

Facultative sociality in a subterranean rodent, the highland tuco-tuco (*Ctenomys opimus*)

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Understanding why social relationships vary among conspecifics is central to studies of animal behaviour. For many species, patterns of space use provide important insights into social behaviour. To characterize the social organization of the highland tuco-tuco (*Ctenomys opimus*), we used visual observations and radiotelemetry to quantify spatial relationships among adults in a population at Laguna de los Pozuelos, Jujuy Province, Argentina. Specifically, we sought to confirm anecdotal reports that these subterranean rodents are social, meaning that adults share burrow systems and nest sites. Our data indicate that the animals live in spatially distinct groups, although the number of individuals per group varies markedly. Although these relationships were robust with regard to location (above vs. below ground) and type of data (visual vs. telemetry), some groups identified during the daytime fissioned during the night. We suggest that the population of *C. opimus* at Pozuelos is facultatively social, meaning that individuals display predictable, adaptive differences in social relationships with conspecifics. More generally, our findings add to the growing number of subterranean species of rodents recognized as social, thereby generating new opportunities for comparative studies of these animals aimed at assessing the causes and consequences of variation in social organization.

ADDITIONAL KEYWORDS: behaviour – Ctenomyidae – home range – social – space use – subterranean – telemetry.

INTRODUCTION

The social environment in which an animal lives can have profound effects on multiple aspects of its biology, including access to mates and other resources (Le Boeuf & Peterson, 1969; Farentinos, 1972; Monaghan, 1985; Creel & Creel, 1995), exposure to predators and pathogens (Griffin, 2004; Prado *et al.*, 2009; Habig *et al.*, 2018), and response to environmental challenges (Madison *et al.*, 1984; Madison & McShea, 1987; Schradin *et al.*, 2006; Rabosky *et al.*, 2012). Accordingly, intraspecific variation in social behaviour may have significant effects on survival and fitness (Lott, 1991). A fundamental component of the social

environment is the number of conspecifics with which an individual interacts on a regular basis. Although studies of social structure have typically focused on characterizing a species as solitary or social, the number and frequency of social relationships can vary markedly among conspecifics (Chapman *et al.*, 1995; Creel & Winnie, 2005). Facultatively social species—those in which solitary and group-living animals co-occur in a population and individuals display predictable variation in the extent to which they interact with conspecifics—provide an important opportunity to assess the consequences of differences in the nature or magnitude of social interactions. Potential effects of such variation include but are not limited to differences in stress physiology (Creel *et al.*, 2013; Woodruff *et al.*, 2013), gut microbial

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diversity (Tung *et al.*, 2015; Moeller *et al.*, 2016; Raulo *et al.*, 2018), and overall health and immune function (Bartolomucci, 2007; Kappeler *et al.*, 2015), indicating that facultative differences in social environment may play a significant role in determining the fitness consequences of interactions with conspecifics.

Because direct observations of social interactions are not possible for all species, numerous studies have employed spatial associations among individuals as a proxy for social relationships (Radespiel, 2000; Blundell *et al.*, 2002; Lusseau *et al.*, 2006; Hinze *et al.*, 2013; Scillitani *et al.*, 2013; Farine & Whitehead, 2015; Lacey *et al.*, 2019). Patterns of space use can generate critical insights into patterns of social behaviour. For example, by determining which animals overlap spatially, such analyses can reveal the potential for interactions among specific individuals. Analyses of the temporal patterning of spatial overlap can generate additional insights; social interactions are expected to differ depending on whether individuals use the same portion of the habitat simultaneously (e.g. savanna baboons (Stammach, 1987)) vs. at different points during the 24-h cycle (e.g. coyotes (Atwood & Weeks, 2003)). Further, in some taxa, spatial relationships may vary with ecological context (e.g. above- vs. below-ground activity in ground squirrels (Smith *et al.*, 2018)), with associated implications for social interactions. As a result, for many species, characterizing variability in spatial relationships among members of a population may reveal the extent to which social relationships vary.

To assess potential variability in social relationships among highland tuco-tucos (*Ctenomys opimus*), we examined patterns of space use within a population of this species from Jujuy Province, Argentina. Like other members of the rodent family Ctenomyidae, highland tuco-tucos are subterranean, meaning that individuals spend much of their time in below-ground burrows (Nevo, 1979; Lacey *et al.*, 2000). Although most of the > 60 known species of tuco-tucos (Parada *et al.*, 2011) have not been characterized with respect to social structure, those that have been studied have generally been found to be solitary, with each adult occupying its own burrow system and displaying minimal if any spatial overlap with other adults (e.g. *Ctenomys australis* (Zenuto & Busch, 1998); *Ctenomys haigi* (Lacey *et al.*, 1998); *Ctenomys talarum* (Cutrer *et al.*, 2006)). A notable exception to this solitary lifestyle is the colonial tuco-tuco (*Ctenomys sociabilis*), burrow systems of which are routinely occupied by multiple adult females and, in many cases, a single adult male (Lacey *et al.*, 1997; Lacey & Wiczorek, 2004). This interspecific variation in social structure, including pronounced differences between species that occupy the same general habitat (*C. sociabilis* and *C. haigi* (Lacey & Wiczorek, 2003)), makes the

genus *Ctenomys* an important comparative system for exploring the causes and consequences of variation in social behaviour.

Although the highland tuco-tuco has been described as solitary based on the capture of no more than one adult per burrow system in southern Peru (Pearson, 1959), our anecdotal observations of populations of *C. opimus* in northern Argentina suggest that these animals engage in some degree of burrow sharing. Highland tuco-tucos from the latter region are unusual in that they emerge completely from their burrows to forage, with the result that they are visible above ground for extended periods of time. Direct visual observations indicate that multiple adults may use the same burrow entrance when foraging but that individuals vary with regard to the number of conspecifics with which they interact. To quantify the social structure of *C. opimus* and to assess individual variation in the frequency of social interactions, we used a combination of visual observations and radiotelemetry to document spatial and social relationships among members of this species. Specifically, we sought to confirm that adults in our study population engage in burrow sharing (a criterion for sociality in subterranean species (Lacey, 2000)) and determine whether patterns of social interaction vary with temporal (daytime vs. night-time) or ecological (above vs. below ground) context. Our analyses suggest that highland tuco-tucos from northern Argentina are characterized by an intermediate form of social structure not previously described in *Ctenomys*. Further, the animals display marked inter-individual variation in social behaviour that provides a foundation for future studies aimed at exploring the adaptive function of potential facultative sociality in these animals.

