



Dynamic spatial overlap in a solitary subterranean rodent: the Anillaco tuco-tuco (*Ctenomys* sp.)

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Despite striking diversity in mammalian social behavior, studies of social organization have often dichotomized species by identifying them as either solitary or social (i.e., group living). This tendency has been particularly pronounced for subterranean rodents, the majority of which have long been assumed to be solitary. As a result, variation in social organization has likely been underestimated for these animals, particularly for species in which patterns of space use suggest limited or temporally dynamic opportunities for interactions among conspecifics. Here, we characterize patterns of space use in a population of tuco-tucos (*Ctenomys* sp.) from Anillaco, La Rioja Province, Argentina. Although these animals have been the subject of extensive research regarding circadian patterns of activity, spatial and social relationships among free-living individuals have not been documented. Analyses of radiotelemetry data from 17 individuals monitored during the breeding season (December 2015) revealed that partial overlap of individual home ranges was common, occurring between male–female as well as female–female pairs of animals. Spatial relationships, however, were dynamic, with both home range sizes and overlap changing on a daily basis. Although members of the study population did not meet the criteria typically used to identify group living in subterranean species, they were not completely solitary. Instead, the animals displayed an intermediate form of social organization characterized by persistent partial overlap of the areas occupied by different adults. These data add to the growing comparative picture of social variation in *Ctenomys* and suggest that further studies of these animals should contribute to improved understanding of the factors underlying differences in mammalian social systems.

Key words: *Ctenomys*, home range, social systems, space use

A pesar de la gran diversidad en el comportamiento social de los mamíferos, estudios sobre su organización social frecuentemente dicotomizan a las especies al definir las ya sea como solitarias, ya sea sociales (es decir: que viven en grupos). Esta tendencia ha sido particularmente acentuada en roedores subterráneos, en los cuales la mayoría de las especies han sido clasificadas como solitarias. A consecuencia de este esquema, es probable que variaciones en la organización social hayan sido infravaloradas en estos animales, particularmente en aquellas especies en las cuales los patrones de uso del espacio sugieren oportunidades limitadas o temporalmente dinámicas para las interacciones entre conespecíficos. En este trabajo, caracterizamos el patrón de uso de espacio de una población de tuco-tucos (*Ctenomys* sp.) de Anillaco, en la provincia de La Rioja, Argentina. Aunque estos animales han sido objeto de estudio de considerable número de investigaciones sobre el patrón circadiano de actividad, el uso del espacio y la organización social de individuos silvestres no habían sido documentados. El análisis de datos de radiotelegrafía colectados de 17 adultos durante un período de 9 días durante la temporada reproductiva (diciembre de 2015), reveló que era común la sobreposición parcial de los territorios de los individuos, ocurriendo entre

pares macho-hembra, así como hembra-hembra. Sin embargo, las relaciones espaciales eran dinámicas ya que el uso del espacio por los individuos y la coincidencia entre ellos cambiaba diariamente. Aunque los miembros de la población estudiada no cumplieron con el criterio comúnmente usado en roedores subterráneos para diagnosticar que viven en grupo, los individuos tampoco eran completamente solitarios. En cambio, mostraron una forma intermedia de organización social caracterizada por una coincidencia parcial persistente entre los territorios ocupados por diferentes adultos. Estos datos amplían el creciente cuadro comparativo de la variación social en *Ctenomys* sugiriendo que estudios adicionales en estos animales contribuirían a una mejor comprensión de los factores subyaciendo las diferencias entre los sistemas sociales de los mamíferos.

Palabras clave: *Ctenomys*, sistemas sociales, territorios, uso de espacio

Animal social systems are strikingly diverse, encompassing a wide array of spatial and social relationships among conspecifics (Wilson 1975; Faulkes et al. 1997). One component of this diversity is a species' social organization, which describes variation in group size and composition (Kappeler 2019). Despite well-documented variability in these parameters, studies of social organization frequently dichotomize species by characterizing them as either solitary or group living (Lacey and Sherman 1991; Lacey et al. 1997). Although this distinction can be analytically useful, it obscures considerable variation in behavior that may be informative regarding the ecological and evolutionary bases for differences in social organization (Doody et al. 2012). Further, variation in group size and composition may have important implications for other elements of social systems, including social structure (e.g., nature and frequency of social interactions), mating systems (e.g., number of mates per individual), and parental care systems (e.g., potential for alloparental care—Kappeler 2019). As a result, efforts to characterize fully the social organization of a species are essential to understanding the totality of its social system (Kappeler 2019).

Often, initial insights into a species' social organization come from analyses of spatial relationships, notably patterns of home range overlap (Smith and Ivins 1984; Lacey et al. 1997; Schradin and Pillay 2005). Patterns of space use can be reliable indicators of the tendency to live alone versus in groups (Madison 1980; O'Brien et al. 2020), although these data may not fully capture intermediate forms of social organization, particularly when overlap of individual home ranges is temporally dynamic (Chapman et al. 1995; Creel and Winnie 2005; O'Brien et al. 2020). Spatial relationships can vary over multiple time scales, including from day to day (Richard et al. 2014; Johann et al. 2020). Daily changes in home range overlap may arise due to variation in factors such as resource availability (Ullmann et al. 2018; Zehnder et al. 2018) and reproductive opportunities (Travis et al. 1995; Lacey and Wiczorek 2001). Because such variation has the potential to alter social interactions among conspecifics, evaluating short-term changes in spatial relationships may be critical to understanding a species' social organization and, more generally, its social system.

The use of spatial data to characterize social organization as well as the tendency to dichotomize solitary versus group-living species have been particularly pronounced among studies of subterranean rodents (Nevo 1979; Lacey 2000).

