

NEST AND SPACE USE IN A HIGHLAND POPULATION OF THE SOUTHERN MOUNTAIN CAVY (*MICROCAVIA AUSTRALIS*)

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We examined the spatial and social structure of a high-altitude population of the scarcely known southern mountain cavy (*Microcavia australis*) in Argentina. We used radiotelemetry techniques to monitor nest use at night and daily home ranges and examine whether southern mountain cavies form nesting associations that are socially cohesive groups. We further timed our observations to breeding time of our study population (September–November) to assess opportunities for communal breeding. The nighttime telemetry of 24 radiotagged cavies revealed 7 nesting associations (i.e., communal nesting). These included 1–4 breeding females and 1 or 2 breeding males. Nesting associations were stable in terms of identity of individual members and in the location of putative nest sites. Most associations used a single nest site, but some shared 2 or 3. We noted that all nest sites were located under dominant shrubs, but use of nest sites was unrelated to variation in shrub cover. Nest sites with more burrow entrances were more frequently used by radiocollared cavies. During the day, home ranges of cavies overlapped more with ranges of nest mates than with those of non-nest mates, implying that nesting groups were socially cohesive units. This study confirmed that southern mountain cavies are communally nesting, and, because communal nesting occurs during breeding time, our findings support the idea that cavies engage in communal care of young.

Key words: communal nesting, group living, home-range overlap, home-range size, *Microcavia*, nest site, nest use, social structure, southern mountain cavy, space use

Social systems of rodents range from solitary-living species to social and highly gregarious forms, in which individuals interact frequently, and share feeding areas and a burrow system or a den (Armitage 1999; Bennett and Faulkes 2000; Lacey 2000; Solomon 2003). As a result, females of several rodent species engage in communal nesting and breeding, meaning that they use and rear their young together in shared nests (Hayes 2000; Solomon and Getz 1997). Benefits of this behavior may include protection of young from predation and infanticide, improved thermoregulation, increased intake of milk and growth of young, and adoption of young whose mothers die (Ebensperger 2001, 2003; Hayes 2000; Lewis and Pusey 1997).

Examining how communal nesting varies across species is essential for comparative approaches aimed at examining the current utility (i.e., current fitness benefits) of this behavioral strategy to face current (and past) social and ecological conditions (Blumstein and Armitage 1998; Ebensperger and Cofré 2001). However, most available field data and theory developed from social rodents come from the study of a limited number of taxonomic groups, typically from African mole-rats (Bathyergidae) and North American squirrels and marmots (Sciuridae). Therefore, data from other taxonomic groups are essential to assess the generality of hypotheses posed to explain rodent social living in general (Ebensperger 1998, 2001). One such group corresponds to the New World Hystricognathi (guinea pigs, degus, and viscachas). These rodents are interesting study subjects because they include species that vary morphologically and physiologically and use a great variety of habitats (Mares and Ojeda 1982; Redford and Eisenberg 1992). More importantly, patterns of morphological, physiological, and

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ecological diversity seem to covary with patterns of social organization and behavior (Ebensperger and Cofré 2001; Lacher 1981; Redford and Eisenberg 1992; Trillmich et al. 2004).

Cavies include 14 extant species, comprising 5 genera (*Cavia*, *Galea*, *Kerodon*, *Microcavia*, and *Dolichotis*) and collectively grouped in the family Caviidae (Woods 1993). Comparative studies on these New World hystricognaths still disagree about the relative importance of ecology and phylogeny in molding the social and breeding organization of these rodents (e.g., Rowe and Honeycutt 2002; Trillmich et al. 2004). Regarding social organization, early studies suggested that these surface-dwelling caviids were socially noncohesive, meaning that they form rather passive aggregations about clumped resources (Lacher 1981; Rood 1972). However, these studies also suggested that social attraction might contribute to group formation, particularly in the case of the southern mountain cavy (*Microcavia australis*). Based on visual observations of both free-living and captive animals, Rood (1970, 1972) indicated that female *Microcavia* generally displayed amicable social interactions, they may share home bushes, and nurse each other's offspring indiscriminately. These data are intriguing because they raised the possibility that southern mountain cavies are communally nesting and breeding rodents. However, data on the frequency of home bush (nest) sharing and opportunity for communal breeding were not provided. Thus, a major objective of our study was to use radiotelemetry techniques to examine whether cavies form nesting associations and whether these associations correspond to socially cohesive groups. Second, and to assess opportunities for communal breeding in this species, we timed our observations to breeding time of our study population.

