Habitat use by colonial tuco-tucos (*Ctenomys sociabilis*): specialization, variation, and sociality

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Understanding habitat requirements has implications for numerous aspects of a species' biology, including where individuals live and how they behave. Specialization for mesic, resource-rich habitats known as mallines is thought to have favored group living in the colonial tuco-tuco (*Ctenomys sociabilis*), a subterranean rodent that is endemic to Neuquén Province in southwestern Argentina. To explore the proposed relationship between mallines and sociality in this species in greater detail, we characterized the habitats occupied by *C. sociabilis* at 3 locations representing the extremes of this species' geographic range. Specifically, plant composition and vegetative structure were characterized for 57 occupied burrow systems distributed across the 3 sampling localities. Our data indicate that *C. sociabilis* is not restricted to mallines. Although significant variation in vegetation was detected among the 3 study sites, the majority of active burrow systems surveyed at each site occurred in nonmallín habitats. In addition to providing the first species-wide survey of habitat use by *C. sociabilis*, our data yield new insights into the role of habitat specialization in promoting sociality in this behaviorally unusual species of ctenomyid rodent.

Key words: *Ctenomys sociabilis*, habitat, mallín, sociality, subterranean rodents

Knowledge of the habitats in which a species occurs can provide valuable insights into its biology, including aspects of its ecology, behavior, and conservation. With regard to social behavior, the distribution of critical resources—including suitable habitats—is thought to be an important factor favoring group living in numerous species (Emlen 1982; Koenig et al. 1992). Specifically, if resources such as suitable habitat are rare or patchily distributed, the costs of dispersing may be high enough that individuals benefit by being philopatric and remaining in their natal group (Emlen 1982, 1991). As a result, for social species, understanding patterns of habitat use may yield critical insights into the reasons for group living.

Specialization for mesic habitat patches has been suggested to be an important ecological factor favoring group living in the colonial tuco-tuco (*Ctenomys sociabilis*). Although more than 50 species of tuco-tucos (Rodentia: Ctenomyidae) occur in sub-Amazonian South America (Reig et al. 1990; Wilson and Reeder 2005), *C. sociabilis* is the only ctenomyid for which quantitative evidence of group living is available (Lacey et al. 1997; Lacey and Wieczorek 2004). This species is endemic to Neuquen Province, Argentina, where it occupies open habitats in the eastern foothills of the Andes mountains. In their initial description of *C. sociabilis*, Pearson and Christie (1985) noted that the animals were associated with wet meadows known locally as "mallines." Subsequently, using comparative data from *C. sociabilis* and the syntopic but solitary *C. haigi*, Lacey and Wieczorek (2003) postulated that the patchy distribution of mallín habitat favors philopatry and group living in the former species.

Although intriguing, this analysis was based upon data from a limited portion of the geographic distribution of *C. sociabilis*. Mallines are found throughout the range of this species but the relationship between mallín habitats and the occurrence of colonial tuco-tucos has not been assessed at this scale. Thus, the primary objective of this study was to determine whether *C. sociabilis* is associated with mallín habitats throughout its range. Accordingly, we quantified the plant species and vegetative structure associated with currently occupied burrow systems of colonial tuco-tucos at 3 localities representing the extremes of this species' geographic distribution. In addition to providing the first general characterization of the habitats used by this species, our data yield potentially important insights
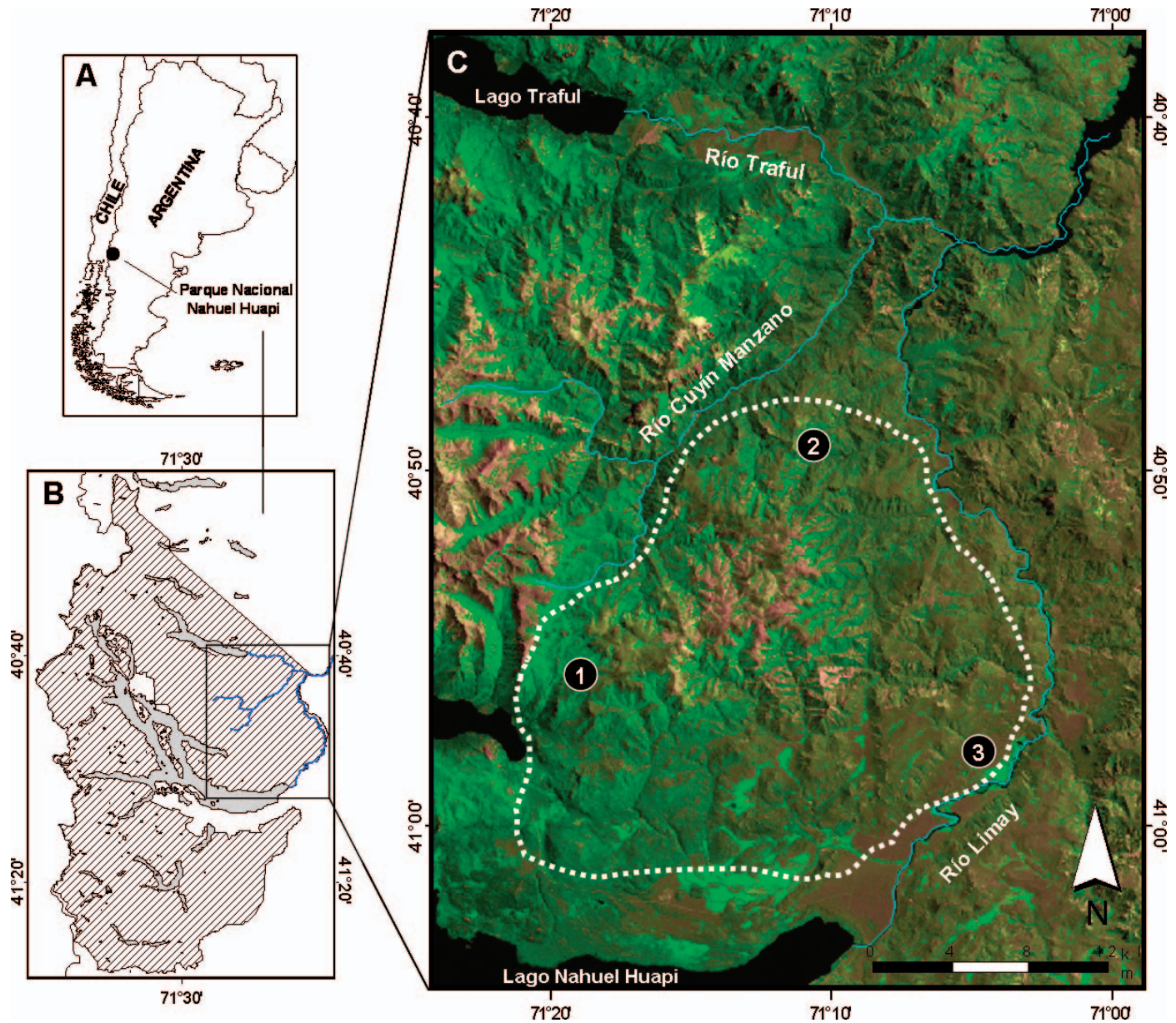
FIG. 1.—Maps depicting the location of the study area in Nahuel Huapi National Park, Neuquén Province, Argentina. In A), the location of the park in southwestern Argentina is indicated. In B), the location of the study area (rectangle) within the park (hatched area) is denoted. In C), the known geographic distribution of *C. sociabilis* is indicated by the dashed line. Within this area, the locations of the 3 focal study sites are denoted by numbers, with 1 = Paso Coihue, 2 = La Lipela, 3 = Rincón Grande.

