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Variable social organization among tuco-tucos (genus *Ctenomys*) in the *opimus* clade

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Comparative studies of closely related species provide a powerful means of identifying the ecological and demographic factors associated with variation in mammalian social systems. Although most members of the subterranean rodent genus *Ctenomys* are thought to be solitary, the highland tuco-tuco (*C. opimus*) is group living, meaning that multiple adults share a burrow system and underground nest site. These animals are part of the *opimus* clade, a monophyletic collection of four named species that occur in northwestern Argentina and adjacent portions of Chile and Bolivia. As a first step toward generating a comparative assessment of social organization within this clade, we characterized spatial relationships among members of a population of *Ctenomys* at Antofagasta de la Sierra, Catamarca Province, Argentina. Based on geographic location and natural history, these animals were expected to be part of the *opimus* clade; analyses of mitochondrial cytochrome-b sequences from our study population confirmed this general phylogenetic placement. Radiotelemetry data indicated that the animals at Antofagasta were group living, with up to three adult females and one adult male sharing a burrow system. In contrast to other group-living ctenomyids, however, individuals did not consistently share nest sites. Comparisons of these data with re-analyses of spatial relationships among members of the population of *C. opimus* studied by O'Brien et al. (2020) revealed several intriguing differences in social organization, potential explanations for which include short-term responses to variable demographic and ecological conditions as well as more enduring responses to differences in local selective pressures. Further comparative analyses of these populations and, more generally, members of this subclade of *Ctenomys* will help to elucidate the factors contributing to variation in social behavior within this speciose and geographically widespread genus.

Key words: *Ctenomys opimus*, group living, social organization, tuco-tucos

Los estudios comparativos de especies estrechamente relacionadas proporcionan un recurso eficaz para identificar los factores ecológicos y demográficos asociados con la variación en los sistemas sociales de los mamíferos. Aunque se cree que la mayoría de los miembros del género de roedores subterráneos *Ctenomys* son solitarios, el tuco-tuco andino (*C. opimus*) vive en grupos, lo que significa que varios adultos comparten el sistema de túneles y el nido (O'Brien et al. 2020). Esta especie forma parte del clado *opimus*, un grupo monofilético con cuatro especies reconocidas, distribuidas en el noroeste de Argentina y partes adyacentes de Chile y Bolivia. Como primer paso para generar una evaluación comparativa con base filogenética de la organización social dentro del clado, caracterizamos las relaciones espaciales entre los miembros de una población de *Ctenomys* en Antofagasta de la Sierra, Provincia de Catamarca, Argentina. En base a su ubicación geográfica e historia natural, se esperaba que estos animales fueran parte del clado *opimus*. Así, los análisis de las secuencias del citocromo

b mitocondrial de nuestra población de estudio confirmaron esta ubicación filogenética general. Los datos de radiotelemetría revelaron que los animales de Antofagasta viven en grupo, con hasta tres hembras adultas y un macho adulto compartiendo el sistema de túneles. Sin embargo, a diferencia de otros ctenomidos que viven en grupo, usualmente los individuos no compartieron regularmente los nidos. La comparación entre los datos de este trabajo con los nuevos análisis de las relaciones espaciales entre los miembros de la población de *C. opimus* estudiados por O'Brien et al. (2020) revelan diferencias notables en la organización social, cuyas potenciales explicaciones incluyen respuestas a corto plazo debido a la variabilidad en la demografía y en las condiciones ambientales, así como también respuestas a largo plazo como resultado de diferentes presiones de selección locales. Futuros análisis comparativos entre estas poblaciones y entre miembros de este clado de *Ctenomys* ayudarán a dilucidar los factores que contribuyen a la variación en el comportamiento social dentro de este género específico geográficamente extendido.

Palabras claves: *Ctenomys opimus*, organización social, tuco-tucos, vida en grupo

Social organization describes the tendency for conspecifics to live in groups and encompasses measures of both group size and group composition (Kappeler 2019). These aspects of behavior are generally thought to reflect the ecological and demographic settings in which animals occur (Emlen 1982; Lacey and Sherman 2007; Blumstein 2013). For example, patchily distributed resources (e.g., food, shelter) may favor the aggregation of individuals in the habitat, resulting in the formation of social groups (Alexander 1974; Johnson et al. 2002). Concomitantly, intersexual differences in dispersal or mortality may affect adult sex ratios, resulting in groups that are biased toward males or females (Dobson 1982; Clutton-Brock and Lukas 2011). Such ecological and demographic conditions can vary markedly over relatively small spatial and temporal scales, suggesting that variation in social organization is likely to occur within as well as among species (Lott 1991; Maher and Burger 2011; Schradin et al. 2018). As a result, comparative studies—particularly those of conspecifics or closely related species that differ behaviorally—can provide important insights into the extrinsic factors underlying differences in social organization (Felsenstein 1985; Foster and Cameron 1996; Nee et al. 1996).

Tuco-tucos are rodents in the genus *Ctenomys*, which ranges from Peru and Bolivia to Tierra del Fuego (de Freitas et al. 2021). More than 60 species of *Ctenomys* are currently recognized (Bidau 2015; D'Elia et al. 2021), all of which are subterranean. Although the majority of these taxa have not been characterized with respect to social organization, tuco-tucos—like other subterranean rodents—have generally been assumed to be solitary, meaning that each adult occupies its own burrow system (Nevo 1979; Busch et al. 1989; Lacey 2000). While several species of *Ctenomys* have been confirmed as solitary (e.g., *C. australis*: Cutrera et al. 2010; *C. haigi*: Lacey et al. 1998; *C. minutus*: Kubiak et al. 2017; *C. talarum*: Cutrera et al. 2006), at least two examples of group living have been identified (*C. opimus*: O'Brien et al. 2020; *C. sociabilis*: Lacey et al. 1997). In these latter taxa, multiple adults share the same burrow system and underground nest site, thereby creating opportunities for social interactions that are unlikely to occur in solitary species (Lacey 2000; Kappeler 2019). This marked variation in social organization among congeners suggests that comparative studies of tuco-tucos provide an important opportunity to elucidate ecological and demographic correlates of differences in social behavior. To date, however, few such comparative studies have been conducted for *Ctenomys*; published comparisons (e.g., Lacey and Wieczorek 2003; Cutrera et al. 2010) have focused on criteria other than phylogenetic relationship to select taxa for study, making it challenging to disentangle the effects of current environmental conditions from those of evolutionary history.