METHODS

STUDY SITE

The population of highland tuco-tucos (*C. opimus*) studied was located in Monumento Nacional Laguna de los Pozuelos (hereafter referred to as Pozuelos), Jujuy Province, Argentina (22°34' S, 66°01' W; elevation: 3600 m). Pozuelos is located in a high Andean valley containing a mosaic of tola (*Parastrephia* sp.) shrubland and more open areas dominated by salt grass (*Distichlis* sp.). The study site consisted of an approximately 1.5 ha area of salt grass habitat bordered to the east by the Río Cincel. The site was bounded to the west by tola habitat and to the north and south by the remnants of adobe walls used historically to contain livestock. Annual rainfall at the site was ≤ 200 mm, with most precipitation occurring between December and March (Mascitti, 2001). Data for this study were collected between 24 December 2009 and 9 January 2010.

ANIMAL CAPTURE AND MARKING

All procedures 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) as well as the guidelines of the Association for the Study of Animal Behaviour for the treatment of animals in behavioural research (Buchanan *et al.*, 2012). Members of the study population were captured using tomahawk-style live traps baited with carrots. Open traps were placed at active burrow entrances, as identified by the presence of recently excavated soil and fresh faecal pellets as well as observations of animals using those entrances. Trapping was conducted during daylight hours; open traps were monitored continuously, and animals were retrieved immediately upon capture. The location of each capture was recorded using a hand-held GPS unit (accuracy ~ 6 m). Additionally, we recorded each capture locality using a Cartesian coordinate system (8 m x 8 m grid cells) that had been established on the study site prior to the start of trapping. This grid was also used to record the locations of animals during radiotelemetry studies (see below) and thus documenting capture localities with the same coordinate system allowed us to more accurately relate captures to home ranges estimated from telemetry data.

Upon first capture, each animal was marked for permanent identification with a uniquely coded PIT tag (IMI-1000, Bio Medic Data Systems, Inc., Seaford, DE) that was inserted beneath the skin at the nape of the neck. PIT tags were read using a hand-held scanner (DAS 4000 Pocket Scanner, Bio Medic Data Systems Inc.). For visual identification, each animal was also marked by applying human hair dye to the fur in a unique combination of colour patches; dye marks typically lasted 2–3 weeks before needing to be redone. Each time that an animal was captured, its sex and body weight were recorded. Data on body weight were used to determine the apparent age (juvenile vs. adult) of each individual. For adult females, reproductive status was assessed based on the appearance of the external genitalia (sexually receptive), the ability to palpate fetuses (pregnant), or the presence of enlarged mammae (lactating). In contrast, because the testes of male tuco-tucos do not descend externally (Zenuto, 1999), the reproductive status of adult males in the study population could not be determined based on visual examination.

RADIOTRACKING OF STUDY ANIMALS

All adults captured were fitted with radio transmitters (G3-1V transmitters, AVM Instrument Company, Colfax, CA) that were affixed using plastic cable ties

as collars. The weight of the transmitter and collar together (~ 7 g) represented < 5% of the body weight of each individual (males: 364.0 ± 47.8 g, $N = 10$; females: 309.4 ± 39.1 g, $N = 16$), as recommended for studies of small mammals (Sikes *et al.*, 2016). Collared animals were released at the point of capture, after which their locations were determined using R1000 receivers (Communications Specialists, Inc., Orange, CA) and 3-element hand-held Yagi antennas (AVM Instrument Company). Radio fixes were collected multiple times per day, with a minimum of 1 h between successive recordings. For each fix, the location of an individual was recorded to the nearest half meter using the 8 m x 8 m grid system established on the study site. Analyses of telemetry data for transmitters placed at known locations revealed this procedure to be accurate within 0.5 m; these analyses also confirmed the consistency of spatial data collected by different researchers ($N = 5$). Because these assessments were made under ideal conditions (e.g. daylight, immobile object), we used a more conservative error estimate when analysing our telemetry data; all fixes occurring within a 1 m radius of each other were treated as the same location. Radio fixes recorded between sunrise and sunset (07:00–20:00 h) were categorized as daytime data points, whereas fixes recorded from sunset to sunrise (20:00–07:00 h) were designated as night-time points. During daylight hours, if a collared individual was sighted above ground at the time that a telemetry fix was made, that datum was noted as a visual sighting of the animal and the location at which the animal was observed was recorded. Although we did not detect evidence of above-ground activity during the night, we were not confident of the accuracy of visual observations conducted in the dark and thus we restricted comparisons of visual vs. telemetry data to localities recorded during daylight. At the end of all data collection, individuals were recaptured, and their radio collars were removed.

SPATIAL RELATIONSHIPS

Patterns of space use were analysed using 95% minimum convex polygons (MCPs) generated with the *adehabitatHR* package in R (Calenge, 2019). To determine the number of telemetry fixes required to generate robust estimates of individual home ranges, we examined the relationship between number of fixes analysed and MCP size for a random subset of six animals from our study population; this sample size is comparable to other studies that have examined space use in relation to the number of data points per individual (Santos & Lacey, 2011; Lacey *et al.*, 2019). To explore the temporal consistency of individual home ranges, we generated distinct daily MCPs (daytime radio fixes only; $N = 5$ successive days) and

then quantified the percent overlap for MCPs for the same individual; this comparison was conducted for a subset of six animals for which we had \geq ten fixes per day for at least 5 successive days.