into the ecological bases for group living in this behaviorally unusual species of ctenomyid rodent.

MATERIALS AND METHODS

Study area.—The study was conducted in Nahuel Huapi National Park, Neuquén Province, Argentina. Data were collected in November–January of 2007 and 2008. This corresponds to the austral spring–summer, which is the portion of the year when animal activity and food resources are greatest (E.A. Lacey, in litt). The study area (40°47′ to 40°59′S and 71°03′ to 71°20′W) comprises the current known

geographic distribution of the colonial tuco-tuco (Fig. 1). The area is bounded to the east by the Limay River, to the south by Lake Nahuel Huapi, to the north by the Traful River and Lake Traful, and to the west by dense montane forest (Pearson and Christie 1985). The habitat in this region consists primarily of precordilleran steppe, which extends from the high-precipitation (1,000 mm per year) eastern edge of the Andean–Patagonian forest to the low-precipitation (300 mm per year) western edge of the Patagonian steppe; the mean annual isotherm for this region does not exceed 10°C (Bran 2000; Cabrera and Willink 1980). Precipitation occurs primarily in winter, largely as snow, with a sharp west–east

gradient caused by the rain shadow of the Andes (Bran 2000; Cabrera and Willink 1980). Vegetation in the area generally is consistent with precordilleran steppe habitat and is dominated by small shrubs and bunch grasses such as *Festuca pallescens* (coirón dulce), *Stipa speciosa* (coirón amargo), *Mulinum spinosum* (neneo), and *Acaena splendens* (cepa caballo; Bran 2000; León et al. 1998). Toward the western end of the study area isolated groves of *Austrocedrus chilensis* (ciprés de la cordillera) occur and, at higher altitudes, stands of deciduous *Nothofagus pumilio* (lenga) are common (Bran 2000; León et al. 1998).

Within the study area, 3 localities were chosen for detailed investigation. These sites formed the apices of the roughly triangular geographic distribution of *C. sociabilis* (Fig. 1) and thus they encompassed the variation in topography and climate present within the range of this species. As a result, we expect that these sites also encompassed much of the variation in habitat experienced by the study species. Because our data were collected as part of the 1st quantitative assessment of the geographic distribution of *C. sociabilis*, sampling focused on the extremes of this species' suspected range. Given the limited area ($\sim$700 km^2) in which *C. sociabilis* occurs (Fig. 1) and given that our sampling regime encompassed the west–east rainfall and habitat gradient that predominates in this region (Ezcurra and Brion 2005; Martín and Mermoz 2005; Mermoz et al. 2009), it is unlikely that this emphasis on the distributional limits of the study species caused us to overlook significant variation in the types of habitats occupied by colonial tuco-tucos.

With regard to the 3 sites selected for detailed study, the distance between adjacent sites was $\sim$18 km. Paso Coihue (southwestern site) and La Lipela (northern site) were more mesic ($>$1,100 mm annual precipitation) and consisted of hilly cordilleran terrain characterized by deep valleys separated by steep, heavily vegetated slopes. Although *Nothofagus* forest was present at both sites, Paso Coihue was characterized by a dense understory of bamboo (*Chusquea*), whereas forested areas at La Lipela were more open and brushy. In contrast, Rincón Grande (southeastern site) was more arid ($<$800 mm annual precipitation) and was characterized by rolling hills and open, level plains.

Identifying burrow systems.—At each focal locality, we searched for burrow systems occupied by colonial tuco-tucos by walking through the habitat; the minimum distance traversed at each locality was 20 km. Surveys did not follow a predetermined pathway and, although we attempted to include all major vegetation types present in the region (Martín and Mermoz 2005), no quantitative assessment of the prevalence of different habitat types was conducted. Because previously published studies suggested that *C. sociabilis* is associated with mallín habitat (Lacey and Wieczorek 2003; Pearson and Christie 1985), our surveys targeted mallín areas but included the intervening habitat traversed while walking from one mallín to the next. Thus, although mallín habitat likely is overrepresented in our samples, the intervening areas

examined provided a relatively unbiased sample of the other habitats present at each focal locality.

