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Spatial relationships among free-living cururos (*Spalacopus cyanus*) demonstrate burrow sharing and communal nesting

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Spatial relationships among conspecifics can provide insights into numerous aspects of social behavior. Spatial data may be particularly important for characterizing the behavior of difficult-to-study species such as subterranean rodents, direct observations of which are challenging. To characterize the social organization of the cururo (*Spalacopus cyanus*), a subterranean species in the rodent family Octodontidae, we used radiotelemetry to quantify spatial relationships within populations of this species located in Parque Nacional Bosque Fray Jorge and Santuario de la Naturaleza Yerba Loca, Chile. Specifically, we sought to determine if adults in this diurnal species share burrows and subterranean nests, the two criteria typically used to identify subterranean rodents as social. Analyses of radio fixes collected during February–March 2003 revealed that cururos at both Fray Jorge and Yerba Loca shared nighttime nest sites; cluster analyses of these data identified multiple spatially distinct subsets of adults in each population. Overlap of minimum convex polygons constructed from radio fixes collected during daylight hours suggested burrow sharing by animals in both populations. Cluster analyses of overlap values revealed the same spatially distinct groups of individuals identified from analyses of nest sharing; in addition, these analyses revealed one cluster of animals in each population that was not evident from analyses of nighttime data. Collectively, these results confirm that cururos are social, with adults in both study populations sharing burrow systems and communal nests. Our findings add to the growing understanding of social organization in octodontid rodents and reveal a new system for comparative studies of the ecology and evolution of behavioral variation in burrow-dwelling mammals.

La cuantificación de las relaciones espaciales entre conespecíficos puede proporcionar información importante sobre diferentes aspectos del comportamiento social. Específicamente, estas relaciones permiten caracterizar el comportamiento de especies difíciles de observar como los roedores subterráneos, donde la observación directa como método es difícil de utilizar. En este estudio cuantificamos las relaciones espaciales entre los individuos mediante telemetría para caracterizar la organización social del cururo (*Spalacopus cyanus*), un roedor subterráneo de la familia Octodontidae. El estudio se realizó en poblaciones de esta especie en el Parque Nacional Bosque Fray Jorge y el Santuario de la Naturaleza Yerba Loca, en Chile. Concretamente, nuestro estudio buscó determinar si los adultos en esta especie diurna utilizan los túneles y madrigueras subterráneas en forma comunal, dos atributos comúnmente utilizados para caracterizar especies de roedores subterráneos como sociales. Los análisis de coordenadas espaciales para Febrero y Marzo de 2003 indicaron que los cururos en Fray Jorge y Yerba Loca comparten sus madrigueras durante la noche; los análisis de conglomerados de estos mismos datos revelaron agrupaciones de adultos espacialmente distintivas en ambas poblaciones. Complementariamente, la cuantificación de solapamiento espacial a partir de registros de posición durante las horas con luz, también indicó un uso compartido de los túneles subterráneos. Los análisis de conglomerados, basados en valores de solapamiento, revelaron los mismos grupos de individuos espacialmente distintivos comparado con los grupos basados en el uso compartido de madrigueras; además, estos análisis mostraron una agrupación para cada población, no detectada

por los análisis espaciales para las horas de oscuridad. En conjunto, estos resultados confirman que el cururo es una especie social, donde los adultos en ambas poblaciones comparten el uso de un mismo sistema de túneles y anidan comunamente. Estos resultados aumentan nuestro entendimiento sobre la organización social en roedores octodontidos, y sugieren un modelo alternativo e innovador para estudios comparados sobre ecología y evolución de la variabilidad conductual de mamíferos con hábitos subterráneos.

Key words: caviomorphs, cururos, octodontids, social structure, *Spalacopus*, spatial relationships

How animals use space can provide critical insights into patterns of behavior, including patterns of both social structure and social organization (Kappeler et al. 2013; Kappeler 2019). For example, spatial data can be used to assess the extent of overlap between areas occupied by different individuals, thereby indicating whether members of a population tend to be solitary or to live in spatially cohesive groups (Lacey 2000; Gorman et al. 2006; Maher 2009; Ebensperger and Hayes 2016). For species characterized as group living, differences in space use among group mates can yield information regarding important metrics of sociality, such as whether individuals share a communal nest (e.g., Lacey et al. 1997; Ebensperger et al. 2004, 2006). When coupled with information regarding the ages and sexes of conspecifics that co-occur spatially, such analyses can be used to draw inferences regarding multiple aspects of social behavior, including the demographic processes (e.g., natal philopatry) underlying differences in social systems (Smith and Ivins 1983; Linklater and Cameron 2009; Clutton-Brock and Lukas 2012).