Here, we characterize the social organization of a population of tuco-tucos from Antofagasta de la Sierra, Catamarca Province, Argentina (hereafter referred to as Antofagasta). Although the taxonomy of this population has yet to be determined, its geographic location suggests that it is part of the *opimus* clade of *Ctenomys*, a monophyletic lineage occurring in northwestern Argentina that includes two high-elevation Andean species (*C. opimus* and *C. fulvus*) as well as two species (*C. saltarius* and *C. scagliai*) from adjacent, lower-elevation chaco habitats (Parada et al. 2011). Contained within this clade is the population of *C. opimus* at Monumento Nacional Laguna de los Pozuelos, Jujuy Province, Argentina (hereafter referred to as Pozuelos), that has been shown to be group living (O'Brien et al. 2020). Although tuco-tucos at both Pozuelos and Antofagasta occur in open, high-elevation Puna habitats (Mascitti 2001; Carilla et al. 2018; Izquierdo et al. 2018), our observations suggest that these localities differ with regard to several potentially important parameters including the dominant species of vegetation, the distribution of the plants on which the animals forage, and the density of tuco-tucos at each site. Quantitative comparisons of these attributes are lacking but the conspicuous nature of these differences suggests that if current ecological and demographic conditions influence social behavior within *Ctenomys*, then social organization is likely to differ between the populations of tuco-tucos at Antofagasta and Pozuelos.

As a first step toward evaluating potential links between ecological, demographic, and behavioral variation within the *opimus* clade of *Ctenomys*, we used radiotelemetry to quantify spatial relationships among members of the population of tuco-tucos at Antofagasta. By adopting the same field methods employed at Pozuelos (O'Brien et al. 2020, 2021) and by reanalyzing a subset of the spatial data obtained at that locality (O'Brien et al. 2020), we compare directly the social organizations of tuco-tucos at Pozuelos and Antofagasta. To confirm

that animals at the latter site are part of the *opimus* clade and to provide a preliminary assessment of the phylogenetic relationship between the tuco-tucos at Pozuelos and Antofagasta, we examined sequence data from the mitochondrial *cytochrome-b* (cyt-b) locus obtained from animals at these localities. In addition to generating the first description of spatial and social relationships among the tuco-tucos at Antofagasta, these analyses provide the first comparative assessment of social organization within the *opimus* clade, thereby laying the foundation for more extensive exploration of the factors contributing to behavioral diversity within this subset of the genus *Ctenomys*.

Materials and Methods

Antofagasta study site and study population.—Field studies at Antofagasta de la Sierra, Catamarca Province, Argentina (−26.09627, −67.39727, WGS 84, elevation = 3,323 m) were conducted from 8 to 25 December 2019. Antofagasta is located at the southern end of the Puna biome, a high-elevation collection of habitats that is widespread in northwestern Argentina. The climate at the study site is generally cold and dry, with pronounced daily and seasonal fluctuations in temperature (Izquierdo et al. 2018). Mean annual rainfall is less than 200 mm, with most precipitation occurring during the summer (December–February) (Izquierdo et al. 2018).

The ca. 1.5-ha study site was located along the eastern border of the Río Punilla drainage, a low-lying area at the southern end of the valley containing the town of Antofagasta de la Sierra. The site consisted of an open expanse of habitat dominated by saltgrass (*Distichlis* sp.) and sedges (*Amphiscirpus* sp.) (Izquierdo et al. 2018; Morello et al. 2018). The eastern side of the study site was marked by a conspicuous rise that coincided with an abrupt transition to bare, rocky soil that was largely devoid of vegetation. Tuco-tucos were present in both saltgrass and surrounding rocky areas. The animals in saltgrass habitat, like members of the population of *C. opimus* at Pozuelos, were large-bodied, with light-colored pelage. Individuals in this habitat were regularly visible above ground while foraging on surface growing vegetation; while outside of their burrows, these animals were frequently heard emitting vocalizations that were composed of a series of whistle-like, broad-band sounds. In contrast, tuco-tucos in the surrounding, rocky habitat were smaller-bodied, darker in coloration, and were never observed on the surface. Vocalizations by these animals were clearly distinct from those produced by animals in saltgrass habitat, with the former consisting of a grunt-like series of two or three broad-band bursts produced underground. For the purposes of this study, only animals from saltgrass habitat were monitored, although tissue samples for genetic analyses were collected from individuals in both habitat types (see below).

Animal capture, marking.—Trapping of tuco-tucos was conducted from 8 to 25 December 2019. Animals in the focal saltgrass habitat were captured using tomahawk-style live traps baited with carrots and sweet potato. Traps were set at active burrow entrances, as identified based on direct visual observations of animals using a given entrance or by the presence of freshly excavated soil surrounding a burrow entrance. All trapping was conducted during daylight hours. Open traps were monitored continuously by researchers stationed around the periphery of the study site; captured animals were removed as soon as they were detected. Because these animals emerge multiple times per day to forage on the surface, observations of unmarked individuals (see below) were used to determine if further trapping was needed as well as where additional traps should be placed. Several animals were also captured in the adjacent rocky habitat. These individuals were caught by placing a plastic tube trap into the tunnel leading away from a recently plugged burrow entrance (Lacey et al. 1998; Amaya et al. 2021). Tube traps were checked every ca. 2 h and captured animals removed. Burrow entrances at which individuals were caught were then monitored for up to 12 h to detect potential evidence (e.g., plugging of the burrow entrance) of additional animals in the same burrow system. In both habitats, the location of each capture was recorded using a handheld GPS unit (accuracy ca. 6 m). Additionally, the locations of captures in saltgrass habitat were recorded using a grid system that was established on the focal study site at the start of data collection (see below).

All animals captured were permanently marked by inserting a PIT tag (Biomedic Data Systems, Seaforth, Delaware) beneath the skin at the nape of the neck. The sex and body weight of each individual were recorded; apparent age (juvenile or adult) was determined based on body weight and evidence of reproductive activity (O'Brien et al. 2020). For adult females, reproductive status (e.g., pregnant, lactating) was assessed via visual inspection of the external genitalia and palpation of the abdomen (Tassino and Passos 2010; O'Brien et al. 2020); because the testes of male tuco-tucos are never visible externally, the reproductive condition of these animals could not be determined based on the appearance of the genitalia. A nondestructive tissue sample was collected from each individual by removing the distal 1–2 mm of the outer digit of one hind foot (Lacey 2001; Cutrera et al. 2005); tissue samples were stored in ambient temperature EDTA–$DMSO_4$ buffer until analysis.