Southern mountain cavies are found throughout most of eastern Argentina, Patagonia, and southernmost Chile (Tognelli et al. 2001). Habitats include arid lowlands and shrublands up to 2,500 m (Mares et al. 1989). Because communal nesting and nursing of young might be particularly beneficial to individuals living under relatively harsh thermal conditions (extreme cold and snowy during winter, and warm and dry during summer), we chose a high-elevation population of *Microcavia* from middle-eastern Argentina at about 2,400 m altitude.

Long-lasting, expansible nests have been linked to the origin or current maintenance of rodent group-living or both (Alexander et al. 1991; Ebensperger and Cofré 2001; Powell and Fried 1992), where animals may be constrained to live in groups to share burrows that are limited, or benefit through constructing higher-quality nests, decreasing the overall cost of burrow construction, or both (Ebensperger 2001). Because cavies typically excavate their own burrows, which are in association with shrubs (Rood 1970, 1972), we also examined some correlates of nest location that might influence their quality. Specifically, we predicted that cavies will more frequently use nests that are better protected from predators and thermal conditions, that is, nests located under larger shrubs and with a larger number of entrances.

MATERIALS AND METHODS

Study area and capture and marking of study subjects.—The study population was located at Parque Nacional El Leoncito (31°48'S, 69°17'W, altitude = 2,470 m, San Juan Province, Argentina), a protected area in the Argentinean National System of Protected Zones. The study site was characterized by an arid climate (cold and dry) where mean annual precipitation does not surpass 100 mm; winter precipitation (April–August) reaches 75 mm in the form of snow and hail, and summer rainfall (November–December) is less than 10 mm (Le Houérou 1999; Le Houérou et al. 1999). The site consisted of a flat area surrounded by low hills and dominated by scattered thorn bush associations, mostly of jarilla (*Larrea nitida*). Mean bush cover in the area was about 10%. The estimated density of cavies at the study site was 7 ± 1 adults/ha SE (P. Taraborelli, in litt.).

Members of the study population were captured using a combination of single- and double-door Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with pieces of apple. Traps were placed in active runways, usually where they entered jarilla bushes, and near burrow entrances. Traps were opened during morning and evening hours, when these mostly diurnal animals were typically active aboveground (Rood 1970). We avoided trapping animals around noon and during early afternoon hours to minimize the chance of trapped individuals dying through overheating. Traps were checked approximately every 40 min. Trapping was conducted for 10 days during September and for 5 days in November 2004, which corresponds to the portion of the year when females are pregnant or lactating (Rood 1970). For all animals captured, we recorded the individual's body weight and apparent reproductive status. Females were regarded as breeding when perforate, pregnant, or lactating. Males were considered to be breeding when they had enlarged testes; large-sized testes characterize sperm-producing males in this species (S. Velez, in litt.). To characterize spatial relationships among adult individuals, 19 adult-sized individuals ($n = 13$ females, $n = 6$ males) were fitted with 8- to 10-g radiocollars (BR transmitters; AVM Instrument Co., Colfax, California) in September, to which we added 5 more individuals in November 2004 ($n = 4$ females, $n = 1$ male). Weight of radiocollars represented about 3% of study subjects' body weight (mean \pm SE weight of collared cavies = 297 ± 7 g). In both periods, plastic bands used to hold transmitters around females' necks were wrapped with colored tape to allow further visual identification of animals. At the end of each season of data collection, radiocollared animals were recaptured and the transmitters were removed.