Among subterranean rodents, spatial data are an essential component of efforts to assess patterns of social behavior (Lacey 2000; Lacey and Sherman 2007). Because these rodents spend the majority of their lives in underground burrow systems (Nevo 1979), opportunities for direct visual observations of social interactions among free-living animals are limited. As a result, studies of social organization in subterranean species typically rely on analyses of spatial overlap to characterize social relationships. In particular, the degree of spatial overlap among individuals has been used to determine if adults engage in burrow sharing, a key feature distinguishing solitary from social species (Burda et al. 2000; Lacey 2000). Based largely on analyses of this type of information, previous studies have revealed marked variation in social organization among subterranean rodents, including species that are solitary (e.g., *Thomomys bottae*—Bandoli 1987; *Heliophobius argenteocinereus*—Sumner et al. 2008), species that live in multi-female groups (e.g., *Ctenomys sociabilis*—Lacey et al. 1997; Lacey and Wiczorek 2004), and species in which multiple adults of both sexes share burrows and nest sites (e.g., *Heterocephalus glaber*, *Fukomys anselli*, *F. damarensis*, *F. mechowii*—Bennett and Faulkes 2000; Faulkes and Bennett 2007; Skliba et al. 2012; Sumner et al. 2012). This variation in social organization among animals that are otherwise characterized by generally similar life history patterns provides an important opportunity to examine the factors shaping the evolution of mammalian social behavior.

One potential addition to comparative studies of social structure in subterranean rodents is the cururo (*Spalacopus cyanus*). This species, the only truly subterranean member of the family

Octodontidae (Nevo 1979; Ojeda et al. 2013), occupies habitats in central Chile ranging from Andean meadows to coastal scrublands (Contreras et al. 1987; Torres-Mura and Contreras 1998; Lacey and Ebensperger 2007). Cururos have been described as social based on livetrapping studies indicating that multiple adults can be captured within the same putative burrow system, including at the same burrow entrance (Reig 1970; Begall and Gallardo 2000). Radiotelemetry studies of activity patterns of free-living cururos also suggest that adults overlap spatially with one another (Urrejola et al. 2005). None of these analyses, however, have examined directly patterns of space use by members of this species. Accordingly, a detailed assessment of spatial relationships among free-living individuals is needed to determine if cururos are indeed group living and, additionally, if they engage in communal nesting. Clarifying the social organization of this species will contribute significantly to our understanding of the evolution of sociality within the Octodontidae (Rivera et al. 2014; Sobrero et al. 2014) and may reveal a phylogenetically distinct new system for comparative analyses of the adaptive bases for group living in subterranean rodents.

To characterize the social organization of *S. cyanus*, we documented patterns of space use by members of two populations of this species. If cururos are social, then multiple adults of one or both sexes should exhibit regular, extensive spatial overlap indicative of burrow sharing. More specifically, while overlap among members of the same social group (i.e., residents of the same burrow system) should be high, it should be considerably lower among animals from different groups, resulting in 1) a bimodal distribution of pairwise measures of overlap within a population, and 2) the presence of spatially distinct clusters of individuals. If these animals are also communally nesting, then the nest sites used by multiple adults should coincide spatially. Finally, if cururos form behaviorally distinct groups, then analyses of spatial overlap and nest use should reveal the same clusters of associated individuals. To test these predictions, we used radiotelemetry to quantify the home ranges of adults of both sexes in two free-living populations of cururos from central Chile. These data were used to assess the extent of spatial overlap and spatial clustering within populations of conspecifics, with emphasis on evidence of burrow and nest sharing by adults. Our analyses reveal intriguing potential within- and between-population (i.e., intraspecific) differences in space use that may help to elucidate the ecological bases for group living in cururos.

MATERIALS AND METHODS

Study sites.—Spatial relationships were quantified for adults in two populations of cururos (*S. cyanus*). One population was

located in Parque Nacional Bosque Fray Jorge (FJ, 30°39'S, 71°38'W, elevation = 275 m) along the Pacific Coast of north-central Chile (Fig. 1). The other population was located in Santuario de la Naturaleza Yerba Loca (YL, 33°19'S, 70°17'W; elevation = 2,780 m), near the town of La Parva in the Andes Mountains directly east of Santiago (Fig. 1). These sites were selected because they represent contrasting habitat types, thereby allowing exploration of potential relationships between ecological conditions and patterns of cururo behavior. The FJ site encompassed ca. 4.5 ha and was characterized by arid thorn scrub habitat that was dominated by spiny drought-deciduous and evergreen shrubs with a seasonal herbaceous understory (Gutiérrez et al. 1993). Mean annual precipitation at this site was ca. 113 mm. In contrast, the YL site encompassed ca. 2.0 ha of mesic montane meadow dominated by seasonal grasses and alpine shrubs (Quintanilla 1980; Cavieres et al. 2000). Mean annual precipitation at this site was ca. 600 mm. Field work at FJ was conducted from 18 to 28 February 2003; field work at YL was conducted from 1 to 8 March 2003.

