HOME-RANGE AND ACTIVITY PATTERNS OF THE SOUTH AMERICAN SUBTERRANEAN RODENT *CTENOMYS TALARUM*

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Subterranean rodents are characterized by limited individual mobility and patchy distribution of local populations, all of which have been related to the great evolutionary diversification of this group. Because of their secretive habits, radiotracking becomes an essential tool to collect data systematically on characteristics of their space use, rate of movement, and daily patterns of activity. Compared to other subterranean species, the ctenomyids exhibit more activity above the surface. Despite this, a previous study showed that only 25% of the captive individuals analyzed presented rhythmic bouts of activity associated with light–dark cycles. In our study, we used radiotelemetry to explore quantitatively the home-range dynamics and daily movements of the South American Talas tuco-tuco (*Ctenomys talarum*). As expected, the home ranges of males were larger than those of females. However, intraspecific variation in home-range size also was observed between 2 different study sites, possibly reflecting differences in body size and soil characteristics between the study sites. Rhythmicity in activity patterns was confirmed to be polymorphic in this species, as previously observed in captivity, and daily activity was mostly concentrated in the diurnal period. We suggest that the present study will contribute to generating important insights into home-range dynamics and daily patterns of activity of free-living subterranean rodents.

Key words: activity patterns, *Ctenomys*, home range, radiotelemetry

The spatial organization of individuals as well as the use they make of a particular area has been a primary concern of ecology and evolutionary biology. One of the aspects of particular interest is the home range, defined as the area used by an organism during its normal activities, such as food gathering, mating, and caring for young (Burt 1943).

Estimating the size, shape, structure, and degree of overlap of home ranges of individuals within a species provides information about social cohesion (Lacey et al. 1997; Ribble and Stanley 1998), territorial behavior (Schradin and Pillay 2005), and habitat use (Chapin et al. 1998). Moreover, studies of home range have helped to assess the impact of habitat fragmentation on populations of small mammals (Gehring and Swihart 2004) and also have been used to test behavioral hypotheses regarding cycles of population fluctuations in several small mammal species (e.g., microtine rodents—Sera and Gaines 1994). Despite the fundamental nature of the home range to a species' biology, determining aspects of its size and structure remains difficult in certain groups, such as subterranean rodents. For these small mammals with secretive habits, radiotracking becomes an essential tool to collect data systematically on their behavior and, particularly, characteristics of their space use and rate of movement.

In addition to providing a means to collect information regarding the home range of a species, radiotelemetry has been used to determine patterns of daily activity of several small mammal species in their natural habitats (e.g., Blanchong et al. 1999; Gehring and Swihart 2004; Urrejola et al. 2005). On the one hand, the rhythm of activity of an animal during a 24-h cycle is regulated by endogenous mechanisms synchronized with environmental variables (zeitgeber) such as light irradiance (Argamaso et al. 1995; Bunning 1973) and thermal conditions (Rezende et al. 2003). On the other hand, the magnitude of predation pressure (Halle 2000) and characteristics of the social stimuli (Bennett 1992) that an animal encounters in its natural habitat also may play a significant role in determining the times an individual will be active throughout the day.

Subterranean rodents are characterized by limited individual mobility and a patchy distribution of local populations (Lacey et al. 2000). At the physiological level, although physical

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parameters such as light intensity and temperature remain largely unchanged in the burrows (Buffenstein 2000; Marhold and Nagel 1995), a great number of subterranean species exhibit bimodal patterns of activity throughout 24-h cycles (e.g., *Thomomys bottae* [Reiter et al. 1994], *Georychus capensis* [Lovegrove and Muir 1996], and *Spalacopus cyanus* [Urrejola et al. 2005]). However, others are arrhythmic and exhibit patterns of activity in periods without a clear association with light–dark cycles or even temperature changes (e.g., *Heterocephalus glaber* [Davis-Walton and Sherman 1994]).