The presence of *C. sociabilis* was determined on the basis of the size and configuration of burrow entrances (burrow openings $\sim$7.5 cm in diameter, with multiple open entrances located in proximity to one another—Lacey et al. 1997). No other species of tuco-tuco is known to occur within the study area and no other rodents in this region construct burrow entrances with the same configuration (Pearson 1995; Pearson and Christie 1985). As a result, it is unlikely that these criteria resulted in the incorrect assignment of burrow systems to *C. sociabilis*. To determine if a burrow system was currently occupied, we looked for fresh (moist) mounds of dirt around burrow openings or the presence of fresh (moist) soil plugs within burrow entrances. Fresh mounds and plugs typically are generated daily; because exposed soil dries quickly, the presence of moist mounds or plugs is indicative of animal activity within the last 24 h (Pearson and Pearson 1993). In addition, because *C. sociabilis* is diurnal and produces a distinctive, birdlike alarm call that is emitted above ground (Pearson and Christie 1985), we typically waited at each area of apparent tuco-tuco activity for a period of 20–30 min to obtain visual and auditory confirmation that animals were present. Burrow systems that did not provide evidence of current activity were recorded as unoccupied; long-term field studies of *C. sociabilis* (e.g., Lacey and Wieczorek 2003, 2004) indicate that unused burrow entrances quickly deteriorate and thus unoccupied burrow systems must have contained tuco-tucos within the past 1–2 years.

For each location at which evidence of *C. sociabilis* (occupied and unoccupied burrow systems) was detected, we recorded a global positioning system (GPS) coordinate (WGS 84, accuracy 5–7 m) using a hand-held Garmin ETrex GPS unit. On the basis of the spatial distribution of burrow systems monitored as part of long-term behavioral studies of this species (Lacey and Wieczorek 2004), clusters of burrow entrances located within a 10-m radius of one another were counted as part of the same burrow system and were assigned to the same GPS locality. In contrast, clusters of active burrow entrances separated by $>$10 m were considered distinct and were recorded as separate GPS coordinates.

Microhabitat characterization.—To characterize the habitats occupied by *C. sociabilis*, we selected 57 burrow systems at which tuco-tuco activity was detected for detailed analysis. At Rincón Grande, this included a subset ($N = 21$) of the burrow systems monitored as part of long-term studies of the behavioral ecology of *C. sociabilis* (Lacey and Wieczorek 2004). At Paso Coihue and La Lipela, preliminary surveys were used to identify the locations of occupied burrow systems, after which a subsample of localities was randomly selected for analysis; the total number of localities characterized at each of these sites (Paso Coihue $N = 21$; La Lipela $N = 15$) was comparable with that examined at Rincón Grande.

At each occupied burrow system, we established a 200-m^2 rectangular plot centered on the point at which the GPS fix for that locality was taken. Plot size was based on the estimated

Mallín

Mixed grasses

Shrub

Fig. 2.—Photos of the 3 habitat types to which occupied burrow systems of *C. sociabilis* were assigned during field surveys. For each burrow system examined, a 200-m² rectangular plot was established (axes denoted by red strings in each photo) and vegetation within that

area occupied by a single adult female *C. sociabilis* (E. A. Lacey, in litt.). We then assigned the area within the plot to 1 of 3 habitat types previously defined for this part of Argentina (Bran 2000). The 3 habitat types (Fig. 2) to which these localities were assigned were: mallín–herbaceous vegetation and hydrophilic grasses such as *Carex* spp., *Juncus* spp., and *Poa pratensis*, with <20% bare soil; shrub–woody vegetation, primarily of *Berberis* spp. and *Senecio* spp., with >20% bare soil; and mixed grasses–herbaceous and shrubby vegetation, often including numerous grasses, with equal proportions of vegetation and bare soil.

To provide a more quantitative assessment of the habitat at each locality sampled, within each 200-m² plot we established 5 2-m² subplots; 1 subplot was placed at the center of the 200-m² plot, with the remaining 4 subplots placed 8 m away along each of the 4 cardinal compass directions. Within each subplot, percent cover was estimated for shrubs (e.g., *Senecio bracteolatus*), woody herbs (e.g., *M. spinosum*), herbs (e.g., *Trifolium*), and bare soil. Because grasses (e.g., *Poa)* and graminoids (e.g., *Carex*) are smaller and more cryptic, percent cover for these vegetation types was estimated using 2 0.25-m² quadrats nested within each 2-m² subplot. Percent cover for all vegetation types was estimated visually following the method of Braun-Blanquet (Newton 2007). Values for each vegetation type were averaged across subplots to yield a mean percent cover for each 200-m² plot sampled.

Digital habitat data.—Digital data layers are now routinely used to assess environmental parameters, including patterns of habitat use by species of conservation concern (Breininger et al. 1991; Danks and Klein 2002). To compare habitat types identified by digital environmental data with our field measures of habitats occupied by *C. sociabilis*, the GPS locations of all burrow systems detected (occupied and unoccupied) were used to construct a digital layer depicting the occurrence of this species at the 3 focal sampling localities. By superimposing maps of burrow system localities onto existing environmental data layers for this region obtained from the Delegación Regional Patagonia (Administración de Parques Nacionales, S. C. de Bariloche, Argentina), we were able to determine values for annual precipitation (isohyet), elevation, and major vegetation type (e.g., steppe grassland; Martín and Mermoz 2005) for each of the 3 study sites. Comparisons of digital layers and quantification of environmental parameters were completed using the Geoprocessing techniques available in ArcView GIS 3.2 (ESRI 1998).

Data analysis.—To determine if the vegetative structure of mallín and nonmallín (shrub and mixed grass habitats pooled) habitats differed, we used a generalized linear model (GLZ) with a normal distribution and a log link function (McCullagh and Nelder 1989) to compare these habitat types with respect to

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plot assessed. Assignments of habitat types were based on the identities of the plant species present and the overall percent cover by vegetation versus bare soil, as described by Bran (2000).

TABLE 1.—Number of burrow systems sampled and associated environmental conditions at each focal study site. Data on elevation and precipitation were obtained by plotting the location of each burrow system (occupied and unoccupied) detected on environmental layer data obtained from the Administracion de Parques Nacionales Argentinas. Numbers in parentheses are ranges.

Site	Number of burrow systems	Number (%) of active burrow systems	Elevation (m above sea level)	Precipitation (mm/year)
Paso Coihue	128	45 (35)	$1,428 \pm 197$ (1,095–1,813)	$1,553 \pm 50$ (1,500–1,600)
La Lipela	90	29 (32)	$1,389 \pm 84$ (1,146–1,511)	$1,193 \pm 25$ (1,100–1,200)
Rincón Grande	147	59 (40)	793 ± 39 (747–887)	670 ± 61 (600–800)

mean percent cover by each of the 5 vegetation types considered (shrubs, woody herbs, herbs, grasses, graminoids) plus mean percent bare soil. These analyses were completed using study site and habitat type (mallín versus non-mallín) as categorical variables under a full factorial model. Significant differences in vegetative structure revealed by the GLZ analyses were then examined in greater detail by comparing vegetation types or study sites directly using Kruskal–Wallis or Mann–Whitney U-tests. GLZ and post hoc comparisons were completed using Statistica 5.1 (StatSoft 1997).