To determine if patterns of space use differed when animals were above vs. below ground, separate MCPs were constructed for above-ground sightings vs. telemetry fixes (animals not visible above ground) for the same individual. Because visual observations were only possible during daylight, the radio fixes used in this comparison were also restricted to those collected during the daytime. Only data from individuals for which \geq ten visual observations had been obtained were included in this analysis. The sizes of MCPs constructed from visual vs. telemetry data from the same individual were then compared and the percent overlap between these MCPs was calculated. Distinct pairwise estimates of spatial overlap between different individuals were generated for both MCPs based on visual observations and those based on telemetry fixes. Because overlap between pairs of animals may not have been symmetric, estimates of percent overlap of MCPs were calculated from the perspective of each individual.

To characterize circadian patterns of activity within the study population and to determine if spatial relationships among individuals differed between day and night, radio fixes were collected hourly for a period of 5 days and nights (120 consecutive hours). Separate MCPs were then constructed for daytime and night-time fixes for each individual; to avoid potential biases resulting from differences in data collection methods, only telemetry data used for these analyses. The sizes of daytime and night-time MCPs for the same animal were compared and the percent overlap between these MCPs was calculated. Based on evidence (see *Results*) that members of the study population are diurnal, the nest site for each individual was identified as the most frequently recorded (modal) x and y coordinates obtained during night-time telemetry fixes (Urrejola *et al.*, 2005). The percentage of fixes that an animal spent at its putative nest site was calculated using the standard 1-m error distance described above. To account for the unknown sizes of nests (i.e. the potential for animals to change locations while remaining in the nest), the percentage of fixes falling within 5 m of the modal x and y coordinates for each animal was also calculated and this value compared to the percentage of fixes assigned to the nest using the more conservative 1 m error distance.

SOCIAL NETWORK ANALYSES

To identify spatially distinct groups of animals and to assess potential variation in social relationships among members of the study population, we used

social network analyses (Wey *et al.*, 2008; Krause *et al.*, 2009) to identify the number of significant social interactants per individual. Specifically, pairwise measures of percent overlap between MCPs for different animals were used to generate association matrices that were then analysed with SOCPROG (Whitehead, 2009) to identify hierarchical spatial clusters of individuals. The fit between association matrices and the resulting clusters was assessed using the cophenetic correlation coefficient, with values \geq 0.8 considered indicative of a strong correspondence between these data sets (Bridge, 1993). Social groups were identified using the maximum modularity criterion, which provides a measure of the degree to which the study population was divided into distinct spatial units (Newman, 2006; Whitehead, 2008). Cut-off values for significant spatial associations among individuals were generated by SOCPROG for each data set examined. Graphical depictions of networks among spatially clustered individuals were generated using the R package igraph (Csardi & Nepusz, 2006). To compare relationships during the day vs. the night, separate network analyses were conducted for each temporal period. To compare relationships when animals were above vs. below ground, separate analyses were conducted using daytime spatial data collected visually vs. via telemetry; only individuals with \geq ten visual observations were included in these analyses.

STATISTICAL ANALYSES

Normality of the data was assessed using Shapiro-Wilks tests, after which parametric or non-parametric statistics were used as appropriate. Statistical analyses were performed using R v. 3.5.0 (R Core Team, 2013). All means are reported \pm 1 SD.

RESULTS

A total of 26 adults (10 males, 16 females) were monitored via telemetry over a period of 17 days. The mean number of days per animal on which telemetry data were collected was 8.9 ± 3.9 (range = 3–15) for males and 8.2 ± 3.9 (range = 2–16) for females. The number of animals under study increased over successive days as more individuals were captured and marked and thus our data set included multiple days in which all 26 adults were monitored concurrently. An additional eight adults observed on the study site were not captured ($N = 4$) or were captured too late in the field season to generate substantial telemetry data ($N = 4$). Thus, overall, telemetry data were obtained from 76.5% of adults in the study population. The individuals that were not monitored were scattered

throughout the study site suggesting that any impact of these animals on our analyses should have been evenly distributed among the spatial clusters of individuals detected (see below). Further, comparisons of capture localities and localities at which unmarked animals were typically sighted suggested that these unmonitored individuals were unlikely to have overlapped spatially with the apparently solitary individuals identified by our social network analyses (see below). For animals monitored via telemetry, the mean number of daytime radio fixes recorded per individual was 62.9 ± 30.7 (range = 16–123); the mean number of visual sightings per individual was 12.9 ± 7.2 (range = 0–24). Analyses of daytime telemetry data from a randomly-selected subset of individuals ($N = 6$) revealed that estimated home range size stabilized after ~ 30 radio fixes (Supporting Information, Fig. S1). Radio collars for four individuals (two males, two females) ceased functioning before night-time telemetry data could be collected. As a result, data regarding night-time spatial relationships were available for only 22 individuals, with 29–30 night-time telemetry fixes recorded for each of these animals.

VISUAL OBSERVATIONS VS. TELEMETRY

Analyses of the subset of 12 individuals for which both visual and telemetry data were available revealed no significant tendency for home range sizes based on telemetry data to differ from those based on direct visual observations (Wilcoxon Signed Rank Test, $N = 12$, $V = 60$, $P = 0.1$ (Supporting Information, Fig. S2)).

CONSISTENCY OF SPACE USE

Analyses of daytime telemetry data collected across 5 successive days ($N = 6$ individuals with \geq ten fixes per day) revealed that the mean overlap for MCPs for the same individual ranged from 33.0% to 52.5%, with a mean coefficient of variation of 0.56 among the animals sampled (Fig. 1). Mean pairwise overlap between MCPs for the different individuals in this sample ranged from 18.5% to 45.8% per day (Supporting Information, Fig. S3).

DAYTIME VS. NIGHT-TIME HOME RANGES

Twenty-two animals were monitored via telemetry for five consecutive days and nights. Paired comparisons of daytime and night-time MCPs revealed a significant tendency for the sizes of night-time home ranges ($90.8 \pm 95.6 \text{ m}^2$) to be less than those for daytime home ranges ($399.3 \pm 334.9 \text{ m}^2$) (Wilcoxon Signed Rank Test, $N = 22$, $V = 250$, $P < 0.001$).