To allow visual identification of animals caught in saltgrass habitat, human hair dye (e.g., Manic Panic, Inc., New York City, New York) was used to give each individual a distinctive combination of colored patches of fur on the cheeks, head, and shoulders. In addition, each adult captured in saltgrass habitat was fitted with a radio collar (see below), such that these animals could be monitored both visually and telemetrically. Upon completion of these procedures, each animal was released at the burrow entrance where it had been captured. All procedures involving live animals were 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.—Prior to release, each adult captured in the focal saltgrass habitat was fitted with a radio collar (TXC-009C transmitters, Telenax Inc., Playa del Carmen, Mexico) weighing ca. 7 g, which represented <2% of an individual's body weight (Sikes et al. 2016; see Results section). After release, collared individuals were located using

an R1000 receiver (Communications Specialists, Orange, California) and handheld 3-element Yagi antenna (AVM Instrument Company, Colfax, California). Multiple localities per animal were recorded daily between 10 and 25 December (N = 14 days); fixes were typically taken between 0600 and 2000 h, with a minimum of 1 h between successive recordings (Lacey et al. 1997; Cutrera et al. 2006). To facilitate identification of subterranean nest sites and to explore daily variation in spatial relationships among members of the study population, radio fixes were collected hourly for 72 consecutive hours from 21 to 23 December 2019. For all fixes, the location of each individual was recorded to the nearest 0.5 m using a Cartesian coordinate system (10 m × 10 m cell size), the axes of which aligned with the east–west and north–south dimensions of the site. Analyses of data obtained for objects placed at known locations revealed this procedure to be accurate to within ca. 0.5 m (O'Brien et al. 2020; Amaya et al. 2021). Because animals were often active above ground during daylight hours, we began each round of data collection by visually scanning the study site from north to south and recording the locations of any individuals that were visible on the soil surface. The locations of the remaining animals were then determined via telemetry, with researchers following a standardized path to traverse the study site while searching for those individuals.

Comparative data from Pozuelos population.—To facilitate direct comparisons of spatial relationships among members of our focal study population at Antofagasta and the population of *C. opimus* at Pozuelos (−22.469347, −65.994279, WGS 84, elevation = 3,600 m), we reanalyzed telemetry data collected at the latter site between 24 December 2009 and 9 January 2010 (N = 17 days). These were a subset of the data used by O'Brien et al. (2020) to demonstrate that the population at Pozuelos is group living; to facilitate comparisons of the populations at Antofagasta and Pozuelos, we restricted our analyses to a portion of the Pozuelos site that was comparable in size to the area monitored at Antofagasta. Data from Pozuelos were collected following the same methods described above to capture, mark, and monitor individuals. In particular, the same scan sampling procedure was used to record the locations of radiocollared individuals at hourly intervals, again with an estimated accuracy of 0.5 m (O'Brien et al. 2020).

Analyses of space use.—For both study populations, home ranges were visualized using minimum convex polygons (MCPs), as generated by the adehabitatHR package in R (Calenge 2015). To confirm that our data were sufficient to yield robust estimates of individual home ranges, we first examined the relationship between the number of radio fixes obtained and home range size (O'Brien et al. 2020; Amaya et al. 2021). We then constructed a 95% MCP for each member of the study population monitored via telemetry using localities recorded throughout the ca. 2-week data collection period. To characterize spatial relationships among individuals, we generated pairwise estimates of percent overlap between 95% MCPs for different animals using adehabitatHR (Calenge 2015); because overlap between individuals may not have been symmetric, percent overlap was calculated from the perspective of each animal included in a pairwise comparison.

Patterns of space use at Antofagasta had not been characterized previously and thus we chose to explore several additional aspects of spatial relationships among members of this population. To identify potential short-term fluctuations in space use (Amaya et al. 2021), we examined daily variation in spatial relationships among members of this population. Using data obtained from 21 to 23 December (the days on which the most data points were collected), we generated a distinct 100% MCP per individual per 24 h of data collection; 100% MCPs were used for these analyses due to the limited number of data points collected per animal during each 24-h period. Based on these 100% MCPs, we then estimated percent daily change in home range size for each animal by calculating the difference in MCP size from one day to the next and dividing by the total area used over all 3 days of data collection. In addition, we estimated percent daily overlap of an animal with itself as well as percent daily overlap between different individuals; estimates of overlap between 100% MCPs were generated using the procedure described above for 95% MCPs.

To examine patterns of nest use by members of the Antofagasta population, we identified the putative nest site for each animal as the single most commonly used location for that individual (Lacey et al. 1997; O'Brien et al. 2020; Amaya et al. 2021). Because the exact dimensions of subterranean nests were not known, we employed a conservative measure in which all fixes falling within a 2.5-m radius of the most common x and y coordinates for an animal were counted as being in that individual's nest. We then compared the locations of putative nests for different individuals to determine if more than one adult used the same nest site.

Social network analyses.—To determine if members of the Antofagasta population occurred in spatially distinct groups, we used social network analyses (Wey et al. 2008; Krause et al. 2009) to evaluate patterns of spatial overlap among individuals. Given the limited number of adult males captured on the study site (see Results section), these analyses were performed for adult females only. Pairwise values for percent overlap between 95% MCPs were used to generate an association matrix that was then analyzed using SOCPROG (Whitehead 2009). The strength of the relationship between the association matrix and the spatial clusters of individuals identified was assessed using the cophenetic correlation coefficient, with a value of ≥0.8 interpreted as evidence of a strong correspondence between these data sets (Bridge 1993). Distinct hierarchical spatial clusters of females were identified using the maximum modularity criterion, with values >0.3 considered indicative of significant spatial clustering within the study population (Newman 2006; Whitehead 2008). Graphical depictions of the results of social network analyses were generated using the igraph package in R (Csardi and Nepusz 2006). The same procedures were used to identify distinct spatial clusters of females among the animals sampled at Pozuelos; although multiple males were present in the sample from this site, we focused social network analyses on females so as to be more directly comparable to analyses of spatial relationships at Antofagasta.

Genetic and phylogenetic analyses.—To determine if the animals at Antofagasta are part of the *opimus* clade of *Ctenomys*, we sequenced a portion of the mitochondrial cyt-b locus for four individuals from our study population: two animals were from rocky habitat and two were from saltgrass habitat. In addition, we sequenced the same portion of the cyt-b locus for two specimens from the population of *C. opimus* studied by O'Brien et al. (2020) at Pozuelos; these represent the first sequence data from the tuco-tucos at this locality and thus provide an essential comparison between our study animals and animals previously identified as *C. opimus*. Detailed information regarding the animals sequenced are given in Appendix I.

For all individuals sequenced, genomic DNA was obtained using a salt extraction procedure (Aljanabi and Martinez 1997). PCR amplification of an 801-bp region of the cyt-b locus was conducted using primers MVZ 05 and MVZ 16 (da Silva and Patton 1993) following the protocol in Cañón et al. (2010). PCR products were purified and then sequenced at the Unidad de Genómica del INTA Castelar in Buenos Aires, Argentina. All sequences generated as part of this study were deposited in GenBank (MZ540021–MZ540026). To include the other species in the *opimus* clade in our analyses and to place sequences from Antofagasta and Pozuelos into a larger phylogenetic context, we used GenBank to obtain cyt-b sequences for an additional 21 specimens of *Ctenomys* chosen to represent the range of currently recognized subclades within this genus (Parada et al. 2011). Also obtained were cyt-b sequences for two species (*Tympanoctomys barrerae*, *Octodon degus*) from the sister family Octodontidae that served as outgroups. GenBank accession numbers for all sequences examined are given in Appendix I.