These species are defined by their tendency to spend the vast majority of their lives in underground burrows (Lacey et al. 2000; Begall et al. 2007). Although the extent to which individuals are active aboveground varies among taxa, the life histories of all rodents identified as subterranean are substantially shaped by their use of underground burrows and nests (Nevo 1979; Lacey et al. 2000; Begall et al. 2007). Subterranean species occur in multiple families in several suborders of rodents (Lacey et al. 2000; Begall et al. 2007). As a result, studies of these animals offer important opportunities to examine the factors associated with evolutionary convergence in basic life history attributes. Behaviorally, although subterranean rodents have generally been assumed to be solitary (each adult occupies its own burrow system and nest site—Nevo 1979; Lacey 2000), studies of a growing number of species are revealing evidence of group living (Smorkatcheva and Kuprina 2018; Lacey et al. 2019; O'Brien et al. 2020). More generally, subterranean rodents range from relatively asocial to highly social and eusocial (Bennett and Faulkes 2000; Lacey 2000; Faulkes and Bennett 2013; O'Brien et al. 2020). Accordingly, comparative studies of these animals offer important opportunities to explore variation in social behavior, including differences in social organization.

Tuco-tucos are subterranean rodents in the genus *Ctenomys* (Reig et al. 1990). More than 60 species of tuco-tucos are currently recognized, ranging in distribution from southern Peru to Tierra del Fuego and from the Andes mountains to southwestern Brazil (Bidau 2015). Collectively, these animals occupy a diverse array of habitats, including high elevation deserts, mesic grasslands, and coastal sand dunes (Reig et al. 1990; Lacey and Ebersperger 2007). All members of the genus *Ctenomys* are subterranean and display numerous adaptations to life in underground burrows (Reig et al. 1990). Although most members of this genus have not been studied with regard to social organization, both solitary (*C. haigi*—Lacey et al. 1998; *C. talarum*—Cutrera et al. 2006; *C. australis*—Cutrera et al. 2010; *C. minutus*—Kubiak et al. 2017) and group-living species (*C. sociabilis*—Lacey et al. 1997; *C. opimus*—O'Brien et al. 2020) have been identified, as has one species in which adults do not share burrows but appear to engage in regular, transitory episodes of spatial overlap (*C. rionegrensis*—Tassinio et al. 2011; Tomasco et al. 2019). These analyses suggest that social organization varies within *Ctenomys*, thereby underscoring the need for species-specific studies of spatial and social relationships. Such information may be particularly important for species in which such relationships tend to be temporally variable,

as these data may help to reveal the context(s) in which adults interact with one another.

Here, we use data on spatial relationships to characterize the social organization of the Anillaco tuco-tuco (*Ctenomys* sp.), which occurs in central La Rioja Province, Argentina. The taxonomy of the study animals remains unresolved. Inspection of multiple specimens collected in and around Anillaco, field observations of behavior and ecology, audio-recordings of vocalizations (Amaya et al. 2016; Amaya and Areta 2018), and analyses of mitochondrial sequence data (T. Sanchez, Facultad de Ciencias Naturales e Instituto Miguel Lillo; and I. Tomasco, Facultad de Ciencias Universidad de la República, pers. comm.) suggest that the area surrounding Anillaco is occupied by a single species of *Ctenomys*. Previously, these animals have been identified as *Ctenomys* cf. *knighti* (Valentinuzzi et al. 2009; Fracchia et al. 2011) or *C. aff. knighti* (Tomotani et al. 2012; Tachinardi et al. 2014). Although a specific taxonomic assignment is still pending, the animals included in this study were all members of a single local population. As a result, the lack of a recognized specific epithet for these animals at this time should not affect the outcome of our analyses of spatial and putative social relationships among adults.

The Anillaco tuco-tuco has been the subject of detailed investigations of vocal communication (Amaya et al. 2016; Amaya and Areta 2018) and circadian patterns of activity (Valentinuzzi et al. 2009; Tomotani et al. 2012; Tachinardi et al. 2014). Understanding of these aspects of the animals' biology would be improved by knowledge of spatial and social relationships among free-living conspecifics. Although anecdotal observations of these animals do not suggest that they are group-living (sensu Pearson and Christie 1985; O'Brien et al. 2020), the density of individuals and the distribution of freshly excavated mounds of soil suggest that some degree of regular spatial interaction among conspecifics is likely. To assess this possibility, we quantified patterns of space use by members of a natural population of Anillaco tuco-tucos, with emphasis on potential overlap of home ranges belonging to different adults. In addition to providing the first quantitative description of the social organization of this species, our data demonstrate that spatial relationships among individuals vary markedly on a daily basis. These findings have important implications for analyses of behavioral variation among ctenomyids, as well as comparisons between these animals and other subterranean rodents.

MATERIALS AND METHODS

Study site.—Field studies were conducted from 5 to 15 December 2015 near Anillaco, La Rioja Province, Argentina (28°48'S, 66°55'W, elevation = 1,365). Average annual temperature in the study area was ~16°C and mean annual rainfall was ~150 mm, with most precipitation occurring during the summer (December–February). Anillaco is located at the northern end of the Monte Desert biome, which is widespread in west central Argentina (Abraham et al. 2009). Vegetation in this region was dominated by shrubs (genera *Larrea* and *Prosopis*), legumes (*Senna aphylla*), and cacti (genera *Trichocereus* and

Tephrocactus—Cabrera 1976; Abraham et al. 2009; Fracchia et al. 2011). The ~3-ha study site was located in an abandoned agricultural field that was dominated by Monte vegetation but that also contained small patches of native grasses (*Eragrostis cilianensis*, *Bouteloua aristoides*).