For each animal monitored, telemetry fixes revealed a single location at which that individual spent a large proportion of time; this location was the same for both daytime and night-time fixes for the same animal. During the daytime, the mean percentage of fixes recorded within a 1-m radius of an animal's most frequently used (modal) location was $8.4 \pm 7.3\%$ ($N = 22$ individuals). When these analyses were repeated using a less restrictive 5-m radius around an animal's modal location, this value increased to $27.4 \pm 21.4\%$. For night-time data, the mean percentages of fixes recorded at an animal's modal locality ($N = 22$ individuals) were $49.6 \pm 20.9\%$ (1-m radius) and $78.9 \pm 16.1\%$ (5-m radius). The tendency for individuals to spend a greater percentage of fixes at a single, modal location during the night was not significant for the 1-m radius around the putative nest (Wilcoxon Signed Rank Test, $N = 22$, $V = 110.5$, $P = 0.87$); however, it was significant for the 5-m radius (Wilcoxon Signed Rank Test, $N = 22$, $V = 210$, $P < 0.001$). Analyses of the maximum distance at which each animal was detected from its modal location indicated that individuals travelled significantly further from their putative nests during the daytime ($60.9 \pm 46.1 \text{ m}$) than during the night ($15.3 \pm 9.49 \text{ m}$; Wilcoxon Signed Rank Test, $N = 22$, $V = 231$, $P < 0.001$). Of the 22 individuals followed via telemetry during the night-time, 18 (81.8%) used a single modal locality during all five nights of data collection. In contrast, the remaining four (18.2%) animals (three males, one female) each used two nest localities; for each of these individuals, the most commonly used nest site was shared with conspecifics whereas the less commonly used nest site was not. The mean percentage of fixes at these animals' primary and secondary locations were $67.5 \pm 9.95\%$ and $31.75 \pm 9.53\%$, respectively. Nest use by these latter four animals was dynamic, with these individuals switching between their primary and secondary nests both within and between nights.

MALE VS. FEMALE HOME RANGES

When all individuals for which daytime telemetry data were available were considered ($N = 26$), mean home range size for males ($773.1 \pm 462.4 \text{ m}^2$; $N = 10$) was greater than that for females ($355.5 \pm 248.15 \text{ m}^2$; $N = 16$); this difference was significant (Mann-Whitney U, $W = 114$, $P = 0.01$). For the subset of individuals ($N = 12$) for which both visual and daytime telemetry data were available, there was no significant difference in mean home range size for males vs. females for either data collection method (visual: Mann-Whitney U, $N = 4$, 8 , $W = 15$, $P = 0.93$; telemetry: Mann-Whitney U, $N = 4$, 8 , $W = 16$, $P = 0.49$). MCPs constructed from night-time telemetry fixes revealed no significant difference between mean home range size for males

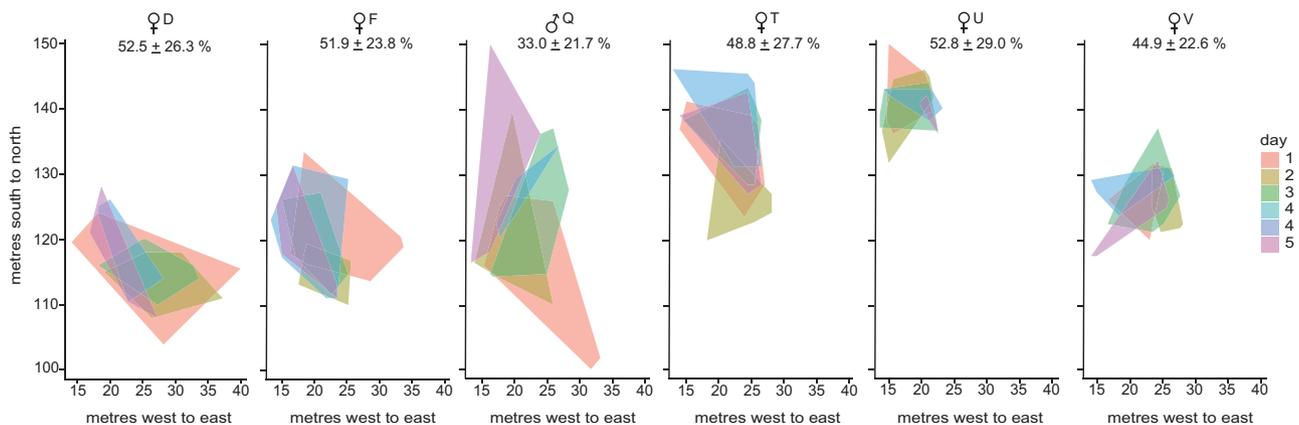


Figure 1. Minimum convex polygons (MCPs) depicting the daytime home ranges of six adult *C. opimus* (one male, five females) monitored via telemetry for 5 consecutive days. The x and y axes denote the location of each MCP on the study site. For each individual, a separate MCP was constructed for each day of data collection; colours shown at right indicate the day corresponding to a given MCP. Percent overlap of MCPs for the same individual over the 5 days examined ranged from 3.8% to 98.8%; individual means are given below the animal ID in each panel of the figure.

($76.9 \pm 76.4 \text{ m}^2$; $N = 8$) vs. females ($98.7 \pm 106.9 \text{ m}^2$; $N = 14$) (Mann-Whitney U, $W = 53$, $P = 0.80$). Maximum distance travelled from the putative nest during the daytime did not differ between males ($69.3 \pm 28.3 \text{ m}$; $N = 8$) and females ($56.1 \pm 54.0 \text{ m}$, $N = 14$; Mann-Whitney U, $W = 74$, $P = 0.23$). Similarly, there was no difference in the maximum distance travelled at night by males ($16.8 \pm 11.5 \text{ m}$, $N = 8$) vs. females ($15.3 \pm 8.1 \text{ m}$, $N = 14$; Mann-Whitney U, $W = 54$, $P = 0.91$).

OVERLAP OF HOME RANGES

Mean percent overlap of home ranges among individuals for which both daytime and night-time telemetry data were available ($N = 22$) was greater during the day ($41.9 \pm 30.6\%$) than during the night ($26.5 \pm 26.6\%$); this tendency was significant (Wilcoxon Signed Rank Test, $V = 604.5$, $P = 0.009$). Mean home range overlap among individuals for which both daytime visual and telemetry data were available ($N = 12$) was $28.8 \pm 28.4\%$ when animals were above ground (visual data) and $42.6 \pm 31.7\%$ when they were below ground (telemetry data); the apparent tendency for overlap to be greater below ground was not significant (Wilcoxon Signed Rank Test, $V = 145$, $P = 0.07$).