The most numerous in species of all subterranean rodents are the South American tuco-tucos (*Ctenomys*), comprising approximately 60 species (Cook and Lessa 1998; Lacey et al. 2000; Reig et al. 1990). One species of this genus, the Talas tuco-tuco (*Ctenomys talarum*), has been studied in great detail in aspects of its ecology and physiology. In particular, *C. talarum* is solitary, is very aggressive, and maintains exclusive territories (Busch et al. 1989). It exhibits a marked intraspecific variation in demographic aspects such as density and adult sex ratio (Busch et al. 1989; Malizia and Busch 1991, 1997; Malizia et al. 1991, 1995) and in the degree of polygyny (Zenuto et al. 1999a, 1999b, 2002). Quantitative assessments of home-range dynamics and movements of free-living *C. talarum* have been primarily based on the size and structure of extensively excavated tunnel systems (Antinuchi and Busch 1992) and mark–recapture techniques (Busch et al. 1989). Compared to other subterranean species, the ctenomyids exhibit more activity above the surface, because they venture away from their tunnels for brief periods to gather vegetation (Busch et al. 2000). Despite this, a previous study regarding the patterns of activity of *C. talarum* in seminatural conditions showed that only 25% of the individuals presented rhythmic bouts of activity associated with light–dark cycles, suggesting that the trait is polymorphic in this species (Luna et al. 2000).

In the present study, we had 3 main objectives. First, we aimed to quantitatively assess home-range size and rates of movement of Talas tuco-tucos in their natural habitat. To determine if there are differences in these traits between the sexes, we used radiotelemetry to monitor movements of these rodents throughout a sand-dune landscape. Second, we compared the radiotracking home-range size with those previously estimated through the excavation of tunnel systems (Antinuchi and Busch 1992) and collected data on plant biomass and soil characteristics. Finally, to estimate patterns of activity in this species, hourly rates of movement were recorded in a 24-h period in both sexes.

Males of *C. talarum* are the more aggressive and territorial sex; they establish hierarchies before the mating season (Vassallo and Busch 1992; Zenuto et al. 2002) and mate with more than 1 female (Zenuto et al. 1999a). This led us to predict that males should have a larger home range because of their larger body size and their competitive search for receptive females (Sandell 1989). Because of their stronger territorial behavior, we expected males to present higher hourly rates of movement and be less likely to present rhythmic activity patterns than females (Bennett 1992; Luna et al. 2000).

The present study is only the 3rd radiotelemetry study of tuco-tucos (the others are of *C. sociabilis* by Lacey et al. [1997] and *C. haigi* by Lacey et al. [1998]) and the 1st to be conducted in *C. talarum*, and thus represents a valuable opportunity to answer intriguing questions regarding the individual movements and patterns of daily activity in natural populations of subterranean rodents.

MATERIALS AND METHODS

Animal capture.—*Ctenomys talarum* is distributed in the sand dunes along the Atlantic coast of Buenos Aires Province, Argentina. Our study was performed from mid-February to mid-April 2005 in a population of *C. talarum* situated in Mar de Cobo (37°45′S, 57°56′W), Argentina. The study site was located in the coastal dune habitat characterized by sandy soils and dominated by *Panicum racemosum*, *Ambrosia tenuifolia*, and *Distichlis scoparia*; a detailed description of the study location is provided by Comparatore et al. (1991). The study period corresponds to the end of the breeding season and half of the nonbreeding season of this subterranean rodent (Busch et al. 1989; Malizia and Busch 1991).

Individual *C. talarum* (mean body weight: 118 g [Busch et al. 2000]) are spatially distributed in groups (Busch et al. 1989). During the present study, all adults present in 2 spatially defined local groups (''clusters'') were captured. To ensure that trapping was complete, plastic tube traps were set at all burrow entrances showing signs of recent activity (e.g., freshly excavated mounds of dirt or fresh soil plugs). Trapping at a given burrow entrance continued until either an adult had been captured or 48 h had elapsed with no evidence of tuco-tuco activity (e.g., plugging of traps or burrow entrances). Each tuco-tuco captured was weighed and sexed, and a radiocollar was placed around its neck. The position at which each individual was captured was recorded to the nearest meter using a 10 × 10-m Cartesian coordinate system established at the grid at the start of trapping. Upon completion of these procedures, the tuco-tuco was released into the burrow system from which it had been captured. When the tuco-tuco was recaptured at the end of the present study, the collar was removed and the individual was weighed again to verify if significant weight loss had happened during the study period.