To determine if plant species composition differed among study sites (locations of occupied burrow systems) or between mallín versus nonmallín habitats, we used the nonparametric multivariate analysis of similarities (ANOSIM; Clarke 1993). ANOSIM is based on the Bray–Curtis similarity index and produces a global R statistic that provides an absolute measure of the distance between data sets. R values approaching 1 indicate that the data sets are strongly differentiated, whereas values approaching 0 indicate that groups cannot be distinguished. The significance of R was determined on the basis of 10,000 permutations of the data set among localities and between habitat types. Differences among the 3 focal sites and between mallín and nonmallín habitats were depicted using nonmetric multidimensional scaling (NMDS) ordination on the basis of Bray–Curtis similarity values. This analysis generates a stress value that reflects the degree of fit between the data matrix and the graphical, 2-dimensional NMDS output. A high stress value (stress = 1) indicates a poor fit, suggesting that the graphical NMDS output distorts the underlying data set (Clarke and Warwick 2001). SIMPER analysis (Clarke 1993) was used to determine the contribution of each species to the mean Bray–Curtis index values used in the NMDS analyses. ANOSIM, NMSD, and SIMPER analyses were conducted using the computer package PAST 1.81 (Hammer et al. 2001).

Throughout the text, means are reported $\pm$ 1 SD. Unless otherwise indicated, $\alpha = 0.05$. When the same statistical test was used multiple times, α was adjusted using the Bonferroni correction procedure (Rice 1989).

RESULTS

A total of 365 burrow systems (occupied and unoccupied) attributed to *C. sociabilis* was identified and their locations recorded as GPS coordinates. The number of burrow systems per study site varied, ranging from 90 at La Lipela to 147 at Rincón Grande (Table 1). The percent of active burrow systems per site ranged from 32% at La Lipela to 40% at

Rincón Grande (Table 1). Burrow systems were found at elevations ranging from 750 to 1,800 m and in areas characterized by precipitation ranging from 600 to 1,600 mm per year (Table 1). Among the focal sites, both elevation and precipitation differed significantly (elevation: Kruskal–Wallis $H = 262.93$, $P < 0.0001$; Dunn post hoc analyses: Paso Coihue versus La Lipela $P > 0.05$, all other comparisons $P < 0.0001$; precipitation: Kruskal–Wallis $H = 331.46$, $P < 0.0001$; Dunn post hoc analyses: all $P < 0.0001$). Within each focal site, however, the locations of occupied and unoccupied burrow systems did not differ with respect to these parameters (elevation: Rincón Grande Mann–Whitney $U = 2461.50$, $P > 0.05$; Paso Coihue Mann–Whitney $U = 1633.00$, $P > 0.05$; La Lipela Mann–Whitney $U = 830.50$, $P > 0.05$; precipitation: Rincón Grande Mann–Whitney $U = 2535.00$, $P > 0.05$; Paso Coihue Mann–Whitney $U = 1717.50$, $P > 0.05$; La Lipela Mann–Whitney $U = 881.50$, $P > 0.05$).

Characterization of habitat types.—On the basis of comparisons of the locations of burrow systems (occupied and unoccupied) with existing digital environmental data layers, *C. sociabilis* occurred in 5 major habitat types (Table 2). At each study site, the majority of burrow systems encountered occurred in herbaceous and woody steppe habitat (Rincón Grande, La Lipela) or in *Nothofagus* forest (Paso Coihue); no burrow systems were encountered in steppe grassland. At all sites, mallines (wet meadows) accounted for ≤11% of burrow systems encountered (Table 2). For occupied burrow systems ($N = 133$), 3% occurred in mallín habitats. Within each focal study site, the locations of active and inactive burrow systems did not differ with respect to habitat type (chi-square tests, Rincón Grande $\chi^2 = 1.71$, $d.f. = 1$, $P > 0.05$; Paso Coihue $\chi^2 = 1.95$, $d.f. = 2$, $P > 0.05$; La Lipela $\chi^2 = 2.31$, $d.f. = 2$, $P > 0.05$).

Habitat characterizations conducted in the field for the subset of 57 occupied burrow systems indicated that the occurrence of *C. sociabilis* in mallín habitats (28% of burrow systems) was significantly greater than expected given the occurrence of these animals in mallín habitats indicated by the digital environmental data (3% of active burrow systems; $\chi^2 = 120.3$, $d.f. = 1$, $P < 0.05$). Field characterizations, however, were consistent with the digital data in revealing that the majority of occupied burrow systems characterized did not occur in mallín habitat (Fig. 3). Although nearly half (48%) of the 21 burrow systems sampled at Rincón Grande were located in mallín habitats, the occurrence of occupied burrow systems in mallines was significantly less at the other 2 study sites (Paso Coihue: 19% of 21 burrow systems; La Lipela: 13% of 15

TABLE 2.—Occurrence of burrow systems (occupied and unoccupied) by vegetation type. For each focal study site, the locations of occupied burrow systems were compared with digital maps of vegetation types. Numbers in parentheses are percentages.

	Number of burrow systems (% occurrence)			
Vegetation type	Paso Coihue	La Lipela	Rincón Grande	Overall
Nothofagus pumilio forest[a]	75 (58.6)	17 (18.9)	0 (0.0)	92 (25.2)
Herbaceous and woody steppe[b]	0 (0.0)	64 (71.1)	131 (89.2)	195 (53.4)
Transitional forest[c]	34 (26.0)	0 (0.0)	0 (0.0)	34 (9.3)
High-elevation deserts[d]	19 (14.8)	9 (10.0)	0 (0.0)	28 (7.7)
Mallín[e]	0 (0.0)	0 (0.0)	16 (10.8)	16 (4.4)
Total	128 (100)	90 (100)	147 (100)	365 (100)

[a] Translated from bosque de lenga, [b] estepa herbácea y arbustiva enana, [c] mosaico de bosques bajos y/o matorrales con herbáceas, [d] semidesiertos de altura, and [e] vegas in Martín and Mermoz (2005).

burrow systems; chi-square tests, frequency of occupied burrows in mallines at Rincón Grande used to determine expected values; Paso Coihue $\chi^2 = 52.85$, $d.f. = 2$, $P < 0.0001$; La Lipela $\chi^2 = 41.90$, $d.f. = 2$, $P < 0.0001$).