EVIDENCE FOR SPATIALLY DISTINCT GROUPS

Analyses of association indices based on overlap of daytime MCPs (telemetry data only) revealed that members of the study population were spatially associated with a mean of 3.7 ± 2.1 conspecifics. Network analyses of the 26 individuals examined generated a cophenetic correlation coefficient of

0.89, indicating a strong correspondence between the association index and patterns of home range overlap. Maximum modularity was 0.71. Based on an association index cut-off of 0.08, these analyses identified five distinct clusters of animals plus one solitary individual (no significant spatial association with conspecifics detected). Mean overlap of daytime home ranges among individuals assigned to the same cluster was $46.1 \pm 31.5\%$ vs. $23.6 \pm 23.4\%$ among individuals assigned to different clusters; this difference in mean percent overlap was significant (Mann-Whitney U, $W = 1129.5$, $P = 0.003$).

TEMPORAL DIFFERENCES IN SPATIAL ASSOCIATIONS

To allow for more direct assessment of potential temporal differences in spatial and social relationships, analyses of daytime spatial associations were repeated using the subset of 22 individuals for which both daytime and night-time telemetry data were available. Analyses of this more restricted dataset generated a cophenetic correlation coefficient of 0.90. Maximum modularity was 0.72 and the association index cut-off was 0.1. These analyses revealed the same five spatially distinct clusters of individuals described above (Fig. 2A); the four individuals excluded from these analyses due to the absence of night-time data included the one solitary individual identified from analyses of all radio-collared animals ($N = 26$; see above). Mean overlap of home ranges among individuals assigned to the same cluster was $46.7 \pm 30.0\%$ vs. $24.1 \pm 24.7\%$ among individuals assigned to different clusters; this difference in mean percent overlap was significant (Mann-Whitney U, $W = 485$, $P = 0.03$).

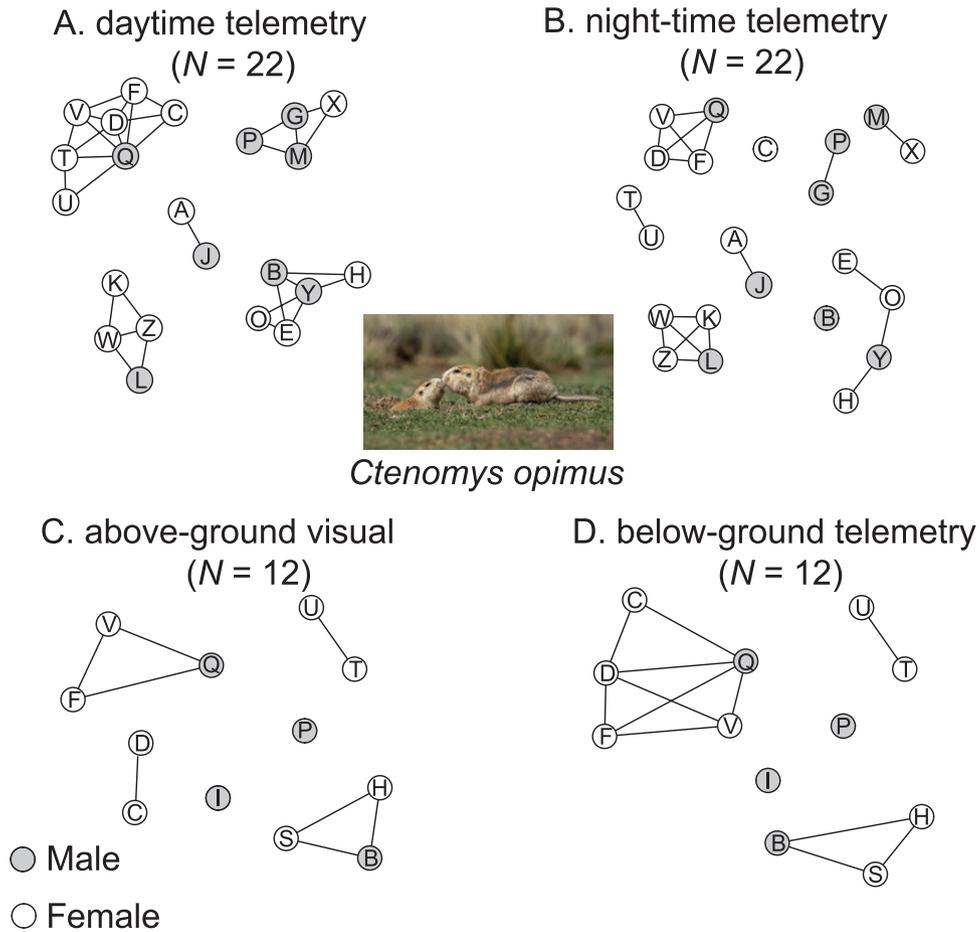


Figure 2. Undirected and unweighted social networks constructed for members of the study population. Networks based on telemetry data from 22 individuals were compared for (A) daytime and (B) night-time radio fixes. Additionally, daytime networks were compared for 12 animals that were (C) sighted above ground and (D) detected below ground via telemetry.