Nighttime telemetry data.—Cavies are diurnal rodents (Rood 1970), and, hence, we used the nighttime locations of radiocollared animals to assess the prevalence of communal nesting by members of the study population. We used night locations of radiocollared animals to infer use and location of putative nests and nesting associations. We determined resting locations once per night, about 2 h after sunset, through homing (Kenward 2001) and using an LA 12-Q receiver and a 3-element handheld Yagi antenna (AVM Instrument Co.). Fixes recorded for radiotransmitters placed at known locations revealed this procedure to be accurate to ± 1 m. Because not all females were captured and collared on the same date, the number of radiofixes per animal varied. In September, the location of each radiocollared cavy was recorded on 9 ± 1 nights (mean \pm SE, $n = 19$ cavies). In November, the location of each radiocollared female was recorded on 10 ± 4 nights ($n = 14$ cavies). To confirm that the animals were not active during the night, we recorded the locations of all radiocollared animals twice every hour on 1 (September) or 2 (November) randomly chosen nights.

TABLE 1.—Nesting associations of female (F) and male (M) southern mountain cavies during 2004 in Parque Nacional El Leoncito (31°48'S, 69°17'W, altitude = 2,470 m), Argentina. Communal nesting involved records of nights where 2 or more cavies were at the same spatial location (i.e., putative nest site).

Nesting association	Group composition (identities of conesting individuals)	Number of breeding cavies		Number of nights all mates were radiotracked	Number of nights with communal nesting observed (% of nights monitored)		Number of nests shared	Distance among nests shared (m)	Total number of nests used by group mates
		Female	Males		Number	% of total			
September									
A	F1, F2, M1	2	1	6	6	100	1		1
B	F3, F4, F5	1	0	7	6	86	2	6	5
C	F6, F7, M2	2	1	6	6	100	1 ^a		3
D	F8, F9	2	0	11	6	55	1		8
E	F10, M3, M4	1	2	7	4	57	3	50 ± 19	5
November									
C'	F6, F7, F11, F12	4	0	7	7	100	1 ^a		1
F	F13, F14, M3	1	1	9	8	89	2	13	4

^a Involved use of the same nest in both study periods.

Locations of putative nests were then transferred to an x-y system of coordinates. By comparing the night locations of radiocollared animals, we determined the number and identities of animals that spent nights at each putative nest site. We measured communal nesting as the percentage of nights 2 or more radiocollared cavies occurred repeatedly at the same location during nighttime.

Correlates of nest location.—Putative nest sites were always located near the base of shrubs. Thus, for every nest site (recorded to have been used by at least 1 radiocollared cavy) we quantified the amount of overhead shrub cover. To do so, we projected the ground area covered by the nearest shrub that covered each nest site. In addition, we quantified shrub height and the total number of burrow entrances surrounding the nest site.

Daytime telemetry.—To determine whether cavies assigned to the same nesting association formed a socially cohesive group when active aboveground, we monitored patterns of space use by radiocollared animals during the day. Unfortunately, these data were obtained during September only because 1 radioreceiver failed during November. After their release, locations of radiocollared animals were determined once every hour from about 0830 to 1330 h, and then from about 1730 to 2000 h. To do so, we used 2 LA 12-Q receivers, each connected to a null peak antenna system (AVM Instrument Co.). Every null peak system had two 7-element Yagi antennas (about 3 m long) positioned horizontally at the ends of a 1.5-m transverse pole. The transverse pole in turn was mounted on a 2-m vertically oriented aluminum pole. We located each null peak system near the top of 2 opposite hills surrounding the flat study area; distance between antenna stations was 161 m. Diurnal locations of every tagged animal were recorded through triangulation (Kenward 2001). Every hour, two 2-observer teams simultaneously recorded bearings of every radiocollared subject ($\pm 0.5^\circ$) using the same previously defined subject sequence. Because cavies and other similarly sized ground-dwelling rodents can detect approaching human observers at rather great distances (e.g., Ebensperger and Wallem 2002; Marquet et al. 1993; Rood 1970), triangulation was preferred over the "homing" technique (see Kenward 2001) to prevent observers from affecting the movement of animals that were active aboveground. Bearings from both antenna stations were then transformed into x-y locations with the software Locate II (Pacer Software, Truro, Nova Scotia, Canada). Data points for each individual were then mapped using the 95% minimum convex polygon algorithm of the software Ranges VI (Kenward et al. 2003).