Animal capture and marking.—All procedures involving live animals were approved by the Animal Care and Use Committee at the University of California, Berkeley, and were consistent with guidelines established by the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016). Members of each study population were captured using handheld nooses constructed from soft, elastic nylon cord (Lacey et al. 1997). Nooses were set at burrow entrances at which cururos were observed foraging. The noose was placed just inside the lip of the burrow entrance and pressed in to the walls of the burrow to hold it in place and to reduce the risk of detection by the study animals. When an individual emerged from the burrow entrance to forage, the noose was pulled tight,

catching the animal just behind the forelegs and preventing it from retreating backwards into its burrow. Captured animals were immediately retrieved and transferred to cloth handling bags. Sex, body weight, and apparent age (adult versus juvenile) were recorded for each individual. For females, reproductive condition (e.g., perforate vaginal opening, pregnant, lactating) was also noted. Upon first capture, all individuals were permanently marked by inserting a uniquely coded PIT tag (IMI 1000 Implantable Microchips, BioMedic Data Systems, Inc., Seaforth, Delaware) beneath the skin at the nape of the neck. Tags were read using a handheld scanner (DAS 4000 Pocket Scanner, BioMedic Data Systems, Inc.).

Radiotracking of study animals.—To quantify patterns of space use, adults in both study populations were fitted with ≤ 5 g radiotransmitters (AVM Instrument Company Ltd., Colfax, California) affixed to cable ties that served as collars. Adults were identified on the basis of body weight (both sexes) and evidence of reproductive activity (females); radiocollars represented $< 5\%$ of the body weights of the individuals collared. Animals were fitted with collars within ~ 10 min of capture and then released at the burrow entrance at which they had been caught. Following their release, collared individuals were located using LA 12-Q receivers and 3-element handheld Yagi antennas (AVM Instrument Company Ltd.). At both study sites, the locations of collared animals were recorded multiple times per day, with a minimum of 1 h allowed between successive fixes; in addition, locations were recorded hourly for three successive nights. Once located, the position of each animal was recorded to the nearest meter using a georeferenced grid (8 m \times 8 m cell size) established at each study site. Fixes of radiotransmitters placed at known locations revealed this procedure to be accurate to within 0.5 m. Because this estimate was generated under ideal conditions (e.g., daylight; stationary object), we used a more liberal error estimate of 1 m when analyzing telemetry data. Thus, all fixes located within a 1 m radius of each other were treated as the same location.

Spatial relationships and identification of social groups.—Free-living cururos are diurnal, displaying little activity between sunset and sunrise (Urrejola et al. 2005; but see Begall et al. 2002 regarding circadian activity in captive cururos). To examine potential differences in diurnal versus nocturnal spatial relationships, we divided radio fixes into those collected at night (2100 to 0700 h) versus during the day (0700 to 2100 h). Data from these temporal periods were analyzed separately, as follows:

- 1) Sharing of night nests: Because cururos spend the vast majority of the night in subterranean nests (Urrejola et al. 2005), shared use of night nest locations provides an important measure of spatial and potential social associations among individuals. For each animal monitored via telemetry, we identified the most commonly used nocturnal location as that individual's putative nest site; comparisons of these locations were used to determine which individuals shared the same nocturnal nest site.
- 2) Nighttime spatial associations: To provide a more quantitative metric of nocturnal nest sharing, for each pairwise



Fig. 1.—Locations of the two study sites in Chile. The shaded area depicts the geographic distribution of *Spalacopus cyanus*.

combination of individuals in a population we divided the number of nighttime fixes during which those animals were detected together at the same nest location by the total number of nighttime fixes during which both individuals were located via telemetry (Ebensperger et al. 2004, 2012). The resulting association matrix was analyzed using SOCPROG (Whitehead 2008, 2009) to generate hierarchical spatial clusters of individuals. The fit between the original matrix and the resulting spatial clusters was assessed using the cophenetic correlation coefficient, with values > 0.8 typically considered indicative of a strong correspondence between these data sets (Bridge 1993). To identify potential social groups, we used the maximum modularity criterion (Newman 2004) generated by SOCPROG as the threshold for recognizing spatially distinct clusters of animals; association index values that exceeded this threshold were considered indicative of significant spatial clustering of individuals.

- 3) Overlap of daytime home ranges: Cururos are active primarily during daylight hours, spending a significantly greater proportion of time outside of their nests and moving significantly greater distances from their nests during the day versus at night (Urrejola et al. 2005). As a result, it was possible that daytime spatial relationships within our study populations differed from those revealed by nighttime radio fixes. To assess this possibility, we used telemetry data collected during the day to construct a 95% minimum convex polygon (MCP) for each individual. MCPs were generated using the *adehabitatHR* package, as implemented in R (R core package—Calenge 2006). The area encompassed by each MCP was then used to calculate values for percent spatial overlap between all pairs of individuals monitored; because overlap of MCPs may not be symmetrical, percent overlap was calculated from the perspective of each individual in a pair of animals (Worton 1987).
- 4) Daytime spatial associations: To provide a more objective measure of daytime spatial relationships, we used the overlaps among 95% MCPs generated for different individuals to construct a spatial association matrix for each study population (Whitehead 2008). These matrices were then analyzed using SOCPROG, with the same metrics (cophenetic correlation, maximum modularity criterion) used to assess the fit between data sets and to identify spatially distinct clusters of individuals (i.e., potential social groups).

