5.2 ± 1.3	0.080	−1.753
♀♀	11.1 ± 2.3	5.8 ± 3.5	0.080	−1.753
♀♂	2.8 ± 0.8	5.4 ± 2.5	>0.1	−0.944
2004				
Overall	15.6 ± 3.4	10.9 ± 2.5	0.059	−1.886
♂♂	24.4 ± 6.6	17.1 ± 6.1	>0.1	−0.405
♂♀	15.2 ± 4.7	12.7 ± 6.7	>0.1	−0.674
♀♀	7.6 ± 1.8	0.0 ± 0.0	0.043	−2.023
♀♂	15.2 ± 5.2	12.7 ± 6.8	>0.1	−0.135

numbers of opposite-sexed animals (males: 2.9 ± 0.3; females: 2.9 ± 0.4). When a male was overlapped by a female, the area of overlap was on average $14.5\% \pm 5.1\%$ of the male's home range. When a female was overlapped by a male, the area of overlap was on average $16.8\% \pm 5.2\%$ of the female's home range.

The greater size of 100% MCPs (Figs. 1a and 1d) indicate that the mice will occasionally venture outside of their 85% MCP home ranges by a considerable distance. In 2003, the 100% MCP home ranges of 4 individuals converged at a similar locality (3 males and 1 female; Fig. 1b), suggesting that there was something distinctive about the habitat at that location. In 2004, 3 individuals (2 males and 1 female; Fig. 1d) exhibited a similar pattern, with their home ranges converging at the same locality noted in 2003.

DISCUSSION

Examination of our data revealed little evidence of sexual dimorphism in size or space use among members of the study population. Measurements of body mass and hind-foot length did not differ between sexes. Most animals tended to nest alone and there was no difference in the home-range sizes for males and females. Female–female home-range overlap was significantly less than expected in 1 but not both field seasons. Male–male home-range overlap was significantly greater than expected in our pooled data set, but only for 100% MCPs. Thus, although some intersexual differences in behavior were detected, overall patterns of space use were not strikingly different for males and females in our study population.

Because of the relatively small number of data points per animal, our data on home-range size and overlap are best viewed as a preliminary assessment of space use by *S. xerampelinus*. We interpreted the 85% MCP contours as the most intensively used portion of the home range, with 100% MCP contours being driven by forays outside of the home range. This is consistent with both empirical and modeling studies that have recommended 85% MCP as the portion of the home range that contains the highest activity for a given individual (Wauters et al. 2005, 2007). However, given our sample sizes, we cannot rule out the possibility that the number of data points per individual used to generate 85% MCPs influenced our findings regarding home-range area and, in particular, home-range overlap. Given that home-range areas (85% or 100% MCPs) did not differ between males and females in either year, however, we believe that our data provide a reasonable representation of intersexual differences in space use. In the male–male overlap data, we should note that 4 males exhibited largely exclusive 85% MCP home ranges, whereas 6 other males had extensive male–male home-range overlap (Figs. 1a and 1c). The extent of individual variation in spatial patterns suggests that space use by males is flexible and may vary in response to external factors (e.g., location of receptive females) or may represent alternative strategies, as have been shown to occur in other rodents (Getz et al. 1993).

Examination of our data suggests that females tend to be more exclusive in their use of space than males. Exclusive space use is one of the criteria used to define territoriality, frequently along with defended area and site-specific dominance (Howard 1920; Kaufmann 1983; Maher and Lott 1995). Data on social interactions between females are needed to determine if exclusive space use in this sex reflects active defense of a territory, or whether it reflects an alternative behavior, such as mutual avoidance or nest-site fidelity. In contrast to female–female patterns, female home ranges overlapped noticeably with those of males. These overlapping distributions may result from active affiliation (both mating and social) or utilization of a common resource. Because each individual overlapped with on average 2 other individuals (representing an average of 20% of each home range), the study population falls between the extremes of solitary and colonial or communal breeding and thus examination of our data suggests a semisocial community of conspecifics.