Sequences were aligned using the default parameters in CLUSTAL X (Thompson et al. 1997), followed by visual inspection of the data for stop codons or reading frame shifts. To characterize haplotype variability within and among species, pairwise distances between sequences were calculated using the *p*-distance method in MEGAX (Kumar et al. 2018). Phylogenetic relationships among the taxa included in our data set were evaluated using maximum likelihood (ML) estimation. The best-fit model of molecular evolution for our data set was identified as (TrN+I+G) based on the Bayesian Information Criterion (BIC) generated by jModeltest2 (Darriba et al. 2012). ML analyses were conducted using IQ-TREE (Nguyen et al. 2015), as implemented on the IQ-TREE web server (Trifinopoulos et al. 2016); analyses were run using the best-fit model of molecular evolution with perturbation strength set to 0.5 and the number of unsuccessful iterations set to 100. Branch support was estimated via 1,000 replicates of ultrafast bootstrapping (BL); branches with bootstrap values >75% were considered well supported (Achmadi et al. 2013; Diez-Nieto et al. 2016).

Statistical analyses.—Statistical analyses were conducted using InfoStat (Di Renzo et al. 2016). Nonparametric tests were used unless the data indicated that parametric analyses were appropriate; *P*-values presented are two-tailed unless otherwise indicated. Throughout the text, means are reported ± 1 *SD*.

Results

Twelve adult tuco-tucos (two males, 10 females) were captured on the focal study site (saltgrass habitat) at Antofagasta, yielding an estimated density of 7.7 adults per hectare, with an adult sex ratio of one male to five females. Although several small individuals that were clearly juveniles were observed on the site, none of these animals were captured. No more than one adult was caught at a given burrow entrance. After being marked and released, each of the animals captured was observed above ground multiple times per day. In contrast, no unmarked adults were observed on the site after these 12 animals were released, suggesting that all adults in the focal study population had been captured. Mean body weight for the males captured was 485.0 ± 7.1 g (range = 480–490 g); for females, this value was 341.0 ± 24.4 g (range = 315–380 g). This difference in body weight between the sexes was significant (Mann–Whitney *U*-test: $U = 20$, $N = 2, 10$, $P = 0.030$). Four of the females captured were pregnant and three were lactating. The remaining three females did not display evidence of reproductive activity (Supplementary Data SD1).

Two females on the focal site at Antofagasta were captured near the end of the data collection period and thus were not fitted with radio collars. Home range boundaries for these individuals were estimated from visual observations of these animals. These data were used solely to place the uncollared animals within the larger spatial context of the study population (Fig. 1); home ranges for these individuals were not included in analyses of home range size or overlap. Although the limited number of visual data points obtained for other members of the study population precluded quantitative comparisons of home ranges estimated from visual versus telemetry data, similar comparisons for a subset of the animals at Pozuelos revealed no consistent differences in home range size based on type of data analyzed (O'Brien et al. 2020). Home range boundaries for the remaining 10 adults at Antofagasta were estimated from telemetry data. A mean of 131.2 ± 49.1 fixes per radiocollared individual (range = 32–177 fixes) was obtained over 10.2 ± 3.9 days of data collection (range = 3–14 days: Supplementary Data SD1). Analyses of home range size as a function of the number of radio fixes analyzed revealed that individual home range sizes stabilized after ca. 50 fixes, which represents approximately 35% of the total number of fixes obtained per individual (Supplementary Data SD2).

Characterization of individual home ranges.—When telemetry data collected over all 18 days of field work at Antofagasta were considered, the mean size of 95% MCPs for males (3,412.3 ± 3,816.6 m^2, $N = 2$) was greater than that for females (654.9 ± 257.9 m^2, $N = 8$). This difference was not significant (Mann–Whitney *U*-tests: $U = 13$, $P = 0.267$; Fig. 1), likely due to the marked difference in home range sizes for the two males monitored. The male with the smaller home range was captured on 23 December 2019, near the end of the study. The total number of fixes obtained for this individual ($N = 32$) was less than the ca. 50 fixes recommended by our preliminary analyses (Supplementary Data SD2) and considerably less than the number of fixes ($N = 171$) obtained for the other male

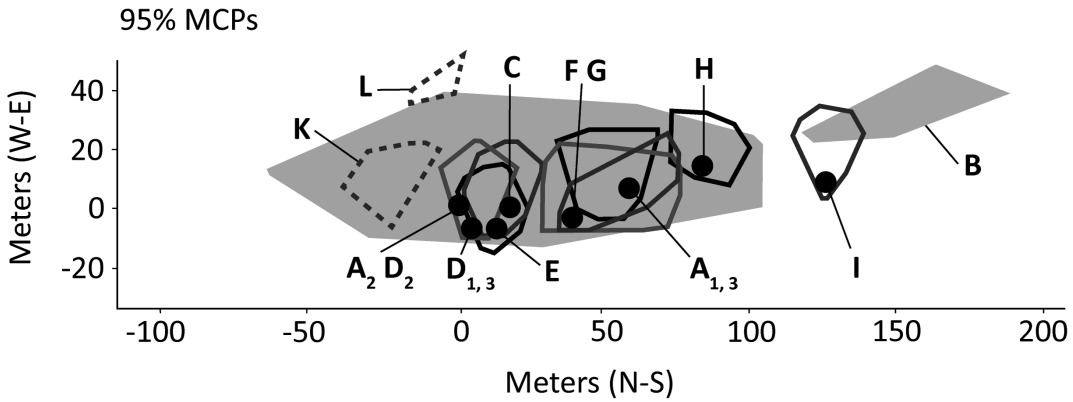

Fig. 1.—Home ranges for 12 adult (two male, 10 female) tuco-tucos from Antofagasta de la Sierra, Catamarca Province, Argentina. Home ranges are based on radiotelemetry data collected from 8 to 25 December 2019. Home ranges were calculated using 95% minimum convex polygons (MCPs). Filled polygons depict home ranges for males while unfilled polygons depict those for females. Letters correspond to individual animal IDs provided in Supplementary Data SD1–SD5. Black circles depict nest sites. For animals A and D, the nights during which each nest was used are indicated with numbers (nights 1, 2, and 3); no other animals used more than a single nest site during data collection. Polygons denoted by dotted lines indicate the approximate home ranges for two adult females captured too late to be monitored via telemetry; home ranges for these individuals were estimated from visual observations of these animals when they were active above ground.

monitored, suggesting that our analyses may have underestimated the size of the 95% MCP for the male captured late in the study.