Animal capture and marking.—Trapping of the study population was carried out from 3 to 7 December 2015, corresponding to the early austral summer and presumed annual breeding season for Anillaco tuco-tucos. Animals were captured using live traps constructed from a 0.5-m-long piece of PVC pipe (diameter: 0.1 m) that had been fitted with a drop door. When an individual entered a trap, it dislodged a small wooden stick used to hold the door open, allowing the door to close and trapping the animal within the pipe. Traps were set at all active burrow entrances, as identified by the presence of either a fresh soil plug blocking the burrow or a freshly excavated mound of soil surrounding the burrow entrance. Traps were set by opening the burrow entrance and inserting the trap into the adjacent tunnel. Traps were checked at least once every 2 h; traps that had been plugged with soil were emptied then reset. Captured animals were removed from traps as soon they were detected. Individuals then were held in captivity for up to 12 h to ensure that no additional animals were present in the same burrow system. Trapping at a given burrow entrance ended when no further evidence of activity (e.g., freshly excavated soil, plugging of tunnels or traps) had been detected after 12 h; because the study animals are active for short periods throughout the 24-h cycle (Tomotani et al. 2012), this interval should have been sufficient to detect evidence of additional activity within a burrow system.

All animals captured were permanently marked by inserting a PIT tag (Biomedic Data Systems, Seaforth, Delaware) beneath the skin at the nape of neck. Each individual was weighed and its sex and apparent age (juvenile or adult) were determined on the basis of body weight (e.g., Rosi et al. 2000). For adult females, reproductive status (e.g., lactating, pregnant) was assessed via visual inspection of the external genitalia and palpation of the abdomen (Tassino and Passos 2010); because the testes of male tuco-tucos are never visible externally, the reproductive condition of males could not be determined. Each adult was fitted with a radiocollar (GV-13 transmitters, AVM Instrument Company, Colfax, California) weighing 4.5 g, which represented ~4% of an individual's body weight. Upon completion of these procedures, each individual was released into the burrow in which it had been captured. All procedures involving live animals had been approved by the Animal Care and Use Committee at the University of California, Berkeley and followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016).

Radiotracking of study animals.—Telemetry data were collected from 6 to 15 December 2015. Individuals were located using an R1000 receiver (Communications Specialists, Orange, California) and handheld 3-element Yagi antenna. Multiple radio fixes (range: 1–24) were taken daily, typically between 0600 and 2000 h, with at least 1 h allowed between successive fixes (Lacey et al. 1997; Cutrer et al. 2006). To characterize

circadian patterns of activity in the study population, from 9 to 11 December radio fixes were collected hourly for 72 consecutive hours. The location of each individual detected via telemetry was recorded to the nearest half meter using a grid (8 m \times 8 m cell size) labeled with a Cartesian coordinate system. Fixes recorded for radiotransmitters placed at known locations revealed this procedure to be accurate to within 0.5 m. These tests were conducted under ideal conditions (e.g., daylight, stationary object); to account for the greater error expected for data obtained under more variable conditions, a conservative error estimate of 1 m was used when analyzing spatial relationships and nest locations for members of the study population (see below).

Analyses of space use.—Individual home ranges were estimated using minimum convex polygons (MCPs), as implemented in the *adehabitatHR* package in R (Calenge 2006). To assess the ability of our data set to generate robust estimates of individual home ranges, we first examined home range size as a function of the number of radio fixes analyzed. We then used both 100% and 95% MCPs to characterize spatial relationships among members of the study population. Although 100% MCPs are generally considered to be less reliable due to their susceptibility to outlier localities (Linders et al. 2004; Girard et al. 2002; White and Garrott 1990), use of this home range metric maximized our probability of detecting spatial overlap among conspecifics, particularly on a daily basis (see below). In contrast, 95% MCPs are expected to provide more robust estimates of home range boundaries (Linders et al. 2004; Girard et al. 2002; White and Garrott 1990); use of this metric allowed us to evaluate the apparent effects of outliers on patterns of spatial overlap while also enabling us to compare our results to those of previous studies of spatial relationships in tuco-tucos (Lacey et al. 1997, 1998; Cutrera et al. 2006; Tassino et al. 2011; O'Brien et al. 2020).

To quantify spatial relationships among members of the study population, pairwise estimates of percent overlap between MCPs for different individuals were calculated in *adehabitatHR* (Calenge 2019). Because overlap between individuals may not have been symmetric, percent overlap was calculated from the perspective of each animal included in a pairwise comparison. To determine whether members of the study population shared subterranean nests, we identified the nest site for each animal as the single most commonly used location for that individual (Lacey et al. 1997; Urrejola et al. 2005; O'Brien et al. 2020). We then compared these locations to determine if any putative nest sites were used by more than one adult. More generally, we also examined whether areas of overlap between the home ranges of different adults included the putative nest site for one or more of the animals being compared.

To explore potential temporal variation in spatial relationships, we examined changes in daily estimates of range size and overlap as revealed by 100% MCPs; this more inclusive measure of individual ranges was employed due to the limited number of data points collected per individual per day. Analyses were completed for the three successive days of data collection (9–11 December) for which the most telemetry fixes

per individual were obtained. To determine the frequency with which individuals co-occurred spatially, for each pair of animals with overlapping home ranges we calculated the percentage of fixes for which both members of the pair were detected at the same location at the same point in time. In addition, we calculated the minimum distance between members of each pair for each day on which telemetry data were collected.

Statistical analyses.—Statistical analyses were carried out using InfoStat (Di Rienzo et al. 2016). Nonparametric tests were used unless the data met the assumptions for parametric analyses; *P*-values are two-tailed unless otherwise indicated. Throughout the text, means are reported \pm 1 *SD*.