In each field season, multiple home ranges converged on a large log. The distribution of resources on the study grid was patchy, with resource-rich insect habitats such as rotten logs and tree stumps dotting the pasture. *S. xerampelinus* is insectivorous and we suggest that both females and males exhibit intrasexual and intersexual overlap at resource-rich "hot spots." These highly visited areas of the study grid are of interest because they may provide an opportunity for mice of both sexes to obtain information regarding conspecifics, including the sex, age, and reproductive state of neighboring individuals.

The attributes of space use by *S. xerampelinus* that we measured suggest a promiscuous rather than a polygynous or socially monogamous mating system. We had predicted that a promiscuous population would not exhibit sexual size dimorphism, and that male and female home ranges should overlap with multiple members of the other sex; a polygynous population was predicted to be sexually dimorphic, with large, nonoverlapping male home ranges. Our results showed no or minimal sexual dimorphism in body size or space use, male home ranges overlapped substantially with each other, and animals of both sexes had access to multiple potential reproductive partners. Further, we found little evidence for male–female pairs sharing home ranges or nests; coupled with the absence of exclusive space use among males, this observation contradicts patterns characteristic of monogamous rodents. Because 1 male–female pair shared a nest site and home ranges, there may be a capacity for social flexibility, the consequences of which have yet to be explored. A definitive assessment of the mating system of this species will require measuring patterns of genetic parentage in natural populations.

The spatial patterns we observed are consistent with prevailing models for space use among small mammals. The distributions of female rodents are thought to be determined primarily by resource availability (e.g., food and nest sites) or prevention of infanticide, whereas the distributions of males are thought to be determined primarily by those of females (Emlen and Oring 1977; Ostfeld 1990; Wolff and Peterson

1998). When females are widely dispersed, the costs of defending multiple reproductive partners may be high enough that males will forgo territoriality and perhaps even polygyny. Thus, when females show exclusive space use, males may not. Conversely, when females overlap, males may benefit from defense and exhibit exclusive space use. Social monogamy is a notable exception: male–female pairs share home ranges but both exclude same-sexed conspecifics (Ostfeld 1985, 1990). Although the insect-rich resources (e.g., logs and tree stumps) at our study site had a patchy distribution, this was not reflected in the home ranges of females. Infanticide or non–insect-rich resources may have been more important determinants of space use by females. The distribution of females seemed to influence space use by males, most strikingly in the 2nd year. These spatial patterns are consistent with patterns of space use typical of promiscuous rodents (Ostfeld 1985; Waterman 2007).

In sum, our data generate several testable predictions about the mating system and social structure of *S. xerampelinus*. The greater exclusivity of space use by females suggests that these animals may exhibit intrasexual territoriality; future studies can explore this possibility by determining if females exhibit site-specific dominance or active defense of an area (Maher and Lott 1995). We have argued that space use in this species is consistent with patterns characteristic of promiscuous rodents; this can be verified using genetic analyses of paternity and reproductive success. Finally, future studies can examine how space use interacts with the unique calling behavior of this species to structure social and reproductive interactions.

RESUMEN

El ratón silbador de cola larga (*Scotinomys xerampelinus*) es diurno, insectívoro y exhibe un complejo y único comportamiento de llamado el cual es audible para los humanos. Poco se conoce acerca de la estructura social de esta especie. La organización espacial de una población silvestre de ratones silbadores de cola larga fue estudiada mediante con trampas vivas y radiotelemetría. Observamos que hubo un uso espacial exclusivo entre individuos hembras pero no entre individuos machos. Tanto en hembras como en machos, el ámbito de hogar individual (85% mínimo de polígonos convexos) usualmente se superpone con mas de 1 individuo del sexo opuesto. No se encontraron diferencias significativas en la masa corporal, la longitud de la pata trasera o el ámbito de hogar (área), entre individuos machos y hembras. La mayoría de los individuos en la población utilizaron madrigueras individuales. Patrones de uso de espacio y dimorfismo sexual son frecuentemente utilizados para inferir sistemas de apareamiento ínterespecíficos. Nuestros resultados, particularmente la tendencia de superposición de ámbitos de hogar individuales con múltiples parejas potencialmente reproductivas, son consistentes con un sistema de apareamiento promiscuo.

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