In contrast, analyses of night-time telemetry data revealed seven spatially distinct clusters of animals plus two solitary individuals (no significant spatial associations with conspecifics detected; Fig. 2B). All individuals that were spatially associated at night were also spatially associated during the day; the greater number of night-time clusters as well as the presence of the two apparently solitary animals was due to the subdivision of daytime clusters; all individuals that were spatially associated at night were also spatially associated during the daytime (Fig. 2A, B). The cophenetic correlation coefficient for analyses of night-time data was 0.97. Maximum modularity was 0.82 and the association index cut-off was 0.05. Although the mean number of individuals per night-time cluster (2.4 ± 1.2 , $N = 7$ clusters) was less than that for daytime clusters (4.3 ± 2.6 , $N = 5$ clusters), this difference was not significant (Mann-Whitney U, $W = 39.5$, $P = 0.14$). Clusters containing more than one adult were typically female-biased (daytime: 3.2 females per male; night-time: 1.8 females per male),

although there were also daytime ($N = 2$) and night-time ($N = 1$) clusters containing multiple adult males. Mean overlap of home ranges for individuals assigned to the same night-time cluster was $25.3 \pm 26.6\%$ vs. $4.9 \pm 1.2\%$ among individuals assigned to different clusters; this difference in mean percent overlap was significant (Mann-Whitney U, $W = 151.5$, $P = 0.009$).

ABOVE- VS. BELOW-GROUND ASSOCIATIONS

Spatial associations based on MCPs constructed from direct visual sightings (animals located above ground) vs. daytime telemetry fixes (animals located below ground) were completed for the subset of 12 individuals for which ≥ 10 visual sightings were obtained. The cophenetic correlation coefficient for visual data was 0.96 and maximum modularity was 0.60. Based on an association cut-off of 1.5, four spatially distinct clusters of animals as well as two solitary individuals were detected (Fig. 2C). Analyses of daytime telemetry fixes for this subset of individuals revealed three

clusters of individuals plus the same two solitary animals detected from visual observations (Fig. 2D). The cophenetic correlation for the telemetry data was 0.90, with a maximum modularity of 0.51 and an association cut-off of 0.07. The smaller number of clusters detected via telemetry was due to the merger of two distinct clusters revealed by analyses of visual data.

NEST SHARING

Comparisons of the modal night-time location(s) identified for each individual revealed that multiple animals shared the same putative nest site during each night of data collection. Of the 22 individuals monitored during night-time, only two (9.0%) were never detected at the same putative nest as other conspecifics (Fig. 3). In contrast, 16 (72.7%) individuals were consistently found at the same putative nest site with one or more conspecifics. The remaining four (18.3%) animals (three males, one female) had two nest localities each: for each of these animals, the most commonly used nest site was shared with conspecifics whereas the less commonly used site was not. With one exception (Fig. 3C), all individuals that shared night-time nests belonged to the same spatial cluster, as identified from daytime telemetry fixes.

DISCUSSION

Our analyses of spatial relationships indicate that the population of *C. opimus* at Pozuelos is group living. Individual home ranges were larger during the day than at night, but the location at which each animal was most frequently detected (i.e. its putative nest site) was consistent across both time periods. Spatial relationships among individuals did not differ with ecological context, specifically whether individuals were observed above ground or detected below ground via telemetry. Although spatial clusters of animals were generally consistent throughout the 24-h cycle, two daytime clusters appeared to fission at night, with the result that individuals in these groups tended to be associated with fewer conspecifics during the night-time. All individuals that shared a night-time nest site were assigned to the same daytime spatial cluster. In contrast, some animals that were spatially associated during the day occupied different nest sites at night. As a result, while social relationships tended to be linked to occupancy of a shared nocturnal nest site, this was not always the case, indicating that nest site alone was not a reliable predictor of spatial relationships among individuals.

In addition to spatially distinct clusters of individuals, our analyses revealed the presence of several animals that were apparently not associated with conspecifics. Because not all adults in the study

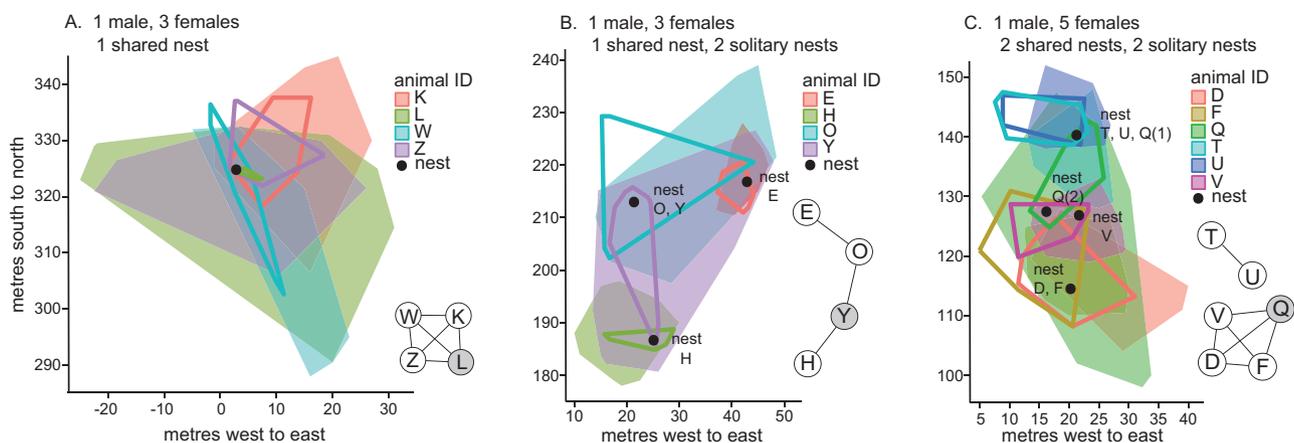


Figure 3. Patterns of nest use vs. home range overlap in *C. opimus*. The 95% minimum convex polygons (MCPs) shown depict home ranges for a subset of adults in the study population. The x and y axes denote the location of each MCP on the study site. Each panel depicts home ranges for individuals assigned to the same spatial cluster based on analyses of daytime telemetry fixes. Each coloured polygon indicates the daytime home range for one of the animals monitored; the polygon outlined in the same colour indicates the night-time home range for that individual. The identities of each animal are shown in each panel. Solid black circles denote nest sites. Social networks from Fig. 2 are included for comparison; individuals in grey are males whereas individuals in white are females. In (A), all individuals (one male, three females) shared a single nest site. In (B), four individuals used three distinct nest sites (one male-female pair and two solitary females). In (C), six individuals occupied four nest sites (two female-female pairs, one solitary female, and one male with two nest sites). In this last group, the nest most frequently used by male Q “Q(1)” was shared with females T and U. The less frequently used nest for this male, “Q(2),” was distinct from the nests used by the females in this spatial cluster.

population were fitted with radio collars, we cannot exclude the possibility that the “solitary” animals detected were in fact associated with individuals that were not monitored via telemetry. Visual observations, however, revealed that the animals for which telemetry data were lacking were scattered throughout the study site and did not occur in close proximity to apparently solitary individuals, suggesting that our identification of the latter was correct. More importantly, even if all adults in the study population had been followed via telemetry, variation in the number of individuals per spatial cluster would still have been evident, as would the tendency for some spatial clusters to fission during the night. Thus, while our data may not have captured the full composition of all spatial clusters of individuals, we believe that the general patterns revealed by our analyses are robust and provide a reasonable reflection of spatial and social structure in the study population.