Telemetry data for a subset of eight animals (one male, seven females) were also analyzed on a daily basis using fixes collected over 72 consecutive hours. Two radiocollared animals (one male, one female) were excluded from these analyses due to intermittent problems detecting their collars; these individuals were each characterized by <10 fixes per day. Comparisons of 100% MCPs generated on a daily basis revealed that the size of the area used by an animal varied somewhat across successive days, with this variation being greatest for the sole male included in these analyses (Supplementary Data SD3). Consistent with this, the mean percent change in daily home range size for the male was 29.3 ± 17.0%, which was greater than the mean values for six of the seven females monitored (Supplementary Data SD3). Although small sample sizes precluded formal statistical comparisons of these data, the mean percent change for the male did not fall outside of the 95% confidence interval (CI) for females (13.7%, 45.8%), suggesting that daily changes in home range size did not differ between the sexes. Based on comparisons of 100% MCPs, the mean percent daily overlap of the male with himself was 70.0 ± 37.6%, compared to mean values for females ranging from 53.2 ± 16.0% to 92.3 ± 7.7% (Supplemental Data SD3). The mean value for the male fell outside of the 95% CI for females (80.8%, 92.1%), suggesting that spatial overlap of an individual with itself was greater for females.

Spatial overlap among individuals.—Comparisons of 95% MCPs generated using data obtained over the entire 18-day data collection period at Antofagasta revealed overlap between the home ranges of 16 pairs of animals, including eight female–female and eight male–female pairs (Fig. 1). No overlap was detected between the two males monitored (Fig. 1; Supplementary Data SD4). Mean percent pairwise overlap did not differ between female–female (47.4 ± 29.2%) and male–female pairs (46.4 ± 42.9%: Mann–Whitney *U*-test: $U = 123$, $N = 8,8$, $P = 0.404$). When overlap was examined on a daily basis, the identities of overlapping individuals were generally consistent across days (Supplementary Data SD5). These analyses revealed six overlapping male–female pairs; five (83.3%) of these pairs overlapped spatially on all 3 days of data collection (Supplementary Data SD5). Of the seven overlapping female–female pairs detected, five (71.4%) displayed spatial overlap on all 3 days of data collection (Supplementary Data SD5).

Nest sites and nest sharing.—Each of the individuals (one male, seven females) at Antofagasta monitored via telemetry for 72 consecutive hours was characterized by a single most commonly used location that was identified as that animal's putative nest site. The mean percentage of fixes recorded at an individual's putative nest (37.7 ± 11.1%, range = 15.3–50.0% of fixes) was markedly greater than that for the animal's second most frequently used location (10.6 ± 5.3%, range = 5.6–19.4% of fixes), with a significant tendency for individuals to spend a greater percentage of fixes in their putative nest during the nighttime (75.6 ± 5.5%, range = 69.4–84.6% of fixes) versus the daytime (24.0 ± 5.1%, range = 15.4–30.6% of fixes: Wilcoxon signed rank test $Z = -2.53$, $N = 8$, $P = 0.01$). As a result, nest sharing was assessed based primarily on fixes collected at night. Although six (75%) of the eight animals monitored used a single nighttime nest location throughout the data collection period, the male and one female changed nest locations on the second night (Fig. 1); by the third night of data collection, both individuals had returned to the putative nest at which they were detected on the first night.

Comparing the locations favored by different members of the study population revealed that most individuals did not consistently share putative nest sites with other adults. During the nighttime, only two (28.6%) of the seven females monitored were detected together at the same nest site; these individuals shared the same apparent nest during all nights of data collection, co-occurring at this location for 10 (33.3%) of the 30 nighttime fixes recorded (Fig. 1). In contrast, these females

were found together in the nest during only three (7.1%) of the 42 daytime fixes recorded. Nest sharing was also detected for the male and one female on the second night of data collection (Fig. 1). These were the same two animals that changed nest locations from the first night to the second, ending up at the same location on the second night; these individuals were never detected together in a nest during the daytime. Overall, although four (50.0%) of the eight animals monitored shared a nest with another adult during at least one night of data collection, nest sharing was detected on only eight (33.3%) of the 24 nest-nights (number of individuals times number of nights) monitored.

Identification of spatial clusters of animals.—Analyses of the association matrix for overlap of individual home ranges (95% MCPs) revealed the occurrence of four spatially distinct clusters of females within the study population at Antofagasta (Fig. 2). The cophenetic correlation coefficient for these analyses was 1.00 and the maximum modularity was 0.67, providing evidence of both a strong correspondence between the association matrix and patterns of overlap among individual home ranges and the presence of spatially distinct sets of individuals. The mean number of females per cluster was 2.0 ± 1.6 (range = 1–3; Fig. 2). Within clusters, mean percent overlap of 95% MCPs for different females was 62.7 ± 13.0% (N = 6 females in two