Pairwise estimates of percentage home-range overlap among individuals and nesting associations also were calculated using Ranges VI.

Statistical analysis was performed using Statistica 6.0 (StatSoft Inc., Tulsa, Oklahoma). Because most variables did not fit the assumptions of normal distribution and homogeneity of variances, we used nonparametric statistics throughout. All statistical tests were 2-tailed. Data are presented as mean \pm SE.

All observations recorded during this study were carried out according to current Argentinean laws (National Law 14346, National Park permit 105). In addition, we followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) during our procedures.

RESULTS

Nesting associations.—Monitoring the locations of these animals hourly throughout 3 nights revealed that all but 2 nighttime radiofixes (total radiofixes = 80) occurred at locations previously identified via telemetry as putative nest sites. A single male recorded during November was responsible for this unusual activity that involved short-range movements (2–3 m). Thus, and as suggested previously (Rood 1970, 1972), members of the study population restricted their activity between sunset and sunrise.

Based upon the nighttime locations of a total of 24 radiocollared cavies, we identified 5 instances of communal nesting (i.e., nesting associations, referred to here as associations A–E) in September 2004 (involving 14 radiocollared animals), and 2 more in November 2004 (associations C' and F, involving 6 radiocollared animals; Table 1). Nesting associations in September involved groups of 2 or 3 cavies and some included 1 or 2 adult males (Table 1). We were unable to capture and to radiocollar all adult cavies in these associations and, hence, the actual mean number of adult animals that share a nest is likely to be larger. All radiocollared males noted to communally nest were breeding animals (i.e., with enlarged testes). In the case of radiocollared females, 3 of 5 groups (A, C, and D) each included 2 breeding females (i.e., pregnant or recently mated individuals). Three more radiocollared females

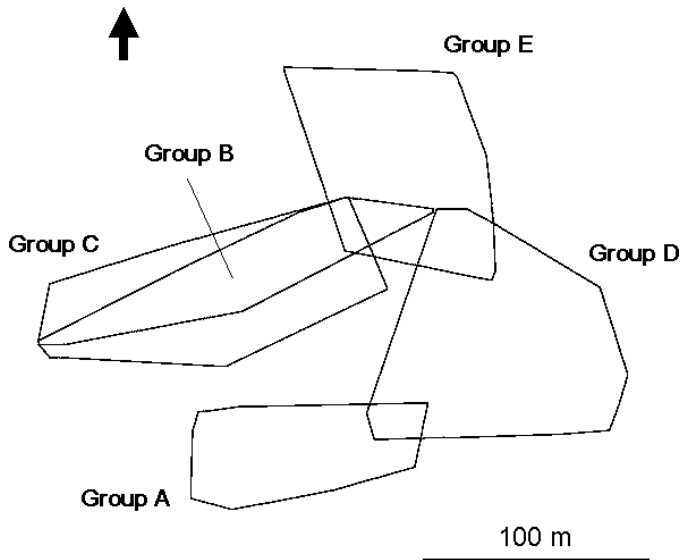


FIG. 1.—Daily home ranges (95% minimum convex polygons) of 5 nesting associations of southern mountain cavies (*Microcavia australis*) during the day. Letter labels for each polygon correspond to association labels in Table 1. Black arrow indicates geographic north. Group home ranges were obtained by radiotracking 10 adult female and 4 adult male cavies during September 2004 at Parque Nacional El Leoncito, Argentina.