Characterization of vegetation structure.—Generalized linear analyses (log-normal GLZ) indicated that the mean percent cover by shrubs, woody herbs, and graminoids did not differ with habitat type (mallín versus nonmallín), study site, or the interaction of these factors (shrubs: habitat Wald stat = 0.36, $P = 0.54$, site Wald stat = 1.03, $P = 0.59$, habitat × site Wald stat = 5.58, $P = 0.06$; woody herbs: habitat Wald stat = 1.20, $P = 0.27$; site Wald stat = 5.92, $P = 0.05$; habitat × site Wald stat = 1.44, $P = 0.48$; graminoids: habitat Wald stat = 1.16, $P = 0.27$; site Wald stat = 3.20, $P = 0.20$; habitat × site Wald stat = 1.09, $P = 0.57$). Similarly, we found no effects of these factors on the mean percentage of bare soil observed (habitat Wald stat = 0.94, $P = 0.33$; site Wald stat = 0.74, $P = 0.69$; habitat × site Wald stat = 0.57, $P = 0.75$). In contrast, the mean percent cover by herbs and grasses differed significantly between habitats and between study sites (herbs: habitat Wald stat = 20.86, $P < 0.0001$; site Wald stat = 28.79, $P < 0.0001$; grasses: habitat Wald stat = 13.23, $P < 0.0001$; site Wald stat = 26.28, $P < 0.0001$); in neither case was the interaction between habitat type and site significant (both $P > 0.05$). Post hoc

analyses revealed that occupied burrow systems at Rincón Grande had significantly higher mean percent cover by grasses than occupied burrow systems at either Paso Coihue or La Lipela (Kruskal–Wallis $H = 24.62$, $P < 0.0001$; Dunn post hoc analyses: Rincón Grande versus Paso Coihue $P < 0.01$; Rincón Grande versus La Lipela $P < 0.0001$, Paso Coihue versus La Lipela $P > 0.05$; Fig. 4a). For herbs, mean percent cover at La Lipela was significantly less than that at the other 2 study sites; mean percent cover by herbs at Rincón Grande and Paso Coihue did not differ (Kruskal–Wallis $H = 18.82$, $P = 0.0001$; Dunn post hoc analyses Paso Coihue versus La Lipela $P < 0.0001$; Paso Coihue versus Rincón Grande $P > 0.05$; Rincón Grande versus La Lipela $P < 0.001$).

Characterization of plant species composition.—Analyses of similarities revealed significant differences between sites with regard to plant species composition at the locations of occupied burrow systems ($R_{global} = 0.514$, $P < 0.0001$; Fig. 5). Post hoc pair-wise comparisons indicated that although Paso Coihue and La Lipela did not differ in terms of plant species composition ($R = 0.005$, $P = 0.3800$; Fig. 5), Rincón Grande differed significantly from both of these sites (Rincón Grande versus La Lipela $R = 0.778$, $P < 0.0001$; Rincón Grande versus Paso Coihue $R = 0.624$, $P < 0.0001$).
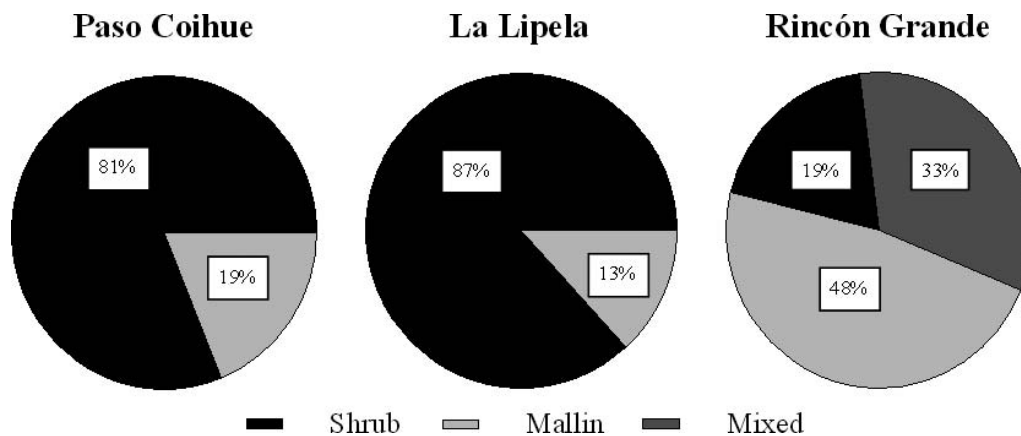