RESULTS

A total of 17 adults (six males, 11 females) were captured on the study site. No more than one adult was trapped at a given burrow entrance and we detected no evidence (e.g., plugged burrow entrances) of uncaptured animals at these locations. Comparisons of individual home ranges (see below) with observations of active burrow entrances suggested that all adults within the study area were captured, resulting in a population density of \sim 7 adults per hectare. Mean body weight for males was 182.8 ± 25.9 g (range = 160 – 228 g) while that for females was 151.3 ± 31.8 g (range = 108 – 227 g); this difference between the sexes was significant (Mann–Whitney *U*-test: *U* = 6, *P* = 0.007; [Supplementary Data SD1](#)). Two of the females captured were pregnant and three were lactating; juveniles were trapped at the same burrow entrances as two of the lactating animals. The remaining six females captured did not display detectable evidence of reproductive activity.

Characterization of home ranges.—We recorded a mean of 105.1 ± 5.1 (range: 96 – 111) radio fixes per collared individual over 9.4 ± 0.7 days (range = 8 – 10 days) of data collection. Analyses of 95% MCPs revealed that home range sizes stabilized after \sim 50 radio fixes, which represented \sim 50% of the total number of fixes obtained per individual ([Supplementary Data SD2](#)). Accordingly, our data should have provided robust depictions of the home ranges for all individuals monitored. Mean home range sizes for males and females did not differ significantly for home ranges based on either 100% or 95% MCPs (Mann–Whitney *U*-tests: 100% MCPs, *U* = 31, *P* = 0.884; 95% MCPs, *U* = 26, *P* = 0.525; [Fig. 1](#); [Table 1](#)) and thus data from both sexes were pooled for subsequent analyses. At the individual level, there was a significant tendency for home range sizes based on 100% MCPs to be larger than those based on 95% MCPs (Wilcoxon signed-rank test, *Z* = 3.57, *P* < 0.0001; [Supplementary Data SD1](#)). On average, the size of an animal's 95% MCP represented $46.9 \pm 22.4\%$ (range = 0.0 – 84.9%) of the size of its 100% MCP ([Supplementary Data SD3](#)).

Spatial overlap among individuals.—When all telemetry data were considered, comparisons of 100% MCPs revealed overlap between the home ranges of 19 pairs of animals, including 10 male–female, seven female–female, and two male–male pairs ([Fig. 1](#); [Supplementary Data SD4](#)). Mean percent pairwise overlap of 100% MCPs did not differ among these