(2 of which had evidence of recent mating) and 2 males with enlarged testes (i.e., most likely breeding) were not detected to nest communally with any other radiocollared cavy. In November we recorded 2 nesting associations. One (C', probably derived from C) involved a total of 4 breeding (postlactating) females, and another (F) involved a breeding male (M3) from previous association E now recorded to communally nest with 2 other females (Table 1), 1 of which (F13) was breeding. Three females (1 lactating and 2 postlactating) and 4 breeding males could not be assigned to any nesting association during this time.

On average, cavies identified as members of the same nesting associations were found together during $>84\%$ ($\pm 20\%$) of nights on which locations of all nest mates were monitored (Table 1). No female was observed to switch from one nesting association to another during the course of this study. Four associations (A, C, D, and C') each shared a single nest, 2 others (B and F) shared 2 putative nests, and 1 nesting association (E) shared 3 nests (Table 1). In the case of nesting associations that shared 2 or more nests, distance between nests varied between 6 and 71 m ($\bar{X} \pm SE = 34 \pm 15$ m). Thus, nesting associations identified during nighttime telemetry were stable in terms of identity of individual members and in the location of putative nest sites.

Nesting site correlates.—The area covered by the overhanging canopy of shrubs above putative nest sites did not predict the total number of visits to a given nest by radiotracked individuals (Spearman's $r = 0.18$, $t = 1.23$, $d.f. = 46$, $P = 0.225$) or the number of different cavies that used that nest (Spearman's $r = 0.04$, $t = 0.29$, $d.f. = 46$, $P = 0.772$). Similarly, shrub height did not predict variation in the number

of times a nest was used by any radiotracked individual (Spearman's $r = 0.22$, $t = 1.52$, $d.f. = 46$, $P = 0.136$) or the number of different cavies that used that nest (Spearman's $r = 0.14$, $t = 0.97$, $d.f. = 46$, $P = 0.339$). In contrast, the number of burrow openings predicted a statistically significant proportion of nest use as measured by the number of times a nest was used by any radiotracked individual (Spearman's $r = 0.41$, $t = 3.07$, $d.f. = 46$, $P = 0.004$), or by the number of different cavies that used a nest (Spearman's $r = 0.33$, $t = 2.40$, $d.f. = 46$, $P = 0.020$). Thus, putative nests with more burrow entrances were more frequently used by radiocollared cavies.

Size and overlap of daily home ranges.—Eighteen individuals were radiotracked during the day, which provided an average of 42 ± 3 radiofixes per animal. If data for all radiocollared cavies are combined, the size of home ranges averaged $4,591 \pm 821$ m² ($n = 18$). On average, radiocollared cavies overlapped $15.1\% \pm 1.1\%$ of their home ranges with those of other cavies. When the influence of sex was examined, males tended to exhibit larger home ranges ($6,737 \pm 1,814$ m², $n = 6$) than females ($3,517 \pm 707$ m², $n = 12$), but not significantly so (Mann-Whitney U -test, $Z = 1.59$, $P = 0.111$). Home-range overlap of males with any other radiocollared subject ($13.0\% \pm 1.3\%$) was similar to that recorded in females ($16.1\% \pm 1.5\%$; Mann-Whitney U -test, $Z = 1.59$, $P = 0.111$). Male home ranges overlapped those of other radiotagged males ($15.7\% \pm 5.3\%$) and females ($11.9\% \pm 1.6\%$) similarly (Wilcoxon-matched pairs test, $Z = 0.73$, $P = 0.463$). Likewise, home ranges of female radiocollared cavies overlapped those of other females ($14.0\% \pm 2.5\%$) and males ($20.0\% \pm 2.7\%$) to similar extents (Wilcoxon-matched pairs test, $Z = 1.02$, $P = 0.308$).