After completing these analyses, we compared the identities of the animals in each spatially distinct cluster of individuals revealed by nighttime versus daytime radio fixes. These comparisons were used to assess the consistency of the results generated by our different analyses and to determine the cohesiveness of social groups across the day and night.

Statistical analyses.—Normality of the data was assessed using Shapiro–Wilks tests, after which we used parametric or nonparametric statistical tests as appropriate. Statistical analyses were performed using Statistica 6.0 (StatSoft Inc., Tulsa, Oklahoma). Throughout the text, data are presented as means ± 1 SD.

RESULTS

A total of 14 adult (8 females, 6 males) and 27 juvenile (14 females, 13 males) cururos was captured at FJ. At YL, a total of 18 adult (8 females, 10 males) and five juvenile (2 females, 3 males) cururos was captured. Because animals were not held in captivity after capture, we could not confirm that all individuals in a burrow system had been caught. Although multiple adults were frequently caught within a few meters of one another, captures of more than one animal at the same burrow entrance were rare; at FJ, two of the 14 adults captured were from the same burrow entrance while at YL two adults were captured at the same burrow entrance on two different occasions ($n = 4$ animals total). In both study populations, the adult females captured included individuals that were pregnant and lactating as well as individuals that showed no external evidence of reproductive activity. The reproductive status of males could not be assessed based on visual examination of the genitalia.

All adults captured at FJ were fitted with radiocollars. In contrast, due to the number of radiotransmitters available for use, only 11 (2 females, 9 males) of the 18 adults captured at YL were fitted with radiocollars. Radio fixes for one animal from FJ revealed no movement following release of this individual, suggesting that the animal had lost its collar; data from this individual were excluded from subsequent analyses, reducing the sample size for this population to 13. Two of the radiocollars deployed at YL failed shortly after release of the animals in question, yielding a final sample size of nine adults for this study population.

The mean number of daytime telemetry fixes recorded per individual was 61.6 ± 13.2 at FJ and 65.3 ± 17.8 at YL; the mean number of nighttime fixes at each site was 30.8 ± 3.6 and 27.9 ± 3.0 , respectively. The mean number of daytime fixes did not differ between the study sites (Mann–Whitney U -test, $Z = -0.702$, $n = 9, 13$, two-tailed $P = 0.484$). In contrast, the mean number of nighttime fixes was significantly greater for FJ (Mann–Whitney U -test, $Z = 2.47$, $n = 9, 13$, two-tailed $P = 0.014$). On average, this represented a difference of three radio fixes per individual, suggesting that the apparently greater nighttime sampling effort at FJ was unlikely to be biologically meaningful.

Home range sizes.—Analyses of telemetry data from a subset of the animals in each study population revealed that the size of the 95% MCP for an individual tended to remain stable after ~ 40 radio fixes (FJ: $n = 6$ animals, YL: $n = 5$ animals; Supplementary Data SD1), suggesting that our data set was sufficient to provide a robust estimate of the area occupied by each animal. Comparisons of the areas encompassed by 95% MCPs revealed no significant differences in daytime home range sizes for males and females in either study population (Mann–Whitney U -tests; FJ: $Z = 1.1$, $n = 5, 8$, two-tailed $P = 0.271$; YL: $Z = 2.0$, $n = 2, 7$, two-tailed $P = 0.178$). As a result, data for males and females in the same population were pooled for subsequent analyses. Based on this pooled data set, mean daytime home range size at FJ was 366.2 ± 504.4 m² versus 722.2 ± 585.0 m² at YL; this difference in daytime home

range size was significant (Mann–Whitney U -test, $Z = -2.08$, $n = 9, 13$, two-tailed $P = 0.0375$).

Nighttime nest locations and nocturnal spatial associations.—Telemetry data revealed that in both study populations, each animal spent the majority of nighttime fixes at a single location that was identified as that individual's nest site (Fig. 2). At FJ, a mean of $88.8 \pm 12.7\%$ of nighttime fixes per individual ($n = 13$ animals) occurred at the putative nest; at YL, this figure was $83.3 \pm 19.8\%$ of nighttime fixes per individual ($n = 9$ animals). The percentage of nighttime fixes recorded at putative nest sites did not differ between the study populations (Mann–Whitney U -test, $Z = 0.534$, $n = 9, 13$, two-tailed $P = 0.534$). Based on these data, four shared nest localities were identified at FJ; two of these sites were used by a male–female pair, one was used by a male and two females, and one was occupied by two adult females. At YL, two shared nest localities were identified; one was occupied by a female and two males while the other was used by two adult males. In both study populations, the remaining adults monitored ($n = 1$ at FJ, $n = 4$ at YL) did not share nighttime nest locations with other collared individuals.