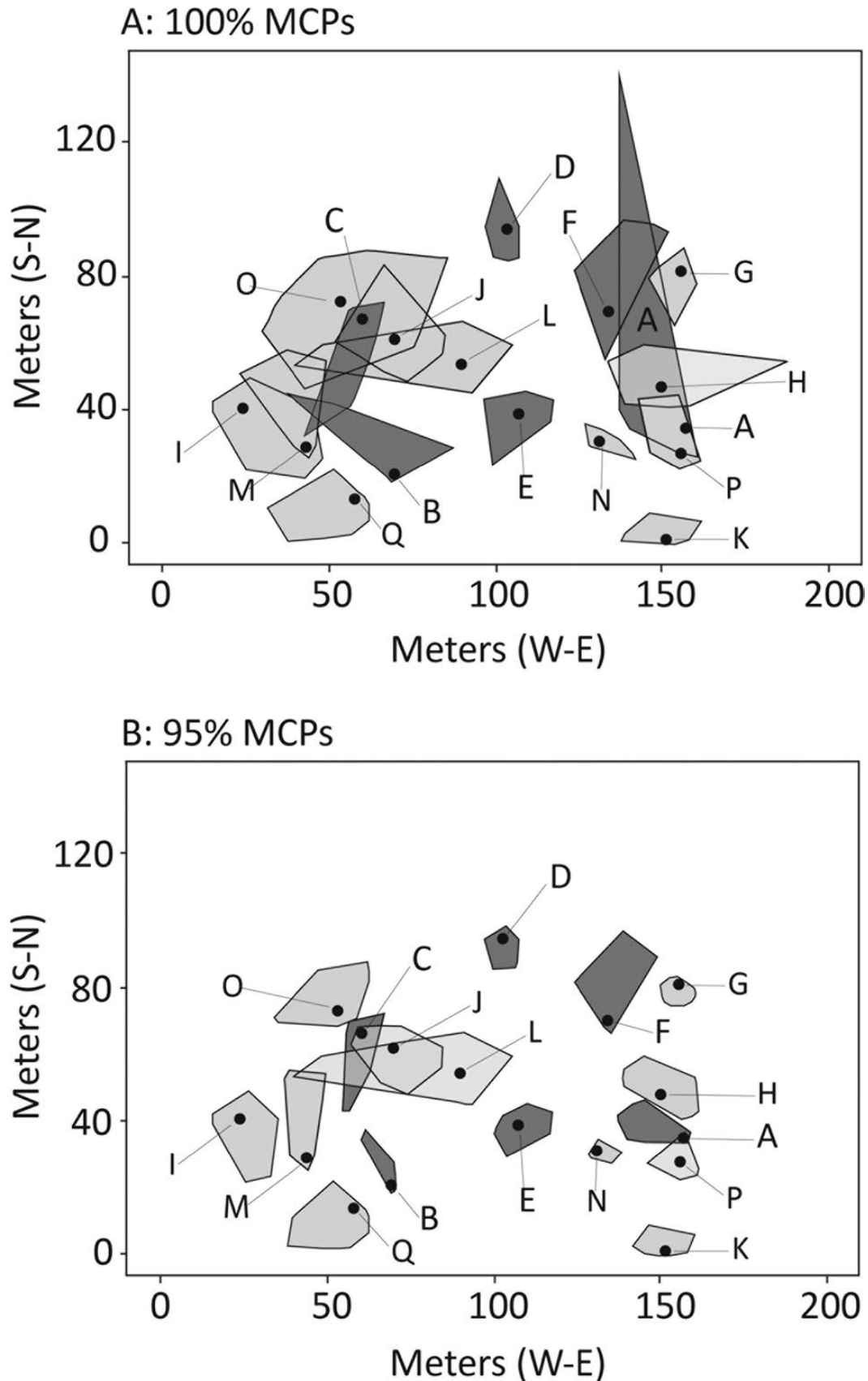


Fig. 1.—Home ranges for six adult male and 11 adult female tuco-tucos from Anillaco, La Rioja Province, Argentina. Home ranges are based on radiotelemetry data collected from 5 to 15 December 2016. Home ranges were calculated using (A) 100% minimum convex polygons (MCPs) and (B) 95% MCPs. In each panel, individuals are indicated with different letters; light gray polygons are females and dark gray polygons are males. The black circle within each home range denotes that animal's putative nest site.

Table 1.—Mean home range sizes for six adult male and 11 adult female tuco-tucos from Anillaco, La Rioja Province, Argentina. Home ranges were calculated from radiotelemetry data using 100% and 95% minimum convex polygons (MCPs). For each sex, mean (\pm SD) home range sizes are shown for each analytical method; the range of values for each mean is given in parentheses. Home range sizes for males and females did not differ (Mann–Whitney U -tests, all $P > 0.05$) for either of the metrics examined.

Sex	Home range size (m ²)	
	100% MCP	95% MCP
Males ($n = 6$)	512.8 \pm 393.7 (154.3–1,267.6)	183.1 \pm 106.9 (73.0–373.8)
Females ($n = 11$)	523.7 \pm 402.3 (65.6–1,500.6)	279.6 \pm 209.5 (37.1–789.5)

categories (Kruskal–Wallis test, $H = 1.8$, $P = 0.407$; Fig. 2). Consistent with the generally smaller sizes of home ranges based on 95% MCPs, fewer overlapping pairs of animals were detected using this metric; although four male–female and two female–female pairs were identified based on 95% MCPs, no overlap between home ranges of males was detected (Fig. 1; Supplementary Data SD4). Mean percent pairwise overlap of 95% MCPs did not differ between male–female and female–female pairs (Mann–Whitney U -test: $U = 16$, $P = 0.999$; Fig. 2). Thus, while both home range estimators revealed examples of pairwise overlap among members of the study population, the number of overlapping pairs identified varied with the metric examined.

Nest sites.—For each individual, radiotelemetry data revealed a single most commonly used location that was identified as that animal's putative nest site. The mean percentage of fixes recorded at the putative nest (32.1 \pm 13.0%, range: 11.7 – 58.7%; $n = 17$ animals) was significantly greater than the percentage of fixes at the second most frequently used location (15.6 \pm 4.0%, range: 9.0 – 21.8%; Wilcoxon signed-rank test, $Z = -5.088$, $P < 0.001$). A distinct putative nest site was identified for each individual monitored, with no evidence of nest sharing among members of the study population (Fig. 1). Analyses of both 100% and 95% MCPs indicated that the nest sites of five animals (two males, three females) fell within the portion of their home range that overlapped with the home range of a conspecific. Putative nests for the majority of individuals ($n = 12$, 70.6%), however, occurred at locations that were never overlapped by another animal, providing further evidence that members of the study population did not share nest sites.

Daily variation in spatial relationships.—When home ranges were examined on a daily basis, comparisons of 100% MCPs revealed that the size and configuration of the area used by an animal often varied markedly across successive days (Fig. 3; Supplementary Data SD5). The mean daily percent change in individual range size was 45.0 \pm 27.4% ($n = 17$ animals monitored for 3 days), while the mean percent spatial overlap of an individual with itself was 55.6 \pm 27.4%. The occurrence of range overlap between different individuals also varied markedly across successive days (Supplementary Data SD6); of 10 overlapping pairs of animals detected, five (50.5%) displayed

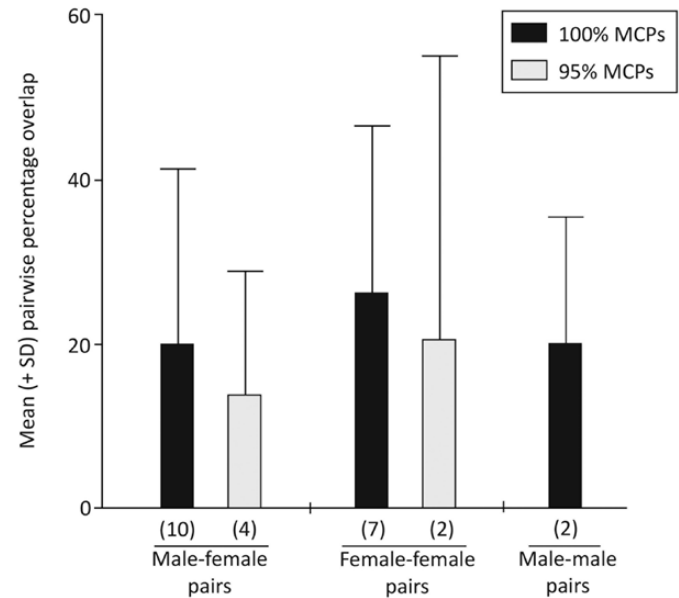


Fig. 2.—Mean percent home range overlap for six adult male and 11 adult female tuco-tucos from Anillaco. Pairwise overlap was calculated separately for male–female, female–female, and male–male pairs. Black bars indicate values based on 100% minimum convex polygons (MCPs); gray bars denote values based on 95% MCPs. Numbers in parentheses are the number of pairs whose home ranges overlapped. No significant differences among means (all $P > 0.05$) were found for either home range metric.

spatial overlap on only a single day of data collection, five (50.0%) displayed overlapping home ranges on 2 days of data collection, and none displayed spatial overlap on all 3 days of data collection. Overall, these findings suggest that spatial relationships among members of the study population were dynamic and varied on a daily basis.