Radiotracking.—Individuals were equipped with G3-1V radiotransmitters (AVM Instruments, Livermore, California), which weighed approximately 5 g and represented 3.5% of body weight ($\pm 0.6\%$ *SD*) on average (variation, 2.5–4.3%). We later located the radiocollared tuco-tucos using a handheld 3-element Yagi directional antenna and an LA12-Q receiver (AVM Instruments, Livermore, California). Fixes were taken 8 times a day from 0900 to 1600 h. To ensure independence of data points (Kenward 1987; Swihart and Slade 1985), intervals between fixes were approximately 1 h. Once located, each individual's position was recorded to the nearest meter using the 10 × 10-m grid (1 × 1-m cell size). We performed fixes of radiotransmitters placed at known locations to estimate the accuracy of the telemetry procedure, which proved to be 0.5 m.

To estimate plant biomass and soil humidity, we used the method of Antinuchi and Busch (1992). In brief, all the vegetation present in a 0.24-m^2 × 0.3-m sample was collected and separated in aerial and subterranean portions. These were dried for 24 h at 80°C and weighed to the nearest 0.01 g. Soil samples were collected from inside the burrow tunnels. Moisture was determined as the difference in weight before and after drying the samples at 80°C to constant weight. Because soil hardness had not been estimated by Antinuchi and Busch (1992), we did so in both their and our study area using a penetrometer, as described by Malizia et al. (1991).

Daily patterns of activity.—For determination of rates of movements within home ranges, tuco-tucos were sequentially relocated every hour during a 24-h period (from 0900 h to 0900 h of the next day). To estimate the hourly rate of movement of the tuco-tucos we calculated the distance moved (in m) between each pair of successive radiofixes, as described by Gehring and Swihart (2004) and Urrejola et al. (2005). As an additional measure of activity we registered the time of day at which we recorded territorial vocalizations typical of male *C. talarum* (Schleich and Busch 2002). All field procedures conformed to guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Animal Care and Use Committee 1998).

Statistical analysis.—We estimated home-range size using the adaptive kernel method (Seaman and Powell 1996; Worton 1989) as calculated by CALHOME (Kie et al. 1996) to obtain 95% home-range contours. For comparative purposes with data on subterranean rodents already published, we estimated 100% minimum convex polygon home ranges using the same software. All tuco-tuco relocations were used in the analysis because the adaptive kernel method is robust to putative violations of independence (Swihart and Slade 1997). In this sense, simulation studies (Swihart and Slade 1985, 1997) suggest that moderate autocorrelation between successive radiofixes does not invalidate the use of the adaptive kernel or the minimum convex polygon (Mohr 1947) to estimate home-range size. Differences in home-range size between males and females were examined using a Student's *t*-test or a Mann–Whitney rank-sum test, in the case where the tests of normality, homoscedasticity, or both were not passed, performed by Sigma Stat Software Analysis Version 3 (RockWare Inc., Golden, Colorado). The minimum number of radiolocations at which home-range size stabilized at the asymptote of accumulation curves was estimated following the methods of White and Garrott (1990) and Gehring and Swihart (2004).

For comparative analyses, 100% minimum convex polygons were calculated (CALHOME—Kie et al. 1996) using data points obtained from excavated burrow systems of *C. talarum* (Antinuchi and Busch 1992). For the present analysis, the spatial coordinates of all the intersections among burrow branches, main tunnel, and feeding tunnels as well as the points corresponding to burrow openings were included. In our study, the burrow systems of the radiocollared tuco-tucos were not excavated as done by Antinuchi and Busch (1992) because the field site of Mar de Cobo is being used as part of an ongoing long-term study of genetic structure of *C. talarum* (Cutrera et al. 2005, 2006) and disturbance in this area needed to be kept at its minimum. Body sizes of females and males were compared within and between study sites using Student's *t*-tests or Mann–Whitney rank-sum tests (in the case where the assumptions of the *t*-test were not fulfilled), as implemented in Sigma Stat Version.

The existence of rhythmic patterns of activity in Talas tuco-tucos was explored using autocorrelation analyses with 5 different lag-times, according to Gehring and Swihart (2004). The influence of 3 temporal periods (characterized by different light intensities: crepuscular, diurnal, and nocturnal) and sex on the mean hourly rate of movement was tested using a repeated-measures analysis of variance (ANOVA) and multiple comparisons were performed using a Tukey unequal N honest significant difference test (STATISTICA Version 3; StatSoft, Inc., Tulsa, Oklahoma). Throughout the text, values are reported as mean ± 1 *SD*.