EFFECT OF ECOLOGICAL CONTEXT: ABOVE- VS. BELOW-GROUND RELATIONSHIPS

Individuals at our study site were often sighted foraging and sunning above ground during daylight hours; this behaviour seemed to be influenced by weather conditions, with animals being most visible on sunny days with little wind. At all other times, individuals were below ground and their locations could only be detected via telemetry. This variability in surface activity allowed us to assess above- vs. below-ground spatial relationships independently of circadian patterns of activity. Our analyses revealed the same clusters of individuals for both above- and below-ground data sets, suggesting that spatial relationships were stable across these ecological contexts. Similar results have been reported for California ground squirrels (*Otospermophilus beecheyi*) (Smith *et al.*, 2018), in which social network connections observed when individuals were above ground were generally the same as those detected when the animals were below ground. This consistency in spatial relationships has important implications for understanding the adaptive benefits of group living members of the study population. More specifically, differences in spatial relationships were not detected when individuals were above vs. below ground, suggesting that the selective pressures favouring group living in this population do not differ significantly according to whether the animals are in their burrows or active on the soil surface.

TEMPORAL VARIATION IN RELATIONSHIPS

Home ranges were smaller, maximum distances travelled from the nest were shorter, and percentages of fixes at putative nest sites were greater during the

night than during the day, suggesting that members of the study population are diurnal. Although most spatial clusters of animals persisted throughout the 24-h cycle, two daytime clusters appeared to fission at night. As noted above, these night-time clusters were subsets of larger, daytime clusters; in no case did an individual spend the night with animals with which it was not associated during the day. Similar variation in daytime vs. night-time patterns of spatial relationships have been described in degus (*Octodon degus*) (Ebensperger *et al.*, 2004) and cururos (*Spalacopus cyanus*) (Lacey *et al.*, 2019). Although this temporal difference in behaviour may increase the complexity of assigning individuals to social groups based solely on patterns of daytime space use, spatial overlap among members of our study population that were assigned to the same daytime cluster was significantly greater than that among individuals assigned to different clusters, suggesting that group membership in *C. opimus* can be reliably determined based on daytime spatial relationships. Nevertheless, comparing diurnal and nocturnal patterns of space use is important because circadian differences in spatial relationships may reflect biologically important differences in activity (e.g. foraging during daylight) that shape interpretations of the adaptive bases for social relationships among individuals. Because the data considered were collected during a single, limited portion of the year, future studies will benefit by assessing spatial and social relationships—including potential circadian differences in these parameters—across multiple seasons and portions of the animals' annual reproductive cycles.

EVIDENCE FOR GROUP LIVING

Spatial relationships among individuals were consistent with the two criteria typically used to identify sociality in subterranean rodents (Lacey *et al.*, 2000). First, members of the study population displayed extensive below-ground spatial overlap, providing evidence that these animals meet the criterion that multiple adults share the same burrow system. Second, most individuals shared their nest site(s) with conspecifics, thereby fulfilling the second criterion for sociality in subterranean species. Because members of the study population were less active at night, sharing of nest sites during this portion of the 24-h cycle may be particularly informative regarding social relationships among individuals (Lacey *et al.*, 2019). Burrow and nest sharing have been used to identify group living in other subterranean species, including colonial tuco-tucos (*C. sociabilis*) (Lacey *et al.*, 1997), naked mole rats (*Heterocephalus glaber*) (Bennett & Faulkes, 2000), Damaraland mole-rats

(*Fukomys damarensis*) (Faulkes and Bennett, 2007), and cururos (*S. cyanus*) (Lacey *et al.*, 2019) and our data provide compelling evidence that the population of *C. opimus* at Pozuelos is also social.

To date, telemetry data have been used to characterize spatial and social relationships for only seven of the ≥ 60 recognized species of ctenomyids (Fig. 4). Of these, four species have been classified as solitary, meaning that each adult occupies its own burrow system (*C. australis* (Cutrera *et al.*, 2010); *C. haigi* (Lacey *et al.*, 1998); *Ctenomys minutus* (Kubiak *et al.*, 2017); *C. talarum* (Cutrera *et al.*, 2006, 2010)). Although occasional spatial overlap among adults has been reported for *Ctenomys rionegrensis*, individuals do not appear to routinely share burrow systems and do not share nest sites (Tassino *et al.*, 2011, Estevan *et al.*, 2016) and thus, we have included this species with the solitary taxa shown in Fig. 4. In contrast, *C. sociabilis* is clearly social (i.e. group living) based on the criteria outlined above, with multiple adults regularly sharing the same burrow system and nest site (Lacey *et al.*, 1997;

Lacey & Wiczorek, 2004; Izquierdo & Lacey, 2008). In comparison, our data suggest that *C. opimus* displays a form of sociality in which individuals share burrow systems and nests but group structure is somewhat more fluid than that in *C. sociabilis*, in which social groups are clearly distinct (i.e. no overlap between animals from different spatial clusters) and there are no differences in the daytime vs. night-time compositions of spatial groups (Lacey *et al.*, 1997; Lacey & Wiczorek, 2004). In contrast, although home range overlap in *C. opimus* was greater for individuals assigned to the same spatial cluster, individuals assigned to adjacent clusters did overlap with one another. Further, the composition of some clusters differed between daytime and night-time, providing evidence of a temporal variability in behaviour not observed in *C. sociabilis*. Collectively, these contrasts lead us to suggest that the population of *C. opimus* at Pozuelos is characterized by an intermediate form of spatial and social structure not previously reported for ctenomyids.