Co-occurrence of individuals.—Despite overlap of home ranges between multiple pairs of individuals, we never detected two animals together at the same location during the same radio fix ($n = 1,793$ fixes for 17 animals). When fixes obtained across all 10 days of data collection were considered, the mean minimum distance between fixes for a pair of animals whose home ranges overlapped was 4.6 \pm 6.8 m (range = 0.5 – 28.5 m; $n = 19$ pairs of animals); mean values did not differ between male–female, female–female, and male–male pairs (Kruskal–Wallis test, $H = 1.5$, $P = 0.468$). Thus, although animals whose home ranges overlapped were often found within a few meters of one another, individuals did not co-occur at the same location at the same point in time.

DISCUSSION

Home ranges of Anillaco tuco-tucos (*Ctenomys* sp.) constructed from radiotelemetry data indicated that although adults in our study population did not share burrow systems or nest sites, partial overlap of home ranges occurred on a regular basis. Although such overlap was most common between males and females, overlap between pairs of females

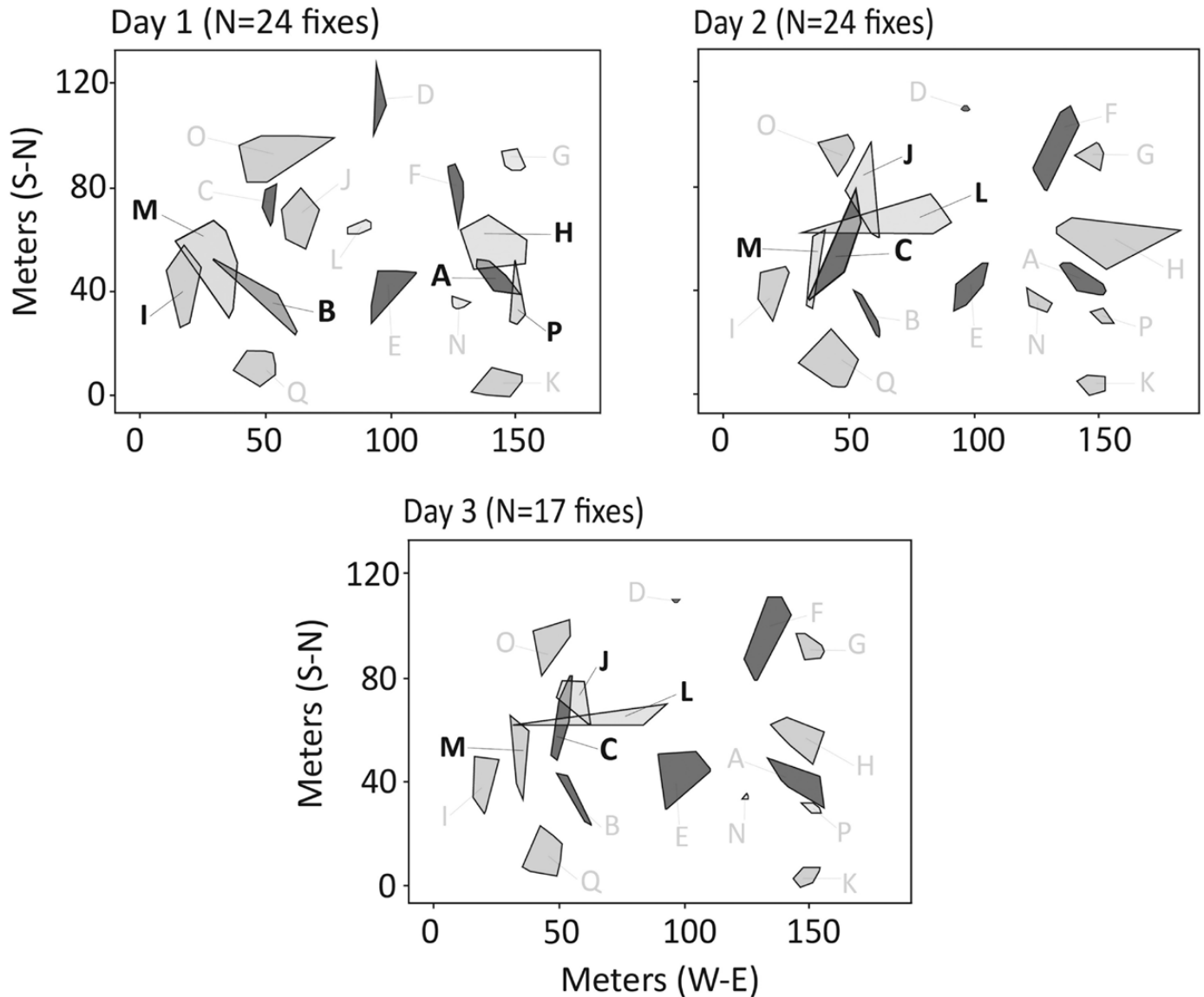


Fig. 3.—Daily home ranges for six adult male and 11 adult female tuco-tucos from Anillaco monitored from 9 to 11 December 2015. Home ranges were calculated using 100% minimum convex polygons (MCPs); daily sample sizes (number of radio fixes per individual) are shown above each panel. Light gray polygons represent females while dark gray polygons represent males. In each panel, individuals are indicated with different letters; identities of individuals whose home ranges overlapped on a given day are shown in bold.

was also detected. Comparisons of home ranges across successive days revealed that spatial relationships among members of the study population were dynamic, with both home range size and overlap varying on a daily basis. While overlap of home ranges belonging to different animals was not uncommon, individuals whose home ranges overlapped did not co-occur at the same location at the same point in time. Collectively, these data suggest that although the tuco-tucos at Anillaco are not group-living, neither are they completely solitary. Instead, the animals appear to engage in an intermediate form of social organization in which regular overlap of home ranges may create opportunities for social interactions but adults do not share burrow systems or nest sites.