RESULTS

Radiotracking.—During the present study, we captured and radiocollared 11 individual *C. talarum* (5 males and 6 females)
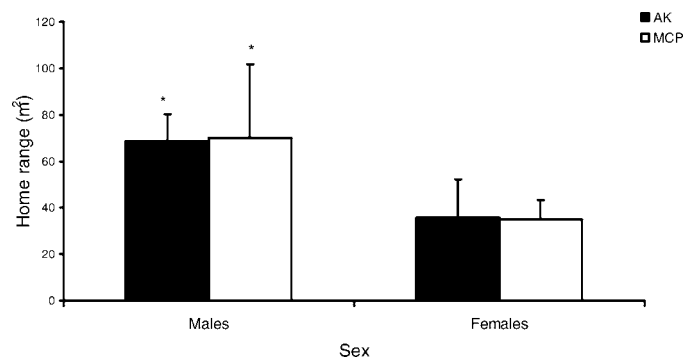
FIG. 1.—Mean values of home-range size (m^2) for males ($n = 5$) and females ($n = 6$) of *Ctenomys talarum*, estimated by adaptive kernel (AK—Worton 1989) and minimum convex polygon (MCP—Mohr 1947) methods. Asterisks (*) denote statistical differences between sexes for the same home-range estimation method ($P < 0.05$). Values are means + *SD*.

that belonged to 2 distinct clusters of tuco-tucos (cluster 1: 2 males and 4 females; cluster 2: 3 males and 2 females). Contour area estimation for 95% adaptive kernel stabilized at approximately 6 days (48 radiolocations per tuco-tuco) and 100% minimum convex polygon home-range area estimation stabilized at 5–6 days (40–48 radiolocations per individual). All individuals were radiotracked for time periods sufficient to provide reasonable estimates of home-range size (average: 8.91 days = 71.28 radiolocations/individual, range 6–11 days). Because 2 radiocollars failed during the study before sequential monitoring could take place, a subgroup of the sample of tuco-tucos used for home-range size estimation (4 males and 5 females) was monitored sequentially for 24 h to determine mean hourly rate of movement within home ranges. No significant change in weight was found in the tuco-tucos after removing the radiocollar at the end of the study compared to their weight at the beginning of the present study (paired *t*-test, $t = 0.082$, *d.f.* = 8, $P = 0.937$).

Home range.—We never captured more than 1 adult at 1 burrow entrance, nor did home ranges of the captured tuco-tucos ever overlap. Significant sexual dimorphism in body size was detected (males: 171 ± 23.02 g, females: 125.83 ± 17.15 g; *t*-test, $t = -3.734$, *d.f.* = 9, $P = 0.005$). Accordingly, the 95% adaptive kernel contour area for adult males (68.74 ± 11.63 m^2) was significantly larger than that of females (35.75 ± 16.47 m^2, *t*-test, $t = 3.81$, *d.f.* = 9, $P = 0.004$; Fig. 1). Minimum convex polygon home ranges also differed significantly between the sexes (males: 70.1 ± 31.6 m^2, females: 34.91 ± 8.49 m^2; Mann–Whitney rank-sum test, $T = 45$, exact $P = 0.04$; Fig. 1).

For both sexes, home ranges estimated from excavated burrows (Antinuchi and Busch 1992) were significantly smaller than those estimated by radiotelemetry (males: *t*-test, $t = 4.53$, *d.f.* = 12, $P < 0.001$; females: Mann–Whitney rank-sum test, $T = 86$, $n = 12$, exact $P < 0.05$; Table 1).

Plant biomass in our study area was not significantly different from that estimated by Antinuchi and Busch (1992) in their study site (results of *t*-test: aerial, $t = -1.18$, *d.f.* = 20, $P = 0.252$; subterranean, $t = 0.095$, *d.f.* = 20, $P = 0.925$; total, $t = 0.578$, *d.f.* = 20, $P = 0.57$; Table 2). However, soil of the