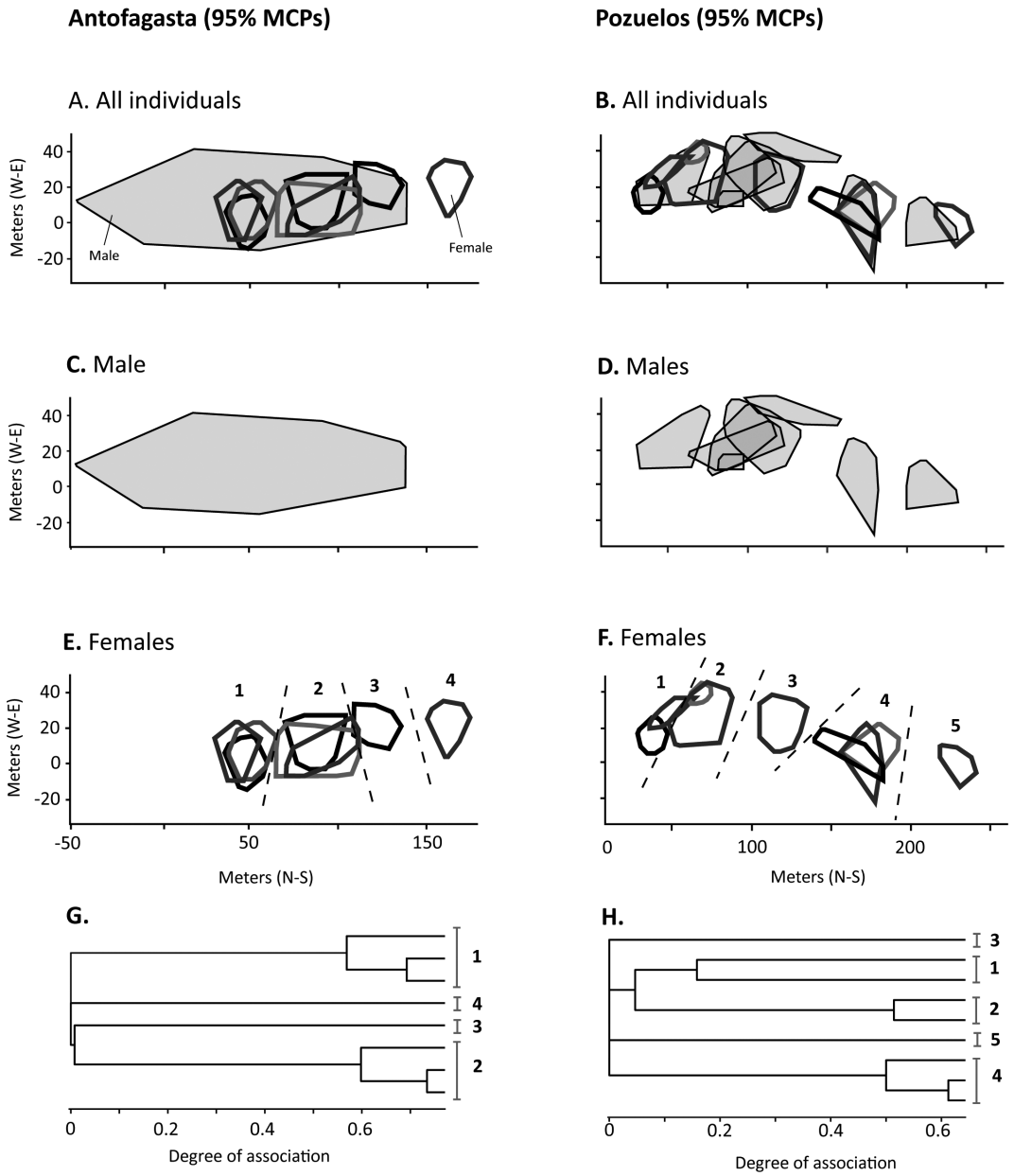

Fig. 2.—Comparisons of spatial and social relationships among tuco-tucos at Antofagasta and Pozuelos. For both populations, home ranges for all individuals sampled (95% minimum convex polygons [MCPs] generated from radiotelemetry data) are shown (A, B), as are home ranges for males only (C, D) and females only (E, F). Dendrograms identifying spatially distinct clusters of females are also shown (G, H); only data from females were analyzed due to the limited number of males in the Antofagasta population. For each population, distinct spatial clusters of individuals are identified with numbers (E, F); the same numbers are used to identify these clusters in the associated dendrograms (G, H).

clusters; Table 1); almost no overlap (1.2 ± 0.9%, N = 3 females) was detected among females belonging to different clusters. The male with the larger home range overlapped with clusters containing one, three and three females; the other male monitored overlapped with only a single adult female (Fig. 1). When visual estimates of home ranges for the two uncollared females were considered, these individuals did not appear to be spatially associated with other adult females although both uncollared animals overlapped with the male with the larger home range (Fig. 1).

Comparisons with Pozuelos population.—Radiotelemetry data were analyzed for a total of 17 adults (eight males, nine females) from the Pozuelos study population. Although the size of the area monitored was similar at both study sites, the density of adults was greater and the ratio of males to females was more equitable at Pozuelos than at Antofagasta (Table 1). Analyses of the association matrix for overlap of individual home ranges (95% MCPs) for the nine females followed at Pozuelos revealed four distinct clusters of animals (Table 1; Fig. 2). The mean number of females per cluster was 1.8 ± 0.8 (range = 1–3; Fig. 2). The mean percent overlap of 95% MCPs for females within the same cluster was 35.3 ± 28.6% (Table 1); although the small number of clusters per study site precluded statistical comparison, this value fell outside the 95% CI for within-group overlap at Antofagasta (50.0–75.4%; Table 1), suggesting that overlap among female cluster mates was less extensive at Pozuelos. While the sample of animals monitored via telemetry at Antofagasta included only a single male, the sample at Pozuelos included multiple males, four of whom displayed considerable spatial overlap (Fig. 2). As noted above, one male at Antofagasta overlapped spatially with three clusters of females. In contrast, at Pozuelos, no male overlapped with more than one cluster of females (Fig. 2).

Phylogenetic placement of study population.—At Antofagasta, both individuals captured in saltgrass habitat were characterized by the same cyt-b haplotype. Similarly, both individuals captured in the adjacent rocky habitat shared a single cyt-b haplotype, as did both individuals from Pozuelos that were sequenced as part of this study. The *p*-distance between animals from saltgrass versus rocky areas at Antofagasta was 5.6%, reflecting 49 sites that differed between the single haplotype detected in each habitat. In contrast, the *p*-distance between animals from saltgrass habitat and those at Pozuelos was 1.5% (12 sites that differed), while that between animals from rocky habitat and Pozuelos was 6.1% (49 sites that differed). ML analyses produced a single most likely tree (lnL = −3,523.662687) for the 29 mitochondrial cyt-b sequences examined (Fig. 3). This tree strongly supported (96% BL) the monophyly of the *opimus* clade and, within this species group, the monophyly (100% BL) of the two high-elevation Puna species (*C. opimus*, *C. fulvus*) relative to the two lower-elevation chaco species (*C. scagliai*, *C. saltarius*). Relationships between the two high-elevation species, however, remain unresolved, with sequences currently identified as *opimus* being paraphyletic with respect to those identified as *fulvus* (Fig. 3). Despite this taxonomic uncertainty, our analyses indicate that the focal study population at Antofagasta (saltgrass habitat) is part of the *opimus* clade, as is the population of tuco-tucos sampled at Pozuelos (Fig. 3). In contrast, the tuco-tucos from rocky habitat at Antofagasta are distinct and, based on the cyt-b sequences examined, appear to be part of the *mendocinus* species group within *Ctenomys*. This outcome is consistent analyses of haplotype differences in indicating that members of the focal, saltgrass population at Antofagasta are more closely related to the animals at Pozuelos than they are to the tuco-tucos in rocky habitat at Antofagasta.

Discussion

Our analyses revealed that the population of *Ctenomys* studied at Antofagasta de la Sierra was group living, with multiple adults sharing burrow systems and, in some cases, subterranean nest sites. Home ranges for the two adult males monitored each overlapped with the area(s) occupied by one or more adult females. Within the larger of these male home ranges, three spatially distinct clusters of adult females were identified. Within clusters, individuals did not consistently share subterranean nest sites, nor did they typically share nest sites with the associated male. Overlap among the females within a cluster occurred on a daily basis, as did overlap between the adult male and the females within his home range, suggesting that these spatial relationships were temporally persistent. Analyses of mitochondrial sequence data confirmed that these animals are part of the *opimus* clade of tuco-tucos, with only a 1.5% difference between cyt-b haplotypes for these animals and the group-living population of *C. opimus* at Pozuelos studied by O'Brien et al. (2020). This phylogenetic relationship, coupled with the

Table 1.—Comparisons of demographic attributes and results of social network analyses for populations of tuco-tucos at Antofagasta and Pozuelos.