Analyses of association matrices constructed from nighttime nest locations generated cophenetic correlation coefficients of 1.00 for both populations; these values indicated a strong correspondence between association indices and the spatial clusters of animals identified based on use of nighttime nest locations. Maximum modularity (used to define significant spatial clusters) was 0.74 at FJ and 0.59 at YL. Based on an association

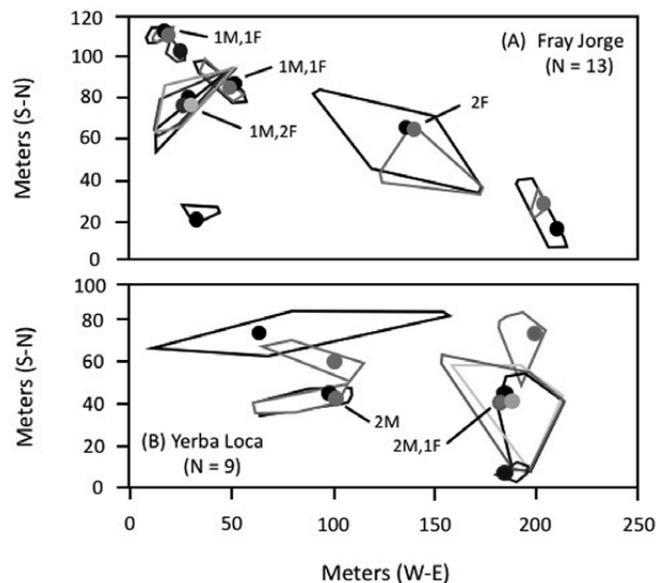
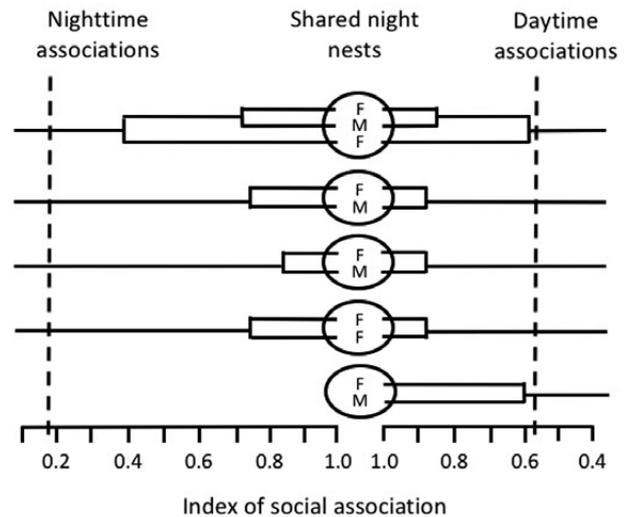


Fig. 2.—Minimum convex polygons (MCPs) for adult cururos (*Spalacopus cyanus*) monitored via radiotelemetry at (A) Fray Jorge and (B) Yerba Loca (number of animals monitored shown in parentheses). In both panels, the 95% MCPs shown were constructed from radio fixes collected during the daytime (x-axis = west to east dimension, y-axis = south to north dimension); different shades of gray denote different individuals whose daytime MCPs overlapped. Circles indicate the locations of nighttime nests for the same animals. For each shared night nest, the number of adults of each sex using that nest is indicated.

index cutoff of 0.17, four spatial clusters of animals were identified for FJ, each of which matched one of the clusters identified based on sharing of nighttime nests alone (Fig. 3A; Supplementary Data SD2). Results obtained for YL were similar; based on an association index measure of 0.84, both clusters identified based on nighttime nest locations were recovered by spatial clustering analyses of nighttime radio fixes (Fig. 3B; Supplementary Data SD2). Thus, overall, sharing of nighttime

A. Fray Jorge



B. Yerba Loca

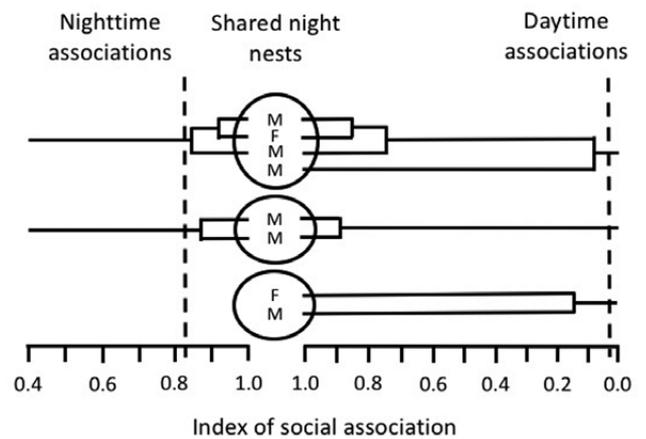


Fig. 3.—Comparisons of spatial clusters of adult cururos (*Spalacopus cyanus*) identified based on sharing of nighttime nests sites versus overlap of daytime 95% MCPs. For both (A) Fray Jorge and (B) Yerba Loca, analyses of daytime radio fixes revealed a cluster of individuals not evident in analyses of nighttime nest sharing. The sexes of animals that shared nighttime nests are indicated in the center of each panel. Nighttime spatial associations (left side of each panel) were identified based on cluster analyses of the frequency of nest sharing by the individuals monitored; daytime spatial associations (right side of each panel) were identified from cluster analyses of the percent overlap of MCPs. Values for the index of social association were generated as part of cluster analyses; in both panels, cutoff values indicative of significant spatial associations are indicated with dashed vertical lines.

nest locations appeared to provide a reasonable metric for identifying nocturnal associations among individuals.