Variability in spatial relationships.—One striking feature of the study population was the variability in spatial relationships

detected. Home ranges based on telemetry fixes recorded throughout the 10-day data collection period revealed that while some animals overlapped spatially with one or more individuals, others displayed no spatial overlap with conspecifics. Overlapping individuals included female–female as well as male–female pairs; individuals that never overlapped with conspecifics also included adults of both sexes. This variability in spatial relationships was more pronounced when home ranges were examined on a daily basis. At this temporal scale, mean overlap of an individual with itself indicated that at least some animals changed the configuration of their home range markedly across successive days. While use of 100% MCPs to characterize individual home ranges has been criticized due to the expected sensitivity of this metric to outlier localities (Linders et al. 2004; Girard et al. 2002; White and Garrott 1990), such

outliers may be particularly informative when exploring variability in patterns of space use and the associated potential for interactions among conspecifics. Consistent with this, overlap between pairs of individuals varied on a daily basis; none of the pairs of animals for which overlap was detected displayed overlapping home ranges on all days examined. Collectively, these findings suggest that spatial relationships among adults in the study population were dynamic, varying temporally as well as among individuals.

To the best of our knowledge, no previous studies of ctenomyids have examined variation in spatial relationships on a daily basis. Although O'Brien et al. (2020) reported daily variation in the extent to which individual *C. opimus* overlapped spatially with themselves, these authors did not characterize variation in relationships among different members of their study population. Patterns of space use over seasonal time scales have been reported for *C. rionegrensis* (Tassinio et al. 2011), although the almost complete turnover of individuals from one sampling period to the next precluded temporal comparisons of relationships among the same subsets of animals. Given the paucity of data regarding short-term variability in space use by ctenomyids, it is possible that the daily changes in home range size, shape, and overlap documented in our study population are not unique to the tuco-tucos at Anillaco. Future studies that explore home range use in *Ctenomys* on a daily basis should prove useful in elucidating how short-term variation in spatial relationships contributes to patterns of spatial and social behavior over the longer time scales typically used to characterize a species' social organization.

Social organization of Anillaco tuco-tucos.—Members of our study population did not share burrow systems or nest sites and thus did not meet the two criteria typically used to characterize subterranean species as group living (Lacey et al. 1997, 2019; Lacey 2000; O'Brien et al. 2020). Although partial overlap of home ranges was not uncommon at Anillaco, this overlap was limited to only a portion (~25%) of an individual's home range and animals that overlapped spatially never co-occurred at the same point in space and time. In contrast, members of ctenomyid species characterized as group living typically share 40% to 70% of their home ranges with conspecifics and individuals routinely co-occur at putative nest sites (*C. sociabilis*—Lacey et al. 1997; *C. opimus*—O'Brien et al. 2020). Similarly, in cururos (*Spalacopus cyanus*), the only subterranean member of the sister family Octodontidae (Reig 1970; Upham and Patterson 2012), overlap of home ranges typically exceeds 70% and individuals are regularly found together at putative nest locations (Lacey et al. 2019). Thus, while overlap of burrow systems was a persistent feature of the population of tuco-tucos at Anillaco, the nature and extent of this overlap were not consistent with patterns of space use in group-living species of ctenomyids.

Spatial relationships among members of our study population also differed from those reported for solitary species of ctenomyids, in which telemetry data have revealed no overlap among home ranges for different adults (*C. haigi*—Lacey et al. 1998; *C. talarum*, *C. australis*—Cutrer et al. 2006, 2010;

C. minutus, *C. flamarioni*—Kubiak et al. 2017). Spatial relationships may be influenced by seasonal changes in reproductive status, with overlap of male–female pairs predicted to be more likely during the breeding season (Ims 1987; Lambin and Krebs 1991). As a result, it is possible that differences in the timing of data collection contributed to the contrast between our findings and those for solitary ctenomyids. As indicated by the presence of pregnant and lactating females, data for this study were collected during the breeding season and it is possible that reproductive opportunities contributed to at least some of the examples of spatial overlap (e.g., male–female pairs) detected. In contrast, studies of space use in *C. talarum* and *C. australis* were conducted during the nonbreeding season (Cutrer et al. 2006, 2010), which may have reduced the potential for detecting spatial overlap between males and females. Data for *C. haigi* and *C. minutus*, however, were collected during the breeding seasons for these species, yet no spatial overlap among adults was reported (Lacey et al. 1998; Kubiak et al. 2017). Thus, while seasonal variation in behavior should be considered when characterizing spatial relationships, differences in the timing of data collection relative to breeding are not sufficient to explain the occurrence of spatial overlap in our study animals but not in other, solitary species of ctenomyids.