	Antofagasta	Pozuelos
A. Demographic attributes		
Size of study area (ha)	1.5	2.0
# adults monitored via telemetry	12	17
Density (adults/ha)	7.7	8.5
Sex ratio (male:female)	1:5	1:1.1
B. Social network analyses		
Cophenetic correlation coefficient	1.00	0.99
Maximum modularity	0.67	0.63
# of distinct clusters of females	4	5
Mean (± *SD*) # of females per cluster (range)	2.0 ± 1.6 (1–3)	1.8 ± 0.8 (1–3)
Mean (± *SD*) % overlap within clusters	62.7 ± 13.0	35.3 ± 28.6

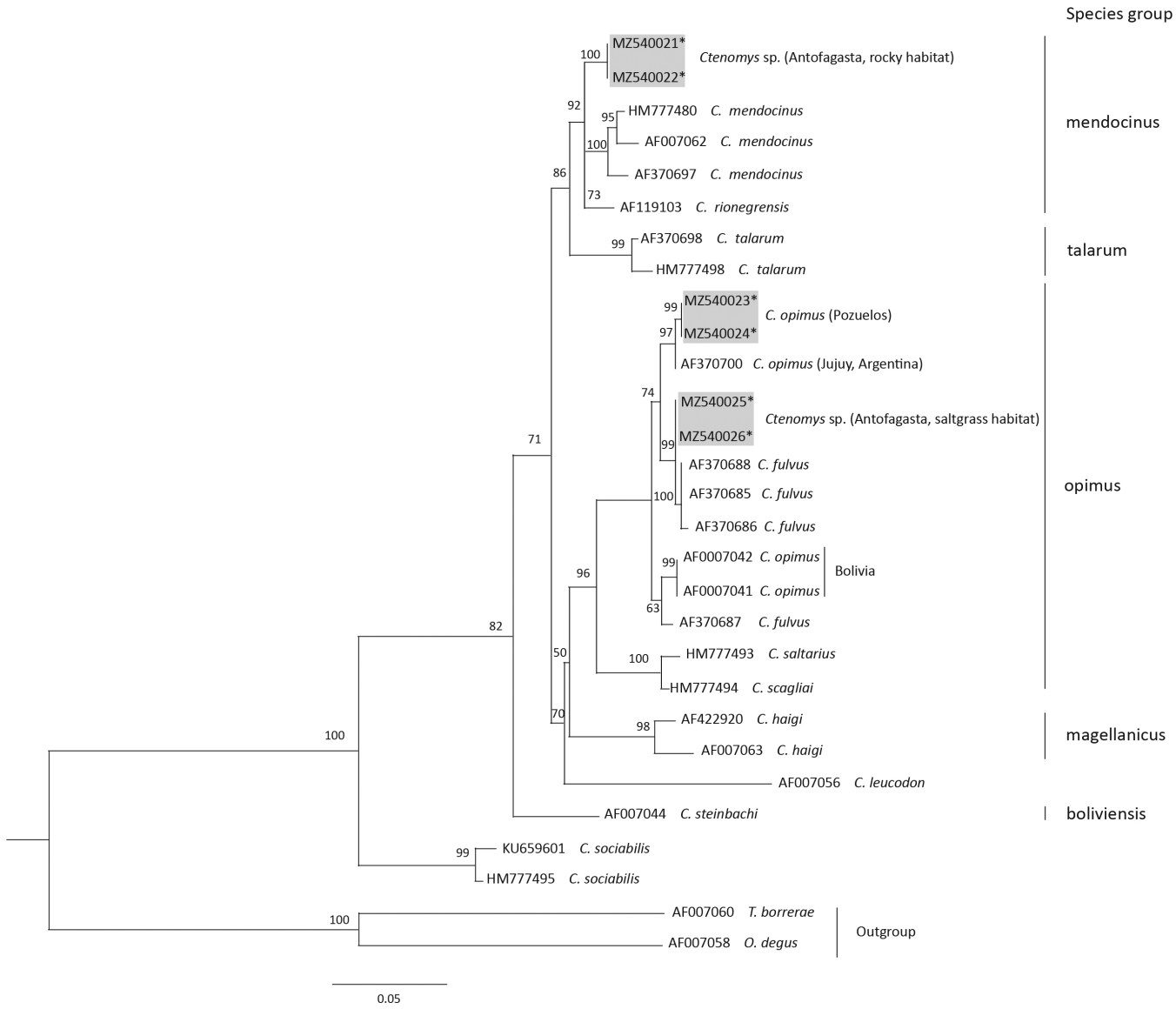

Fig. 3.—Phylogenetic consensus tree obtained from maximum likelihood analyses of 27 partial (801 bp) sequences from the mitochondrial cytochrome-b (cyt-b) locus in *Ctenomys*. Comparable cyt-b sequences from two species in the sister family Octodontidae were used as an outgroup. Gray boxes denote new sequences generated as part of this study. These include sequences for specimens from saltgrass and rocky habitats at Antofagasta de la Sierra, as well as animals from the population of *C. opimus* at Laguna de los Pozuelos studied by O'Brien et al. (2020). Numbers above nodes indicate bootstrap support values (BL); values > 75 are considered evidence of strong support (Achmadi et al. 2013). The GenBank accession number for each sequence is shown; locality data regarding each sequence are provided in Appendix I.

apparent behavioral differences between our study population and the population at Pozuelos (O'Brien et al. 2020), suggests that further comparative analyses of these animals should be informative regarding the factors associated with variation in social organization within the genus *Ctenomys*.

Group living among subterranean rodents is typically identified based on two aspects of spatial relationships among adults: sharing of burrow systems and sharing of nest sites (Lacey 2000). Populations of tuco-tucos previously identified as group living meet both of these criteria (*C. sociabilis*: Lacey et al. 1997; *C. opimus*: O'Brien et al. 2020). In contrast, our data indicate that although adults at Antofagasta share burrow systems, these animals do not consistently share nest sites. Thus, members of this population do not fully conform to both criteria standardly used to diagnose group living in subterranean species, raising the question as to whether this term should be applied to the animals at Antofagasta. From a functional perspective, a key distinction between group living versus solitary species is the opportunity for more frequent and, in some cases, qualitatively distinct social interactions that arises when conspecifics live together (Alexander 1974; Silk 2007; Kappeler 2019). Assuming that the pattern of burrow sharing reported here for animals at Antofagasta is a persistent feature of this population, we suggest that this behavior has the expected impact on the frequency

and, potentially, the nature of interactions among conspecifics. By comparison, opportunities for interactions among members of solitary subterranean species appear to be less common (Lacey et al. 1997; Cutrera et al. 2005) and may be limited primarily to seasonal reproductive contexts (Nevo 1979; Lacey 2000). For these reasons, we assert that the population of tuco-tucos at Antofagasta should be considered group living even in the absence of regular nest sharing by adults.