Daytime spatial overlap and spatial associations.—Radio fixes recorded during daytime hours revealed that individuals also used their night nest locations during the day but that the percentage of fixes spent in the nest during the day (FJ: $41.0 \pm 18.8\%$, $n = 13$ animals; YL: $37.1 \pm 17.5\%$, $n = 9$ animals) was significantly less than during the night (Wilcoxon Signed-Rank test, $Z = -2.659$, $n = 22$, two-tailed $P = 0.008$). For all individuals, the location of the night nest fell within the 95% MCP constructed from daytime radio fixes. For adults assigned to the same spatial cluster based on analyses of nighttime radio fixes, the mean pairwise percent spatial overlap for daytime 95% MCPs was $71.0 \pm 21.3\%$ ($n = 14$ overlaps) at FJ and $83.0 \pm 14.7\%$ ($n = 8$ overlaps) at YL; this difference between populations was not significant (Mann–Whitney U -test, $Z = -1.427$, $n = 8, 14$, two-tailed $P = 0.153$). For adults whose daytime home ranges overlapped but that were not assigned to the same nighttime spatial cluster, mean pairwise percent overlap for daytime MCPs was $18.0 \pm 24.9\%$ ($n = 12$ overlaps) at FJ and $5.1 \pm 7.9\%$ ($n = 10$ overlaps) at YL; this difference between populations was significant (Mann–Whitney U -test, $Z = 2.167$, $n = 10, 12$, two-tailed $P = 0.030$). Within each population, mean percent daytime overlap among animals assigned to the same nighttime cluster was significantly greater than that among individuals whose daytime home ranges overlapped but that were not assigned to the same nighttime cluster (Mann–Whitney U -tests; FJ: $Z = -3.678$, $n = 12, 14$, one-tailed $P < 0.001$; YL: $Z = -3.51$, $n = 8, 10$, one-tailed $P < 0.001$).

Analyses of association matrices based on overlap of daytime MCPs generated cophenetic correlation coefficients of 0.998 for both study populations, indicating a strong correspondence between these matrices and patterns of home range overlap based on daytime radio fixes. Maximum modularity was 0.73 at FJ and 0.60 at YL. Based on an association index cutoff of 0.57, five clusters of individuals were identified at FJ (Fig 3A; Supplementary Data SD3). At YL, an association index cutoff of 0.03 revealed three spatial clusters of individuals (Fig. 3B; Supplementary Data SD3).

Comparisons of daytime and nighttime associations.—In general, the same spatial clusters of individuals were revealed by analyses of nighttime and daytime data (Fig. 3). At FJ, the same four clusters identified from analyses of nighttime nest sharing were evident in analyses of daytime home range overlap. In addition, daytime data revealed a fifth cluster consisting of a male–female pair; although these individuals never shared the same night nest location, the daytime MCP for the female encompassed that for the male, resulting in a significant daytime association for these animals. At YL, the same two clusters identified from analyses of nighttime nest sharing were evident in analyses of daytime overlap. Daytime analyses also revealed a third cluster consisting of a male–female pair and placed a fourth individual (a male) into a cluster of three individuals (2 males and 1 female) detected based on nighttime nest sharing. Members of the new cluster revealed by daytime data did not share a nighttime nest; these individuals had an association index value of 0.14 even

though overlap of their daytime MCPs was minimal ($< 1\%$). The individual added to an existing cluster did not share a night nest location with the other members of the cluster (identified from daytime as well as nighttime data) although the daytime MCP for that individual did overlap ($\sim 25\%$) with those for the remaining animals in the cluster. Thus, while daytime and nighttime data were generally consistent in their identification of spatial clusters of animals, analyses of daytime MCPs tended to be somewhat more inclusive in terms of revealing spatial relationships among individuals in both study populations.

DISCUSSION

Our analyses of spatial relationships in two populations of cururos provide clear evidence that these animals are group living, with adults of both sexes sharing burrow systems and communal nest sites. Individuals that shared the same nighttime nest location displayed significantly greater overlap of daytime home ranges than did individuals occupying different nighttime nests, as expected if cururos live in spatially distinct groups. Analyses of association matrices typically recovered the same clusters of individuals from both nighttime and daytime radio fixes, although in both study populations analyses of daytime data revealed spatial relationships not evident during the night. The similarity in outcomes for both data sets suggests that in general spatial associations among individuals are temporally consistent throughout the 24-h cycle but that some animals may have daytime spatial relationships with conspecifics with whom they do not share a night nest location. At the same time, differences between the study populations with respect to mean home range size and degree of overlap between distinct clusters of individuals raise intriguing questions regarding potential intraspecific variation in spatial structure that may impact patterns of social structure in this species.