Analyses of spatial relationships may also be affected by the duration of data collection, particularly in taxa in which overlap of home ranges does not occur on a regular (e.g., daily) basis. In particular, the absence of spatial overlap in solitary species of ctenomyids may reflect sampling that did not continue long enough to detect periodic instances of overlap among adults. Although the duration of data collection for *C. talarum* (Cutrer et al. 2006) was comparable to that reported here, telemetry data for *C. australis* (Cutrer et al. 2010), *C. minutus* (Kubiak et al. 2017), and *C. haigi* (Lacey et al. 1998) were collected over approximately half as many days, raising the possibility that temporally limited sampling may have contributed to the absence of spatial overlap in the latter three species. Conversely, partial overlap of home ranges was reported for *C. rionegrensis* based on sampling efforts lasting just a few days (Tassinio et al. 2011), indicating that such overlap is readily detected in at least one species of ctenomyid that is not group-living. Although spatial relationships among individuals in our study population varied on a daily basis, examples of overlap were evident on each day examined, indicating that the duration of our sampling efforts was sufficient to capture this aspect of behavior. Collectively, these findings suggest that the tuco-tucos at Anillaco display an intermediate form of social organization in which there is persistent but temporally dynamic spatial overlap between female–female as well as male–female pairs, although adults do not share burrow systems and nest sites.

Implications for comparative studies of social organization.—Among hystricognath rodents, overlap of adult home ranges—particularly between males and females—has been reported for multiple surface- and burrow-dwelling species, including wild guinea pigs (*Cavia aperea*—Asher et al. 2004), southern mountain cavies (*Microcavia australis*—Ebensperger et al. 2006), common

degus (*Octodon degus*—Ebensperger et al. 2004), moon-toothed degus (*Octodon lunatus*—Sobrero et al. 2014), plains vizcachas (*Lagostomus maximus*—Branch 1993), torch-tailed spiny rats (*Trinomys yonenagae*—Santos and Lacey 2011), and Tome's spiny rats (*Proechimys semispinosus*—Adler et al. 1997). Studies of these taxa have revealed a variety of spatial arrangements, comparisons of which have been used to test hypotheses regarding the roles of ecological and phylogenetic factors in shaping the social biology of these animals (Ebensperger and Cofré 2001; Lacey and Ebensperger 2007; Sobrero et al. 2014). In contrast, truly subterranean rodents, including subterranean hystricognaths, have traditionally been assumed to be solitary (Nevo 1979; Lacey 2000). While the most conspicuous exceptions to this statement are social bathyergid mole-rats (Bennett and Faulkes 2000; Faulkes and Bennett 2013), a growing number of studies are revealing evidence of group living in other subterranean hystricognaths, including cururos (Lacey et al. 2019) and at least two species of tuco-tucos (Lacey et al. 1997; O'Brien et al. 2020). Our data regarding spatial relationships among the tuco-tucos at Anillaco add an apparently new variant to the growing comparative picture of social organization in ctenomyids, thereby increasing the importance of this family for comparative analyses of social behavior. Studies that characterize spatial relationships in additional species of tuco-tucos should facilitate understanding of the factors contributing to variability in the social organizations of these and other subterranean rodents.

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SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Home range sizes for six adult male and 11 adult female tuco-tucos from Anillaco, La Rioja Province, Argentina. Home ranges are based on radiotelemetry data collected from 5 to 15 December 2016. For each individual, sex, body weight, and apparent reproductive status are indicated. Individual home range sizes were estimated using 100% and 95% minimum convex polygons (MCPs). Letters correspond to those used to identify the animals in Figs. 1 and 3.

Supplementary Data SD2.—Changes in home range size as a function of the number of data points examined. Data are from radio fixes obtained for six adult male and 11 adult female

tuco-tucos from Anillaco, La Rioja Province, Argentina. Home ranges were estimated using 95% minimum convex polygons (MCPs). The x-axis depicts the percentage of the total number of fixes per individual (mean = 105.1 ± 5.1 , range: 96–111 fixes) used to construct each MCP. The inflection point for each graph indicates the percentage of fixes required to obtain a robust estimate of home range size. Letters correspond to the animal IDs used in Supplementary Data SD1 and Figs. 1 and 3. Bold letters denote males.

Supplementary Data SD3.—Percent change in home range size for six male and 11 female tuco-tucos from Anillaco that were monitored via radiotelemetry. Individuals are identified along the x-axis with different letters; letters in bold denote males. For each individual, the percent change in home range size (m^2) is shown for comparisons of 100% and 95% minimum convex polygons (MCPs) for that animal.

Supplementary Data SD4.—Pairs of adults with overlapping home ranges as identified using 100% and 95% minimum convex polygons (MCPs). Data for male–female, female–female, and male–male pairs are shown. Because the overlap between pairs of individuals was not symmetric, the mean \pm SD percent overlap is shown for each pair. Letters correspond to the animal IDs used in Supplementary Data SD1 and Figs. 1 and 3.

Supplementary Data SD5.—Daily home range sizes for six adult male and 11 adult female tuco-tucos from Anillaco, La Rioja Province, Argentina, that were monitored from 9 to 11 December 2016. Home ranges were calculated using 100% minimum convex polygons (MCPs); daily samples sizes (number of radio fixes per individual) ranged from 17 to 24 fixes per individual. Letters correspond to the animal IDs used in Supplementary Data SD1 and Figs. 1 and 3.

Supplementary Data SD6.—Daily percent pairwise overlap for home ranges for tuco-tucos from Anillaco, La Rioja Province, Argentina, that were monitored from 9 to 11 December 2016. Data for 11 pairs of individuals whose home ranges overlapped on at least 1 day of data collection are shown; because separate values were calculated from the perspective of each member of an overlapping pair, values are presented as means \pm 1 SD. Data for male–female, female–female, and male–male pairs are shown. Letters correspond to the animal IDs used in Supplementary Data SD1 and Figs. 1 and 3.

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