FIG. 3.—Distribution of occupied burrow systems by habitat type. At each focal study site, field surveys were used to determine the percentage of occupied burrow systems occurring in each of 3 habitat types (shrub, mallín, mixed grasses). For Rincón Grande, this represents all (N = 15 per site) active burrow systems detected; for Paso Coihue and La Lipela, this represents a randomly selected subset (N = 21 per site) of the occupied burrow systems at these sites.
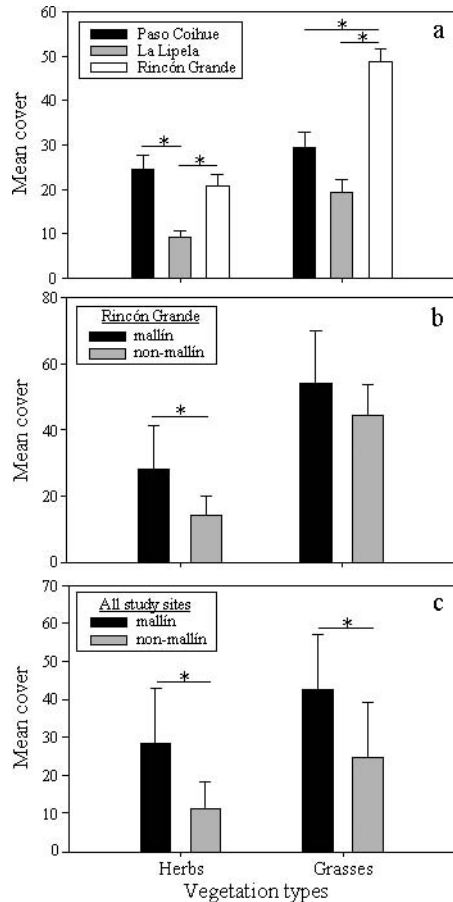
FIG. 4.—Comparisons of mean percent cover by herbs and grasses. In a), data are from the same 57 occupied burrow systems characterized in Fig. 3. In b), data are from 10 mallín and 11 nonmallín localities at Rincón Grande. In c), data are from 16 mallín localities (pooled across study sites) and 16 randomly selected nonmallín localities. * denotes significant ($P < 0.05$) contrasts (statistical results presented in text).
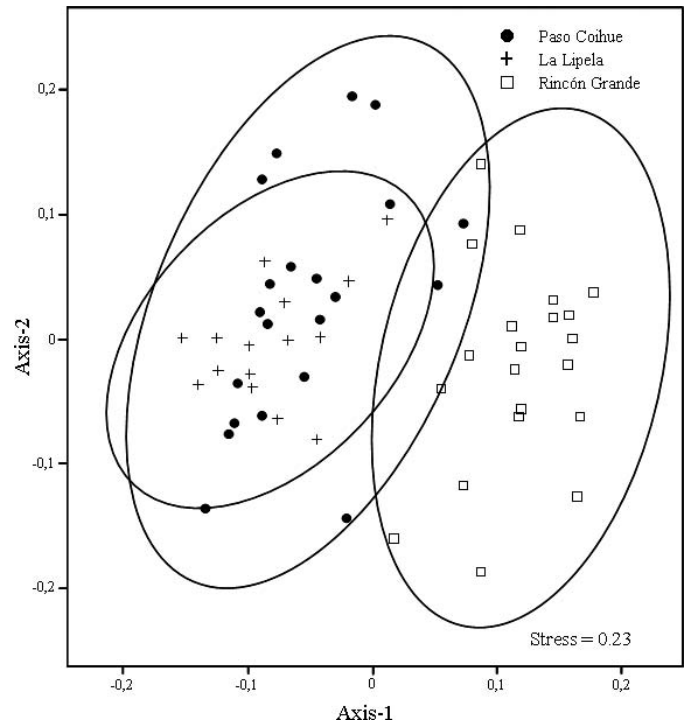

FIG. 5.—Analyses of plant species composition. Shown is the nonmetric multidimensional scaling (NMDS) ordination output from these analyses, which uses the Bray–Curtis dissimilarity index to characterize differences in plant species composition among the study sites. Analyses are based on the percent cover by plant species ($N = 28$) identified during analyses of 57 burrow systems occupied by *C. sociabilis* (Rincón Grande: $N = 21$; Paso Coihue: $N = 21$; La Lipela: $N = 15$). Ellipses denote the 95% confidence interval of each site. The stress value indicates the fit between matrix data and the 2-dimensional plane. High stress indicates a poor fit and that the MDS representation distorts the underlying data.

The SIMPER analysis revealed that, of the 28 plant taxa included in our analyses, 9 accounted for >66% of the overall dissimilarity between sites (Table 3). In particular, mean percent cover by both the shrub *Adesmia boronioides* and the herb *Acaena splendens* was significantly higher at Paso Coihue and La Lipela (*Adesmia boronioides*: Kruskal–Wallis $H = 24.46$, $P < 0.0001$, Dunn post hoc analyses: Rincón Grande versus Paso Coihue $P = 0.019$, Rincón Grande versus La Lipela $P < 0.0001$, La Lipela versus Paso Coihue $P > 0.05$; *Acaena splendens*: Kruskal–Wallis $H = 32.57$, $P < 0.0001$, Dunn post hoc analyses: Rincón Grande versus Paso Coihue $P = 0.0014$, Rincón Grande versus La Lipela $P < 0.0001$, La Lipela versus Paso Coihue $P > 0.05$). In contrast, mean percent cover by the grasses *Stipa speciosa* and *Vulpia australis* was significantly higher at Rincón Grande (*S. speciosa*: Kruskal–Wallis $H = 21.83$, $P < 0.0001$, Dunn post hoc analyses: Rincón Grande versus Paso Coihue $P < 0.0001$, Rincón Grande versus La Lipela $P = 0.001$, La Lipela versus Paso Coihue $P > 0.05$; *V. australis*: Kruskal–Wallis $H = 36.23$, $P < 0.0001$, Dunn post hoc analyses: Rincón Grande

versus Paso Coihue $P < 0.0001$, Rincón Grande versus La Lipela $P = 0.0003$, La Lipela × Paso Coihue $P > 0.05$). Mean percent cover by the remaining 5 of the 9 species identified by the SIMPER analysis did not differ significantly among study sites (Kruskal–Wallis tests, all $P > 0.05$).

Comparisons of mallín and nonmallín habitats.—Given the predicted importance of mallín habitat to *C. sociabilis* and given the results of GLZ and SIMPER analyses of the focal study sites, we compared the mean percent cover of herbs and grasses in mallín versus nonmallín habitats. Because the percentage of occupied burrow systems occurring in mallín habitat was significantly greater at Rincón Grande (Fig. 3), we first compared mallín ($N = 10$) and nonmallín ($N = 11$) habitats for this study site alone. This analysis revealed that mean percent cover by both herbs and grasses was significantly greater in mallín habitat (herbs: Mann–Whitney $U = 20.50$, $N = 10, 11$, $P = 0.012$; grasses: Mann–Whitney $U = 30.0$, $N = 10, 11$, $P < 0.05$; Fig. 4b). We then pooled data for occupied burrow systems in mallín habitats at all 3 study sites ($N = 16$) and compared that information with data from an equal number of nonmallín burrow systems ($N = 16$) that had been randomly selected from across the study sites. The results of this analysis

TABLE 3.—Comparisons of plant species compositions of the 3 focal study sites. For each plant species identified, the mean percent cover at each study site is indicated. Also indicated for each species is its contribution to the overall Bray–Curtis dissimilarity index for the study sites and the cumulative percentage of species composition added by each taxon.