Consistency of spatial clusters identified.—In each study population, daytime data revealed a spatial cluster of individuals that was not apparent from analyses of nighttime data. None of the individuals in these additional clusters shared night nest locations. Instead, spatial associations among these animals were due solely to overlap of daytime MCPs, raising the possibility that spatial relationships during the day differ from those at night. Variation in diurnal versus nocturnal spatial relationships has also been reported for degus (*Octodon degus*—Ebensperger et al. 2004). Members of this species spend much of the daytime aboveground, where they may interact with a larger pool of conspecifics than they do at night, when they occupy subterranean nests. Surface activity by degus, however, is strongly correlated with daylight (Kenagy et al. 2002; Hayes et al. 2007), making it challenging to distinguish the effects of location (above- versus belowground—Smith et al. 2018) from those of circadian variation in behavior. In contrast, because cururos are fully subterranean and rarely leave their burrows, all interactions occur belowground and thus differences in the physical contexts (i.e., above- versus belowground) in which interactions occur cannot explain variation in daytime versus nighttime spatial relationships.

Several factors may have contributed to the greater number of spatial clusters of cururos detected during the daytime. First, use of MCPs to characterize individual home ranges may have led to apparent overlap among individuals that did not actually co-occur spatially or temporally. For example, spatial overlap for the additional daytime cluster of animals identified at YL was minimal and visual inspection of the home ranges for these animals suggested that this overlap was due to the use of polygonal shapes to characterize the areas occupied by each individual (Ford and Myers 1981; Worton 1987; Burgman and Fox 2003). Further, because cururos are diurnal (Urrejola et al. 2005) and are active over larger areas during the day versus at night, the potential for spurious overlap between MCPs, including the potential for overlap among animals that were active in the same area but at different times, should be greater during the day. This explanation, however, does not appear to account for the other daytime-only spatial relationships identified, for which overlap of home ranges was more extensive and consistent. Finally, the two spatial clusters that were not present in analyses of nighttime data involved male–female pairs. Male–female spatial relationships may vary in response to mating opportunities (e.g., Massen et al. 2012) and it is possible that the daytime-only spatial overlaps detected here reflect short-term reproductive interests rather than more enduring social interactions associated with burrow sharing. More generally, patterns of space use may vary among the individuals that share a burrow system (Lovy et al. 2013; Skliba et al. 2016), which could contribute to apparent differences in social relationships among conspecifics. Although additional analyses of circadian variation in space use by cururos are required to determine the full extent to which diurnal and nocturnal associations vary, our findings suggest that data collected during both portions of the 24-h cycle provide reliable indicators of spatial relationships among individuals.

Differences between populations.—Animals in both study populations engaged in burrow sharing and sharing of nighttime nest localities. While overall patterns of space use were similar at YL and FJ, several significant differences in daytime spatial relationships were detected between these populations. For example, daytime home range sizes differed between our study sites, with home ranges at YL being significantly larger than those at FJ. Intraspecific variation in home range size has also been reported for several other subterranean taxa, including three species of ctenomyids (*C. australis* and *C. talarum*—Cutrera et al. 2010; *C. minutus*—Kubiak et al. 2017), which are the subterranean rodents most closely related to cururos (Upham and Patterson 2012). While the intraspecific differences in home range size reported here are not unique to cururos, this variation may prove informative as part of future studies that explore relationships between the ecology and social behavior of these animals in greater detail.

The study populations also differed with regard to the percent daytime overlap among individuals assigned to different spatial clusters. Overlap between clusters was significantly less at YL, indicating that distinct social groups were more spatially dispersed in this population compared to FJ. This finding is

consistent with the larger home range sizes reported for YL in suggesting that animals in this population tended to be more spatially dispersed than those at FJ. Further, the cutoff value used to assign individuals to daytime spatial clusters differed between the study populations, with this value being markedly lower at YL. Cutoff values were based on the estimated maximum modularity for each population, which provides a measure of the extent to which the population was divided into distinct social units (Newman 2004; Whitehead 2008). Maximum modularity was greater for FJ, suggesting that daytime clusters of individuals were more spatially discrete in this population. Collectively, these outcomes suggest that during the daytime, individuals, both within and among groups, were less tightly spatially affiliated at YL. Given that the habitats at the two study sites differ (Quintanilla 1980; Cavieres et al. 2000; Gutiérrez et al. 1993), this intraspecific variation in daytime spatial relationships raises intriguing questions regarding interactions between ecology and social behavior (Maher and Burger 2011).