TABLE 1.—Home ranges (100% minimum convex polygon) estimated for males and females of *Ctenomys talarum* from excavated burrows (Antinuchi and Busch 1992) and by radiotelemetry (present study). Asterisks denote statistical differences between home ranges estimated by the 2 different methods (*t*-test, *, $P < 0.05$; **, $P < 0.001$) for individuals of the same sex.
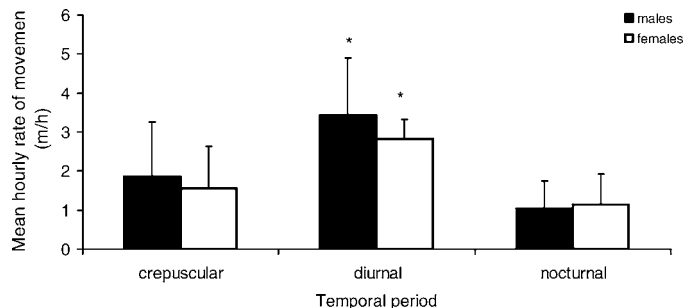
	Females		Males	
	n	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$
Excavated burrows	12	$11.04 \pm 13.18*$	9	$18.01 \pm 11.74**$
Telemetry (m²)	6	34.91 ± 8.49	5	70.10 ± 31.60

area where the radiotracking was performed was significantly softer (*t*-test, $t = -3.82$, *d.f.* $= 34$, $P < 0.001$; Table 2) and less humid ($t = -5.07$, *d.f.* $= 25$, $P < 0.0001$; Table 2) than that where the burrows where excavated by Antinuchi and Busch (1992). In addition, males captured in our study were significantly heavier than males whose burrows were excavated (males from Antinuchi and Busch [1992]: 136.71 ± 13.92 g; Mann–Whitney rank-sum test, $T = 46.5$, exact $P = 0.018$) and the same difference was observed for females (females from Antinuchi and Busch [1992]: 100.64 ± 7.99 g; $t = -4.187$, *d.f.* $= 15$, $P < 0.001$).

Daily patterns of activity.—On the one hand, 56% of the individuals ($n = 5$) did not exhibit significant serial correlation between successive rates of movement at different lag-times ($r = -0.04$–0.29, $P = 0.14$–0.82), whereas 44% ($n = 4$) did present significant autocorrelations ($r = 0.34$–0.52, $P = 0.01$–0.023). On the other hand, there was a significant effect of temporal period on mean hourly rate of movement (repeated-measures ANOVA, $F = 13.67$, *d.f.* $= 2$, $P = 0.005$; Fig. 2), but there was not a statistically significant effect of sex (repeated-measures ANOVA, $F = 0.29$, *d.f.* $= 1$, $P = 0.61$; Fig. 2) or the interaction between these 2 factors (repeated-measures ANOVA, $F = 0.41$, *d.f.* $= 2$, $P = 0.67$). Post hoc comparisons revealed that all significant comparisons were due to those that involved the diurnal period (Tukey test, $P = 0.0006$–0.008). Agreeing with this, male territorial vocalizations were recorded in 19.8% $\pm$ 4% of the scans performed per individual and they were all concentrated during the diurnal sampling period, whereas no vocalizations were recorded during the crepuscular or nocturnal periods.

TABLE 2.—Plant biomass, soil humidity, and soil hardness estimated at the sites where burrows of *Ctenomys talarum* were excavated (Antinuchi and Busch 1992) and where radiotelemetry was performed for this species (this study). Asterisks (*) denote statistical differences between the 2 sites (*t*-test, $P < 0.001$).

	Excavated burrows	Radiotelemetry
Plant biomass (g/m²)		
Aerial	495.40 ± 384.7	323.60 ± 247.4
Subterranean	621.20 ± 124.4	634.00 ± 463.4
Total	$1,116.60 \pm 405.9$	$1,339.80 \pm 1317.2$
Soil humidity (%)	4.44 ± 1.90	$1.15 \pm 0.47*$
Soil hardness (kg/cm²)	10.27 ± 2.94	$5.88 \pm 3.22*$

FIG. 2.—Mean hourly rate of movement (m/h) of males ($n = 4$) and females ($n = 5$) of *Ctenomys talarum* in 3 periods of the day. Asterisks (*) denote statistical differences among periods for individuals of the same sex (repeated-measures analysis of variance with Tukey correction, $P < 0.05$). Values are means $\pm$ *SD*.