Plant taxa	Contribution to dissimilarity	Cumulative %	Mean cover (%)		
			Paso Coihue	La Lipela	Rincón Grande
Acaena splendens	8.53	10.92	10.70	18.30	0.02
Adesmia boronioides	7.89	21.03	8.14	17.00	0.00
Stipa speciosa	6.37	29.20	3.39	1.43	13.30
Berberis microphylla	6.31	37.28	8.90	6.07	11.00
Poa ssp.	6.24	45.28	10.00	9.62	10.00
Mulinum spinosum	5.15	51.88	6.93	8.90	4.02
Senecio bracteolatus	4.78	58.00	0.07	2.66	10.80
Vulpia australis	4.69	64.00	0.00	0.35	10.90
Chiliotrichum rosmarinifolium	3.33	68.27	7.50	1.90	0.00
Festuca ssp.	3.11	72.26	5.17	4.47	0.14
Discaria trinervis	2.90	75.98	0.00	0.60	7.38
Trifolium repens	2.68	79.41	5.87	0.65	1.52
Carex/Juncus	2.37	82.45	0.63	0.53	5.83
Baccharis magellanica	2.23	85.30	3.62	1.90	0.00
Taraxacum officinale	2.00	87.86	3.77	0.90	1.51
Rytidosperma virescens	1.65	89.98	3.64	1.08	0.00
Bromus ssp.	1.63	92.06	1.26	1.70	1.54
Holcus lanatus	1.18	93.57	0.00	0.10	2.93
Agrostis ssp.	1.09	94.97	1.37	1.02	0.77
Hordeum ssp.	0.67	95.82	1.02	0.92	0.04
Carduus thoermeri	0.57	96.55	0.00	0.00	1.35
Maytenus chubutensis	0.55	97.26	1.50	0.00	0.00
Ribes cucullatum	0.52	97.93	1.10	0.53	0.00
Rosa rubiginosa	0.42	98.47	0.00	0.00	1.07
Nothofagus pumilio	0.41	98.99	1.14	0.00	0.00
Apera interrupta	0.36	99.45	0.00	1.03	0.07
Schinus patagonicus	0.27	99.79	0.02	0.00	0.71
Gaultheria pumila	0.16	100.00	0.33	0.00	0.00

were similar in that percent cover by grasses and herbs was significantly greater for mallín versus nonmallín localities (grasses: Mann–Whitney $U = 46.00$, $N = 16$, 16, $P = 0.001$; herbs: Mann–Whitney $U = 35.00$, $N = 16$, 16, $P < 0.0001$; Fig. 4c). Finally, ANOSIM of these data indicated that plant species composition differed significantly between mallín and nonmallín habitats (ANOSIM $R = 0.431$, $P < 0.0001$); this difference was due primarily to the greater abundance of grasses (genus *Poa*) in mallines at all 3 study sites.

DISCUSSION

Our analyses revealed that *C. sociabilis* occurred in mallines at each of our focal study sites, suggesting that these animals are associated with mallín habitat throughout their geographic range. At each site, however, >50% of the occupied burrow systems examined occurred in nonmallín habitats; these habitats differed significantly from mallines in terms of both plant species composition and the mean percent cover by grasses and herbs, indicating that mallín and nonmallín areas were quantitatively distinct. Thus, although our data are consistent with those of Pearson and Christie (1985) and Lacey and Wieczorek (2003) in confirming that *C. sociabilis* occurs in mallines, our findings indicate that, contrary to suggestions by these authors, the animals are not limited to such habitat. Instead, *C. sociabilis* also occurs in areas dominated by woody shrubs that are characterized by a lower percent cover of herbs and grasses than is typical of mallines.

Although our sampling regime was not completely systematic, 2 lines of evidence suggest that our findings provide a reasonable representation of the habitats occupied by *C. sociabilis*. First, given our sampling protocol at Paso Coihue and La Lipela, our data set should have favored burrow systems located in mallín areas yet, at both sites, the majority of the active systems encountered occurred in nonmallín habitats. Second, because Rincón Grande is the site of a long-term study of the behavioral ecology of this species (Lacey 2001; Lacey et al. 1997; Lacey and Wieczorek 2003, 2004) that includes annual censuses of occupied burrow systems, sampling of active burrow systems at Rincón Grande was effectively complete. Even under this intensive sampling regime, ~50% of active burrow systems were located in nonmallín areas. Collectively, these observations suggest that despite potential biases in our sampling protocol, our data are robust in suggesting that *C. sociabilis* is not restricted to mallín habitats.

Digital versus field-based analyses of habitat use.—Our analyses revealed a marked contrast between the percentages of burrow systems assigned to mallín habitat by digital

environmental data layers versus direct, field-based assessments of habitat type. Although multiple authors have questioned the accuracy of digitally based analyses of species distributions (e.g., Araújo et al. 2005; Gogol-Prokurat 2011; Pearson and Dawson 2003), few studies appear to have compared directly the results of digital and field-based assessments of habitat availability. We suspect that the greater use of mallines revealed by our field surveys reflects the greater precision of these habitat data; given the resolution of the digital data layers used (scale 1:250.000; minimum mappable unit = 12 ha—Martín and Mermoz 2005), it seems likely that smaller mallín patches recorded during field surveys were not represented in the digital data, leading to underestimation of use of this habitat type in our digitally based analyses. Although perhaps not surprising, this outcome has potentially important implications for studies that use digital data layers to assess habitat use, particularly for species that favor habitats distributed in small patches.