Evidence for sociality.—Spatial relationships among members of our study populations were consistent with the criteria for group living typically applied to subterranean rodents (Burda et al. 2000; Lacey 2000). Specifically, adults at FJ and YL shared burrows, as evidenced by the extensive overlap of daytime MCPs for individuals of both sexes. Further, adults in both populations shared nest sites; because cururos are diurnal (Urrejola et al. 2005), use of the same location during the night when the animals are inactive should be particularly indicative of communal nesting. Finally, overlap of MCPs for individuals that shared nest sites was significantly greater than that for animals that did not share nests, as expected if cururos live in spatially distinct groups.

The same criteria have been used to characterize other subterranean species of rodents as group living, including colonial tuco-tucos (*C. sociabilis*—Lacey et al. 1997) and multiple species of bathyergid mole-rats (*H. glaber*, *F. anelli*, *F. damarensis*, *F. mechowii*—Bennett and Faulkes 2000; Faulkes and Bennett 2007; Skliba et al. 2012; Sumner et al. 2012). Previous studies of cururos had postulated that this species was social based on captures of multiple animals at the same burrow entrance (Reig 1970; Begall et al. 1999; Begall and Gallardo 2000) and the ability of captive individuals to live together amicably in groups (Begall et al. 1999; de Freitas et al. 2010). Although strongly suggestive of group living, these findings did not provide direct evidence that free-living individuals share burrow systems or nest sites. In contrast, our radiotelemetry data clearly indicate that cururos engage in both of these forms of spatial association and thus provide critical confirmation that members of this species are social.

Implications for sociality in subterranean rodents.—The Octodontidae are widespread in Chile and western Argentina, where they occupy diverse habitats ranging from coastal shrublands to inland salt basins and montane meadows (Lacey and Ebensperger 2007; Ojeda et al. 2016). This family includes nine genera and approximately 13 species (Rivera et al. 2014). Although *Spalacopus* is the only truly subterranean octodontid,

most other members of this family are fossorial and spend at least a portion of their lives in underground burrows (Reise and Gallardo 1989; Ebensperger et al. 2004; Rivera et al. 2014; Frugone et al. 2019). In addition to cururos, other group-living octodontids include common degus (*O. degus*—Ebensperger et al. 2004), Andean degus (*Octodontomys gliroides*—Rivera et al. 2014) and, potentially, moon-toothed degus (*Octodon lunatus*—Sobrero et al. 2014). In contrast, the viscacha rat (*Octomys mimax*—Ebensperger et al. 2008) and the red viscacha rat (*Tympanoctomys barrerae*—Mares et al. 1997) are solitary. Although multiple members of this family have yet to be studied, the behavioral variation already evident among these animals provides an opportunity to explore the factors shaping social organization within the Octodontidae.

The finding that cururos are group living also has implications for studies of social behavior in other lineages of rodents. For example, members of the Ctenomyidae, the sister family to the Octodontidae (Upham and Patterson 2012), are also subterranean and at least one species, the colonial tuco-tuco (*C. sociabilis*), is group living (Lacey et al. 1997). Specialization for subterranean life appears to have evolved independently in ctenomyids and octodontids (Lessa et al. 2008) and thus comparative studies of cururos and group-living tuco-tucos provide an opportunity to explore shared correlates of sociality in these animals. More generally, our findings add to the growing suite of phylogenetically independent examples of group living in subterranean rodents, examples of which include not only colonial tuco-tucos, but also members of the family Bathyergidae (Bennett and Faulkes 2000; Faulkes and Bennett 2007; Visser et al. 2019). Expanding the phylogenetic and geographic scope of these comparisons should increase our ability to elucidate how shared ecological and life history attributes interact with lineage-specific traits to produce convergent patterns of mammalian social behavior.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Home range size as a function of number of telemetry fixes analyzed per individual. Data are shown for adults from (A) Fray Jorge ($n = 6$) and (B) Yerba Loca ($n = 5$). For each animal, 95% minimum convex polygons (MCPs) were constructed for randomly selected subsets of radio fixes, with the number of fixes used ranging from 10 to more than 60 fixes per individual.

Supplementary Data SD2.—Spatial clusters of animals at (A) Fray Jorge and (B) Yerba Loca based on frequency of sharing of nighttime nests. Cluster analyses (SOCPROG—Whitehead 2008) of the percentage of nighttime fixes during which two individuals were found together in the same nest were used to identify spatially distinct clusters of individuals. For each population, the association index cutoff value denoting significant spatial relationships is indicated with a dashed vertical line. Animals whose spatial association index exceeds this value are denoted with brackets.

Supplementary Data SD3.—Spatial clusters of animals at (A) Fray Jorge and (B) Yerba Loca based on overlap of daytime 95% minimum convex polygons (MCPs). Cluster analyses (SOCPROG—Whitehead 2008) of the pairwise percent overlap between MCPs were used to identify spatially distinct clusters of individuals. For each population, the association index cutoff value indicating significant spatial relationships is indicated with a dashed vertical line. Animals whose spatial association index exceeds this value are denoted with brackets; asterisks denote clusters not identified by analyses of nighttime nest sharing.

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