DISCUSSION

Our results confirm that *C. talarum* is solitary. Examination of radiotelemetry data showed that areas occupied by different adults did not overlap and that each individual made use of a different nest site. Because individuals captured for our study were close to each other and belonged to the same spatial cluster, any spatial overlap among adults should have been evident. However, our results demonstrated that each radio-collared adult occupied an exclusive burrow system during the present study (Busch et al. 1989).

Both methods for estimating home-range size showed the same pattern. Male *C. talarum* occupied significantly larger areas than did females. These results agree with the general trend observed across several groups of subterranean rodents (Bandoli 1981; Nevo 1961; Nevo et al. 1982; Reichman et al. 1982; Zhou and Dou 1990; but see Romañach et al. 2005). This difference between sexes has been attributed to differences in body size between males and females and, hence, in their energy demands. This difference in energetic requirements between sexes would, in turn, result in males covering larger foraging areas (McNab 1963; Nevo 1999). In our study, significant differences in body size between the sexes were verified for *C. talarum*. In accordance with previous findings (Zenuto et al. 1999b), males were significantly heavier than females, which could partly explain the differences observed in home-range size between sexes.

An additional factor that has been proposed to affect the differences in home-range size between sexes is the mating system (Fisher and Owens 2000). In a great number of mammalian species, male spatial organization is influenced by the distribution of the females because a male's reproductive success depends mainly on the number of mates he can find and defend (Clutton-Brock 1989; Komers and Brotherton 1997). In *C. talarum* in particular, the mating system is resource-defense polygyny, in which males monopolize resources (territory and foraging areas) that will then be used by reproductive females (Zenuto 1999). In the population of Mar de Cobo, the adult sex ratio is biased to females (Busch et al. 1989), which are spatially distributed in groups (Malizia et al. 1991). These factors make females an economically defendable

resource, through the establishment of a dominance hierarchy among males (Zenuto et al. 2002). Therefore, by occupying larger areas, males increase their chances of monopolizing a higher number of females.

In sum, sexual selection is likely to be one of the main forces driving the observed differences in home-range size between males and females of *C. talarum*, through the effects exerted by body size dimorphism and differential mating behaviors between the sexes, as has been proposed for other solitary mammals (Sandell 1989).

The average size of the home range of Talas tuco-tucos estimated by radiotelemetry was similar to those of other solitary subterranean rodents estimated by the same method (*Ctenomys haigi*: 35.5–38.9 m^2 [Lacey et al. 1998]; *Spalax ehrenbergi*: 63 m^2 [Kushnirov et al. 1998]) but was smaller than that of the colonial tuco-tuco *C. sociabilis* (300–350 m^2 [Lacey et al. 1997]). In strictly subterranean rodents, the area encompassed by the branches and openings of the entire tunnel system of an individual should be the maximal home range of this animal. For *C. talarum*, however, the home-range size estimated by radiotelemetry in our study was significantly larger than that estimated through the excavation of entire tunnel systems (Antinuchi and Busch 1992). However, the present study was performed in a different area close to that used by Antinuchi and Busch (1992).

Intraspecific variation in home-range size across different regions also has been observed in *S. ehrenbergi* (Nevo et al. 1982) and the pocket gopher *Geomys bursarius* (Romañach et al. 2005). This pattern has been related, among several factors, to variation in productivity of the environment. For blind mole rats and pocket gophers, size of their home range was negatively correlated with productivity of the region in which they lived (Nevo 1979, 1991; Nevo et al. 1982; Romañach et al. 2005). In the present study, however, plant biomass at the site where radiotelemetry trials were performed was similar to that of the site where Antinuchi and Busch (1992) excavated entire tunnel systems.

However, soil characteristics were significantly different between the 2 sites. The soil of the site where home ranges were analyzed by radiotelemetry was significantly softer and less humid than the soil of the study site of Antinuchi and Busch (1992). For subterranean rodents, the cost of digging a burrow is 360–3,400 times the cost of walking a similar distance aboveground (Vleck 1979). Although the total cost of digging an entire burrow system appears to be low for *C. talarum* (Antinuchi et al., in press), other studies showed that for Talas tuco-tucos from Mar de Cobo, burrowing in a harder and more compacted soil represents a higher energetic cost (Luna and Antinuchi 2006). Therefore, size of the entire burrow system of a tuco-tuco, and hence its home range, could be affected by soil characteristics, contributing to the intraspecific variation observed in this trait. The same pattern has also been observed in *G. bursarius*, whose tunnel systems were shorter and occupied a smaller area in soils with higher clay content than in sandy soils (Romañach et al. 2005). Moreover, males and females from our study were significantly heavier than those of Antinuchi and Busch (1992); thus, in

accordance to what was proposed by McNab (1963), home-range size in Talas tuco-tucos also may vary intraspecifically in response to the different energetic needs associated with variation in body size.