INDIVIDUAL VARIATION IN SPATIAL AND SOCIAL RELATIONSHIPS

The term *facultative sociality* has been used to describe the behaviour of populations or species in which individuals vary in their degree of spatial and social interaction with conspecifics. Vertebrate species that have been characterized as facultatively social include European badgers (*Meles meles*) (Newman *et al.*, 2011), California ground squirrels (*O. beecheyi*) (Smith *et al.*, 2016), yellow-bellied marmots (*Marmota flaviventris*) (Blumstein, 2013), Amazon red squirrels (*Sciurus spadiceus*) (Eason, 2010), yellow mongooses (*Cynictis penicillata*) (Balmforth, 2004), and eider ducks (*Somateria mollissima*) (Öst *et al.*, 2015). This term has also been used to describe multiple invertebrates, notably some species of carpenter bees (*Ceratina australensis* (Rehan *et al.*, 2010) and *Ceratina calcarata* (Shell & Rehan, 2017)) and sweat bees (*Megalopta genalis* (Wcislo, 1997; Smith *et al.*, 2018)). Our analyses have revealed a similar pattern of spatial and social variation in *C. opimus*, suggesting that this species—at least the population at Pozuelos—may also be facultatively social.

Identifying examples of facultatively sociality, however, may be more challenging than this discussion suggests. Definitions of this term differ and include individual- as well as population- and species-level variation in social behaviour. We suggest that facultative sociality should refer to systems in which members of a population display consistent, predictable, and adaptive variation in spatial and social relationships. Differences in the degree to which animals are spatially and socially connected should not result solely from stochastic factors (e.g. lone animals arising

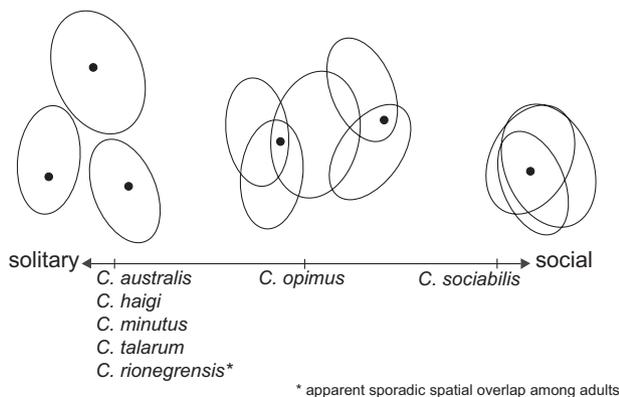


Figure 4. Schematic comparing spatial relationships reported for members of seven species of *Ctenomys* for which telemetry data are available. Each oval represents the home range of one individual; black circles depict the distribution of nests relative to individual home ranges. Apparent social structures range from solitary (no overlap among individuals) to highly social (consistent, almost complete overlap among multiple adults). *C. opimus* at Pozuelos is the first ctenomyid reported to have an intermediate pattern of spatial and social structure, in which individuals overlap extensively but not completely. Figure adapted from Lacey (2000). Citations are as follows: *C. australis* (Cutrera *et al.*, 2010), *C. haigi* (Lacey *et al.*, 1998), *C. minutus* (Kubiak *et al.*, 2017), *C. talarum* (Cutrera *et al.*, 2006; Cutrera *et al.*, 2010), *C. rionegrensis* (Tassino *et al.*, 2011; Estevan *et al.*, 2016), and *C. sociabilis* (Lacey *et al.*, 1997; Lacey and Wiczorek, 2004; Izquierdo and Lacey, 2008). *There is minimal evidence that members of *C. rionegrensis* may engage in occasional spatial overlap (Tassino *et al.*, 2011).

due to mortality of social partners) but should instead reflect adaptive variation in individual responses to intrinsic (genotypic, phenotypic) and extrinsic (ecological, environmental) factors. To determine if apparent differences in degree of social connectedness among highland tuco-tucos meet this more restrictive definition of facultative sociality, future studies of these animals will (1) examine the consistency of individual differences in behaviour over longer timescales, (2) assess the fitness consequences of these differences, and (3) relate individual variation in spatial and social relationships to phenotypic and environmental parameters. These analyses should generate important insights into the factors associated with individual-level differences in social connectedness reported here. More generally, studies of *C. opimus*—in conjunction with analyses of other rodents characterized as facultatively social—should improve our understanding of how behavioural differences among individuals intersect with ecological and demographic factors to produce population-level patterns of social structure.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. Home range size vs. number of telemetry fixes analysed for a randomly selected subset of six individuals. Estimates of home range size are based on 95% minimum convex polygons (MCPs). In general, home range size tended to stabilize at ~ 50% of the total number of fixes for an animal, which corresponded to 29.1 ± 17.4 fixes per individual.

Figure S2. Estimates of home range size (m²) based on 95% minimum convex polygons (MCPs) constructed for a subset of 12 *C. opimus* (four males, eight females) for which both telemetry and visual data were available. Paired comparisons revealed no significant tendency for individual home range sizes to differ between estimates based on telemetry data (grey bars) vs. visual data (white bars) (Wilcoxon Signed Rank Test, $N = 12$, $V = 60$, $P = 0.1$). Further, there were no significant differences in estimated home range sizes for males vs. females for analyses based on either telemetry data (Mann-Whitney U, $N = 12$, $W = 16$, $P = 0.49$) or visual data (Mann-Whitney U, $N = 12$, $W = 15$, $P = 0.93$).

Figure S3. Minimum convex polygons (95% MCPs) depicting the daytime home ranges of six adult *C. opimus* (one male, five females) monitored via telemetry for five consecutive days. The x and y axes denote the location of each MCP on the study site. For each individual, a separate MCP was constructed for each day of data collection. All MCPs for the same day are shown together; colours at right indicate which individual corresponds to a given MCP. Mean daily pairwise percent overlap of MCPs ranged from 18.5% to 45.8% per day; daily means are shown in each panel.