After radiocollared cavies were assigned to a nesting association based on their common use of burrows at night, we noted that individuals overlapped their daily home ranges more with ranges of individuals assigned to the same nesting association ($62.6\% \pm 6.6\%$, $n = 14$ individuals assigned to any nesting association) than with ranges of individuals pertaining to different nesting associations ($9.6\% \pm 1.6\%$), a statistically significant difference (Wilcoxon-matched pairs test, $Z = 3.30$, $P = 0.001$). Thus, individuals that used the same nest sites during the night also used similar areas when active aboveground.

When locations of individuals from the same nesting associations were combined to calculate group home ranges, the extent of daily areas used by nesting associations averaged $5,765 \pm 931$ m² ($n = 5$ nesting associations). Daily home ranges of nesting associations tended to be distinct and overlapped only by $16.1\% \pm 3.1\%$ with ranges of other such associations (Fig. 1).

DISCUSSION

Our results yield new insights into several aspects of southern mountain cavy social structure. For example, examination of our telemetry data indicates that multiple adult females share underground nest sites, confirming that this species is communally nesting. At the same time, areas used aboveground

during the day differ markedly between nest-mate and non-nest-mate individuals, providing additional evidence that nesting associations represent distinct social units. Because communal nesting occurs during the portion of the year when females are breeding, our findings yield strong circumstantial evidence that southern mountain cavies engage in communal care of young. All 4 nesting associations detected that included 2 or more breeding females (A, C, D, and C') used a single nest site. Two more nesting associations that involved a breeding and a nonbreeding female (B and F) used 2 nests that were located in close proximity to one another (Table 1). Putative nest sites were always located near shrubs, but the extent of shrub cover did not influence their use by radiocollared cavies. However, nest sites with more burrow entrances were used more often.

Previous comparative studies on New World caviids suggested that these rodents were socially noncohesive (Lacher 1981; Rood 1972), meaning that they form rather passive aggregations around clumped resources. This view adequately describes the social structure of species recently studied in their natural environments such as *Cavia magna* (Kraus et al. 2003), but not that of others such as *Cavia aperea* (Asher et al. 2004) and *Dolichotis patagonum* (Taber and Macdonald 1992a) where stable social structures have been recorded. However, in the case of *M. australis*, early studies suggested that social attraction contributes to group formation. Visual observations of free-living and captive animals indicated that multiple females displayed generally amicable social behavior, that they shared "home bushes," and nursed each other's offspring indiscriminately (Rood 1970, 1972). Here, we provide direct evidence that multiple females in this diurnal species spend the night at the same location within a burrow system and that communally nesting individuals range over similar areas during the day, providing evidence that nesting associations represent distinct social units. Although we did not excavate these locations to confirm the presence of bedding, food remnants, or other items indicative of a nest, the tendency for females to co-occur at a limited number of sites within a burrow system is consistent with evidence of communal nesting obtained from other subterranean and semifossorial rodents (e.g., Armitage and Gurri-Glass 1994; Lacey et al. 1997; Solomon et al. 1998; Tristiani et al. 2003; Wilkinson and Baker 1988; Wolton 1985) and is strongly suggestive that, in cavies, shared nighttime localities function as nests. If, as examination of our data implies, female cavies share underground nests, then this species can be added to the growing list of social rodents characterized by communal nesting (Hayes 2000; Lacey 2000; Solomon 2003; Solomon and Getz 1997) and future comparative studies should regard this species as truly social (e.g., Rowe and Honeycutt 2002).