Finally, the use of different methods to estimate home-range size in each study site could be an additional factor explaining the differences observed. Subterranean rodents maintain a dynamic equilibrium with regard to burrow length (Andersen 1987; Zinnel 1992). Portions of the tunnels can be plugged and, thus, isolated from the rest of the burrow system for short periods of time, in response to the presence of a predator or because a particular area of the foraging patch is temporally not in use. In addition, burrow length may vary seasonally as individuals refill old burrow sections instead of taking soil out of the tunnels (Sparks and Andersen 1988; Sumbera et al. 2003). These frequent changes in burrow length over short periods of time could have led to the differences observed in our study between the 2 locations. Excavating entire burrow systems provides a snapshot of the burrow system geometry used to estimate home-range size. Telemetry, because it takes place over a longer period of time, can provide a more accurate estimation of home-range size of subterranean rodents, probably resulting in larger size values than those obtained by burrow excavation.

Regarding daily activity patterns of *C. talarum* and contrary to expected, hourly rates of movement did not differ significantly between sexes. Although both sexes are territorial in Talas tuco-tucos, we expected males to show a more continuous and random activity pattern because they exhibit higher aggressiveness and territoriality. One of the possible reasons for the absence of differences in rates of movement between sexes might relate to the time of the year the present study was conducted. Breeding season in *C. talarum* extends from June to February (Busch et al. 1989; Malizia and Busch 1991). During the course of our study, some of the females were still nursing and on several occasions young were observed coming out from the same burrow that was occupied by an adult radio-collared female. In seminatural conditions, nursing females constantly chase their young and retrieve them to the nest (Zenuto et al. 2002), which requires that females travel continuously throughout their burrow system. On the other hand, male *C. talarum* from Mar de Cobo establish dominance hierarchies at the beginning of the breeding season (Zenuto et al. 2002); thus, territorial fights among males are expected to be less frequent during the time of the year when the present study was completed, resulting in less territorial defense and lower rates of movement of males.

An additional factor that could explain the lack of significant differences in rate of movement between sexes is underground predation. As mentioned in other studies (Luna and Antinuchi 2003), snakes such as *Bothrops alternata* (yarará) are frequently found in burrows of *C. talarum*. On these occasions, the tunnels where the yararás were found had been isolated from the rest of the burrow by soil plugs (C. D. Antinuchi, in litt.). Although underground predation on *C. talarum* is less common than that observed aboveground (Busch et al. 2000; Vassallo et al. 1994), both sexes are subject to it. Thus, equal

needs of monitoring and defending burrows through constantly traveling along the tunnels in both sexes also could contribute to the lack of significant differences in rate of movements between them. In sum, all these factors could have attenuated the differences in hourly rates of movement between the sexes in *C. talarum*. Future studies will assess if this pattern changes over the breeding season.

Approximately half of the individuals studied showed a rhythmic pattern of activity, which was multiphasic and showed irregular peaks of activity, similar to what was observed in blind mole rats (Nevo et al. 1982). The remarkable presence of polymorphism in patterns of activity of Talas tuco-tucos observed in our study had already been suggested by Luna et al. (2000) to occur in seminatural conditions. Polymorphism in the presence of circadian rhythms has been previously described in captive blind mole rats, in which the absence of a circadian rhythm reflected an arrhythmic genotype (Avivi et al. 2002; Ben-Shlomo et al. 1995).

The present study is the 1st to provide evidence of intraspecific variation in the presence of rhythms of activity patterns in a free-living subterranean rodent. Previous studies have revealed that kinship and genetic substructure are pronounced in *C. talarum* from Mar de Cobo (Cutrera et al. 2005), particularly for females; significant apportionment of genetic variation was found even at the spatial scale corresponding to clusters of individuals (Cutrera et al. 2005). According to these findings, local groups of individuals may represent genetically distinct units; however, in our study, we found individuals with rhythmic and arrhythmic patterns of activity in the same spatial cluster. This suggests that variation in the presence of rhythmic patterns of activity in *C. talarum* does not seem to be associated with the significant spatial genetic structure found in the Mar de Cobo population.