Habitat use and sociality.—Our characterization of the habitats in which *C. sociabilis* occurs also has potential implications for understanding the distinctive social behavior of this species. *C. sociabilis* is unusual among tuco-tucos in that burrow systems are regularly occupied by multiple adult females and, in some cases, a single adult male (Lacey 2000). Burrow sharing arises due to natal philopatry by females and thus social groups consist primarily of close female kin (Lacey and Wieczorek 2004). Previous descriptions of habitat use by *C. sociabilis* suggested that mallín habitats are important for the social behavior of this species (Lacey and Wieczorek 2003; Pearson and Christie 1985). In particular, Lacey and Wieczorek (2003) hypothesized that the patchy spatial distribution of mallines renders dispersal particularly costly for *C. sociabilis*, which might favor natal philopatry and the formation of social groups.

Our data indicate that specialization for mallín habitats per se is less important than previously assumed but do not negate the idea that a patchy distribution of suitable habitats favors natal philopatry in this species. *C. sociabilis* occurs in the precordilleran interface between the arid steppe grasslands of eastern Patagonia and the temperate mesic forests of the Andes (Mermoz et al. 2009). At the landscape scale, this area consists of a mosaic of steppe, forest, and mallín habitats (Mermoz et al. 2009), with patches of the latter 2 habitat types scattered throughout the prevailing steppe grassland. In our analyses, no burrow systems were detected in steppe habitat, despite the occurrence of this habitat type at all 3 study sites. Thus, even the expanded range of vegetation types reported here may be patchily distributed, with the result that dispersal between suitable areas of habitat is difficult for *C. sociabilis*. Quantitative analyses of the distributions of the different habitat types used by *C. sociabilis* are required to explore the relationship between habitat patchiness and sociality in this species in greater detail.

Variation in habitat use.—Patterns of habitat use may vary temporally, particularly for animals that inhabit temperate environments such as the precordilleran region in which this study was conducted (Bran 2000; León et al. 1998). Seasonal variation in habitat use, however, cannot explain the differences between our findings and those of Lacey and Wieczorek (2003). Data for both studies were collected during the late austral spring and early austral summer and thus reflect the habitats occupied by *C. sociabilis* during the same portion of the year. Further, long-term studies of this species indicate that a social group occupies the same burrow system in consecutive years, with no evidence of changes in the area occupied by a given set of individuals either within or between years (Lacey and Wieczorek 2004).

Habitat use may also vary geographically. Our analyses revealed that the prevalence of *C. sociabilis* in mallín versus other habitat types differed among the 3 study sites. Specifically, active burrow systems in mallín areas were most common at Rincón Grande and least common at La Lipela. This difference may reflect variation in the prevalence of mallín habitats across study sites; the digital environmental layers examined indicated that mallines were more prevalent at Rincón Grande. At the same time, habitat use by *C. sociabilis* may vary across the species' range. Both elevation and precipitation decline sharply along a west–east gradient across the study area; this variation is thought to substantially influence the vegetation in the region (Ezcurra and Brion 2005; Martín and Mermoz 2005) and may contribute to differences among study sites regarding the relative use of different habitat types by *C. sociabilis*. For example, our field observations suggest that mallines at the western (higher elevation, more mesic) end of the species' distribution may be too wet to be occupied by these animals during much of the year. In contrast, at the eastern (lower elevation, more arid) end of the species' distribution, mallines may be among the few habitat types that are mesic enough to support *C. sociabilis*.

To understand fully patterns of habitat use by *C. sociabilis*, future studies of this species should undertake systematic surveys of habitat use versus availability, and should examine the effects of geographic variation in environmental parameters on the specific habitats used by these animals. Dietary analyses indicate that the primary foods consumed by *C. sociabilis* living in mallines are grasses and shrubs associated with mallín habitats (Bonvissuto et al. 2008; Lacey and Wieczorek 2003); further research is needed to determine how food resources differ in nonmallín areas. Variation in the habitats occupied by conspecifics may also be associated with geographic differences in behavior (Busch et al. 2000). Although some species of *Ctenomys* are known to occur in a variety of habitats (Lizarralde et al. 2001; Rosi et al. 2002), studies of these taxa have not typically explored correlated differences in behavior. Consequently, future studies that document social structure in populations of *C. sociabilis* located throughout this species' range may reveal important relationships between habitat type, resource use, and social structure in this species.

Implications for conservation.—*Ctenomys sociabilis* is currently listed as "critically endangered" by the International Union for Conservation of Nature and the Red Book of Mammals of Argentina (Bidau et al. 2008; Díaz and Ojeda

2000), due primarily to its limited geographic range and the generally disjunct distribution of local populations. Although our findings regarding habitat use by *C. sociabilis* do not contradict this conclusion, they do have implications for the conservation of this species. For example, because burrow systems occurring in mallín and nonmallín habitats may respond differently to conservation threats, use of a greater range of habitat types may lead to greater resilience of *C. sociabilis* to deterioration or loss of mallín areas. Although our findings should be viewed positively by conservation biologists and regulatory agencies, further studies are required to characterize directly relationships between habitat use and persistence of populations of colonial tuco-tucos in Nahuel Huapi National Park.

RESUMEN

Comprender los requerimientos de hábitat tiene implicaciones para numerosos aspectos de la biología de las especies, incluyendo donde viven los individuos y como estos se comportan. La especialización en hábitat mésicos, ricos en recursos, conocidos como mallines se cree que ha favorecido la vida en grupo en el tuco-tuco colonial (*Ctenomys sociabilis*), un roedor subterráneo endémico de la Provincia de Neuquén en el suroeste de Argentina. Para explorar en mayor detalle la relación propuesta entre los mallines y la vida social en esta especie, se caracterizaron los hábitats ocupados por *C. sociabilis* en 3 localidades que representan los extremos de la distribución geográfica de la especie. Específicamente, se caracterizó la composición y estructura vegetal para 57 sistemas de madrigueras con animales, distribuidos en las 3 localidades de estudio. Los datos indican que *C. sociabilis* no se restringe a hábitats de mallín. A pesar de que se detectó variación significativa en la vegetación entre los 3 sitios de estudio, la mayoría de los sistemas de madrigueras activos muestreados en cada sitio se encontraron en hábitats no mallínoso. Además de proporcionar el primer muestreo amplio de hábitat para *C. sociabilis*, nuestros datos podrían ofrecer nuevas perspectivas sobre el papel de la especialización de hábitat en la promoción del comportamiento social inusual de esta especie de roedor ctenómido.

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