That most females in our study population were reproductive during data collection and our ongoing mark-recapture program at El Leoncito indicate that most female cavies breed each year (P. Taraborelli, in litt.). As a result, it seems likely that this species is a plural breeder, with little or no reproductive skew among female nest mates (Hayes 2000). Further, nest sharing by recently lactating females suggests that allonursing of young

may occur, as has been reported for some free-living members of this species (Rood 1970). Some potential ways by which social southern mountain cavies might cooperate have been suggested, including social thermoregulation and the collective detection of predators (Rood 1970, 1972; P. Taraborelli, in litt.). As may occur in other neotropical hystricognaths (Ebensperger et al. 2004; Macdonald 1981; Rood 1972; Taber and Macdonald 1992b), we concur with Rood (1970) that communal care of young, including allonursing, represents a potential additional form of cooperation that may influence costs and benefits of sociality in this species.

Putative nest sites with more burrow entrances were used more frequently by the same individuals and by a larger number of individuals. Because we did not measure social group size precisely (i.e., not all group members were identified), it is not known whether nest sites with more burrow entrances were occupied by larger social groups, a potential consequence if cavies cooperate to excavate burrows. Cooperation during burrow digging has been hypothesized to play a role during the evolution of rodent group-living (Ebensperger and Bozinovic 2000; Ebensperger and Cofré 2001; Ebensperger and Blumstein 2006), so our future efforts will include assessing this possibility for *M. australis*. Additional efforts that expand our findings to other populations will be useful to verify if group-living in *Microcavia* varies predictably with relevant ecological factors, as implied in most comparative studies within Caviidae (Lacher 1981; Trillmich et al. 2004).

RESUMEN

Examinamos la estructura espacial y social de una población andina del cuis chico (*Microcavia australis*) en Argentina. Utilizamos radiotelemetría para cuantificar el uso de madrigueras durante la noche, el ámbito de hogar durante el día, y verificamos si los grupos comunitarios identificados (individuos que anidan juntos) establecen unidades sociales cohesivas. Las observaciones se realizaron durante el período reproductivo para evaluar además la potencialidad de que exista reproducción cooperativa. El seguimiento nocturno de 24 cuises marcados con radiocollares permitió detectar siete asociaciones comunitarias compuestas por 1–4 hembras reproductivas y entre 1 o 2 machos reproductivos. Las asociaciones detectadas fueron estables en términos de la composición de sus integrantes así como de la ubicación de las madrigueras utilizadas. La mayor parte de las asociaciones usaron una madriguera pero algunas usaron 2 o 3. Todas las madrigueras estaban localizadas bajo la cobertura de arbustos. Cada cuis utilizó más aquellas madrigueras con un mayor número de entradas. Durante el día, el ámbito de hogar de cada cuis se sobrepuso más con el de cuises de la misma asociación y menos con los de cuises de otras asociaciones. Nuestro estudio confirmó que *M. australis* comparte sus madrigueras comunitariamente, que estas asociaciones tienden a ser estables, socialmente cohesivas, y muy probablemente, que los adultos realizan cuidado cooperativo de sus crías.

ACKNOWLEDGMENTS

We are indebted to the Sistema de Parques Nacionales de Argentina, particularly to park rangers of Parque Nacional El Leoncito, for providing all the necessary facilities during fieldwork. We are specially thankful to Park Ranger A. J. Sandobal ("Petty") who assisted with logistics during fieldwork. L. Hayes kindly helped with calculating minimum convex polygons in Ranges VI. Comments and suggestions made by D. Blumstein and 1 anonymous reviewer improved a previous version of our article. Funding was provided partially by Fondo Nacional de Desarrollo Científico y Tecnológico grant 1020861 (LAE), Program 1 of Fondo de Investigación Avanzada en Áreas Prioritarias 1501-001 (FB), Proyecto de Investigación Científica y Tecnológica grant 01-11768, and by Consejo Nacional de Investigaciones Científicas y Técnicas-Proyecto de Estímulo a la Investigación grant 06261.

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Submitted 7 December 2005. Accepted 6 March 2006.

Associate Editor was Nancy G. Solomon.