Because daily activity patterns in surface-dwelling rodents are related to, and sometimes depend on, the presence of environmental factors such as light intensity (Honma and Hiroshige 1978), photoperiod (Aschoff 1966), and temperature (Degen 1996; Gordon 1993; Ilan and Yom-Tov 1990; Refinetti 1995), it has been assumed that the absence of rhythms of activity is a common trait among subterranean rodents (Nevo et al. 1982). However, as the number of studies on this particular topic increases, conflicting evidence is obtained. Some subterranean rodents follow the expected pattern of random activity patterns; this is the case in *Geomys attwateri* (Cameron et al. 1988) and *Heterocephalus glaber* (Davis-Walton and Sherman 1994). However, other fossorial rodents display a well-defined pattern of activity, either nocturnal (such as *Octodon bridgesi* [Verzi and Alcover 1990] and *O. lunatus* [Muñoz-Pedreros and Yáñez 2000]) or diurnal (e.g., *Tachyoryctes splendens* [Jarvis 1973], *Aconaemys fuscus* [Pearson 1983], *Cryptomys damarensis* [Lovegrove and Muir 1996], and *Spalacopus cyanus* [Urrejola et al. 2005]). In addition, discrepancies between results obtained in the field and in captivity have been observed in a great number of studies that deal with rhythms of activity in subterranean rodents (e.g., *Octodon degus* [Kas and Edgar 1999; Kenagy et al. 2002], *G. bursarius* [Benedix 1994; Vaughan and Hansen 1961], and *Arvicanthis niloticus*

[Blanchong et al. 1999; Smale et al. 2003]), suggesting that daily activity patterns are not at all consistent among different species of subterranean rodents and possibly reflect unique historical as well as ecological constraints, in spite of the proposed similarities of the subterranean niche in which they live (Buffenstein 2000; Nevo 1999). Thus, further research is needed to identify the factors that determine such a great variation (both at the intra- and interspecific level) in patterns of activity in subterranean rodents.

Examination of our data demonstrates that home-range size of Talas tuco-tucos varies intraspecifically in relation to sex, body size, and soil characteristics. Regarding patterns of activity, this is the 1st study in free-living subterranean rodents to confirm that the presence or absence of rhythms of locomotor activity can be a polymorphic trait, at least in *C. talarum*. We consider that additional studies on the proximate factors (e.g., physiological, neuroendocrinological, etc.) that influence home-range size and patterns of activity are required to further elucidate the adaptive basis of the intra- and interspecific variation reported by this and other studies on subterranean rodents.

RESUMEN

Los roedores subterráneos se caracterizan por su limitada movilidad individual y la distribución en parches de sus poblaciones locales, lo cual ha sido relacionado con la gran diversificación evolutiva de este grupo. Debido a sus hábitos subterráneos, la radiotelemetría constituye una herramienta esencial para recolectar datos sistemáticamente sobre características del uso del espacio, tasas de movimiento y patrones diarios de actividad. Comparados con otro roedores subterráneos, los ctenómidos exhiben mayor actividad sobre la superficie. A pesar de ello, un estudio previo demostró que sólo el 25% de los tuco-tucos evaluados en cautiverio presentaron actividad rítmica asociada con ciclos de luz-oscuridad. En este estudio, utilizamos radiotelemetría para explorar cuantitativamente la dinámica del home range y los patrones de movimientos diarios del tuco-tuco de los talas sudamericano (*Ctenomys talarum*). De acuerdo a lo esperado, el home range de los machos fue de mayor tamaño que el de las hembras. Sin embargo, se observó también variación intraespecífica en el tamaño del home range entre dos sitios de estudio diferentes, posiblemente asociada a diferencias en el peso corporal y en las características del suelo entre los dos lugares. Se confirmó que la ritmicidad en los patrones de actividad diaria es un rasgo polimórfico en esta especie, como ya había sido observado en cautiverio, y la actividad se concentró principalmente durante el período diurno. Este estudio contribuye a generar importantes conocimientos sobre la dinámica de home range y los patrones diarios de actividad de roedores subterráneos en condiciones naturales.

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