Behavioral variation within the opimus *clade.*—Currently, the *opimus* species group of tuco-tucos contains four named forms (Parada et al. 2011; Bidau 2015). No data regarding social organization are available for *C. saltarius* or *C. scagliai*, each of which is known from only a few locations in Salta and Tucuman Provinces in northwestern Argentina (Bidau 2015). Behavioral information regarding the other two species in this clade—*C. fulvus* and *C. opimus*—is limited to studies of a single population at Laguna de los Pozuelos in Jujuy Province, Argentina, that has been identified as *C. opimus* (O'Brien et al. 2020, 2021). The animals at Pozuelos are group living but, as revealed here, the spatial and social structure of this population differs from that at Antofagasta in several potentially important ways. In particular, while social groups at Antofagasta were strongly female biased in composition, groups at Pozuelos are regularly composed of multiple adults of both sexes (O'Brien et al. 2020, 2021). The maximum number of adults that overlapped spatially at Antofagasta was four; in contrast, larger clusters are common at Pozuelos, where up to 24 adults have been assigned to the same group (O'Brien et al. 2021). Conversely, although no truly lone animals were evident at Antofagasta, individuals that do not overlap spatially with conspecifics are a persistent feature of the population at Pozuelos (O'Brien et al. 2021). As already noted, sharing of nest sites was not common at Antofagasta; based on the data provided in O'Brien et al. (2020), members of the population at Pozuelos shared nests at approximately double the rate (53 of 70, or 75.7% of nest-nights) reported for Antofagasta. Collectively, these findings suggest that although the tuco-tucos at both Antofagasta and Pozuelos can be characterized as group living, these populations differ with regard to several key elements of social organization.

Behavioral differences between the animals at Antofagasta and Pozuelos may reflect multiple factors, including short-term responses to variable ecological and demographic conditions as well as longer-term, evolved differences in social organization. With regard to current conditions, differences in two key demographic parameters—population density and adult sex ratio—may have contributed to the observed differences in spatial relationships between animals at these localities. For example, the more female-biased sex ratio at Antofagasta may allow individual males to maintain exclusive access to a greater number of females, including females belonging to adjacent but distinct spatial clusters (Emlen and Oring 1977; Davies 1991). Concomitantly, the lower population density at Antofagasta may enable greater spatial separation of groups, as suggested by the lesser degree of overlap among members of different spatial clusters in this population versus at Pozuelos (O'Brien et al. 2020). If these differences in behavior are shaped by immediate demographic conditions, then we would expect spatial and social relationships in both populations to vary with short-term (e.g., annual) changes in sex ratio and population density, as has been reported for several other species of group-living rodents that occur in variable environments (Randall et al. 2005; Ebensperger et al. 2012; Schradin et al. 2012, Pinho et al. 2019). Although ecological factors (e.g., abundance and distribution of food resources) were not assessed as part of this study, short-term changes in these conditions may have similar effects with regard to spatial and social relationships and these interactions should be explored as part of future studies of the tuco-tucos at Antofagasta and Pozuelos.

Because our characterization of the population at Antofagasta is based on data collected over a limited time period, it is not known if the demographic attributes reported are typical of this locality. Data gathered at Pozuelos over five successive years indicate that the values for population density and adult sex ratio considered here are typical for this population, as is the occurrence of multi-male social groups (O'Brien et al. 2021). Clearly, longer-term studies are required to determine if the same is true for the population at Antofagasta and to evaluate the temporal persistence of the reported demographic differences between populations. Over time, consistent differences in demographic and ecological attributes may lead to the emergence of distinct selective pressures on spatial and social relationships at each locality (Kappeler et al. 2013; Schradin 2013); such selective differences may, in turn, contribute to different patterns of social organization at Antofagasta versus Pozuelos. Long-term monitoring of the demography, ecology, and behavior of each population combined with potential experimental manipulations of key demographic and ecological parameters should help to reveal the extent to which the differences in social organization described here reflect short-term responses to variable environmental conditions versus more enduring patterns that may arise due to differences in the selective pressures experienced by members of each population.

Comparisons with other ctenomyids.—Within *Ctenomys*—as in other lineages of subterranean rodents—group living is thought to be relatively rare (Nevo 1979; Lacey 2000). Radiotelemetry studies have confirmed that multiple species of tuco-tucos are solitary, meaning that each adult occupies its own burrow system and subterranean nest (e.g., *C. haigi*: Lacey et al. 1998; *C. talarum*: Cutrera et al. 2005; *C. australis*: Cutrera et al. 2010; *C. minutus*: Kubiak et al. 2017). This includes two species (*C. rionegrensis*: Tassino et al. 2011; *C.* sp. from Anillaco, Argentina: Amaya et al. 2021) in which brief but regular overlap of adults has been detected, although individuals do not share burrow systems or nests. In contrast, only *C. sociabilis* (Lacey et al. 1997) and the population of *C. opimus* at Pozuelos (O'Brien et al. 2020, 2021) have been shown to be group living. *Ctenomys sociabilis* is similar to the animals at Antofagasta in that (i) groups are composed of multiple adult females but only a single adult male and (ii) the adult sex ratio is strongly female biased (Lacey and Wieczorek 2004). The social organizations of the two taxa differ, however, in that individual male *C. sociabilis* are never associated with more than one spatially distinct cluster of females, even when population

density reaches values comparable to that at Pozuelos (Lacey et al. 2019). Thus, while both *C. sociabilis* and the population at Antofagasta are characterized by female-biased groups, they display marked differences in spatial relationships that may have implications for understanding how ecological and demographic factors interact to favor group living in each species.

Although no complete phylogeny has been constructed for *Ctenomys*, available analyses are consistent with our data in suggesting that *C. sociabilis* is basal to other members of this genus and is not closely associated with the *opimus* species group (Parada et al. 2011; Gardner et al. 2014; Sanchez et al. 2019). As a result, it seems likely that group living in *C. sociabilis* has arisen independently from that in members of the *opimus* clade, such that comparative studies can be used to identify general factors favoring group living in both of these lineages (Harvey and Pagel 1991; Miles and Dunham 1993; Stayton 2015). In contrast, because the animals at Antofagasta and Pozuelos are more closely related, behavioral differences between these populations are better suited to evaluating the environmental factors contributing to divergence in social organization (Miles and Dunham 1993; Martins 1994). Our analyses of spatial and social relationships within the population of tuco-tucos at Antofagasta and our comparisons of this population with that at Pozuelos provide the first phylogenetically informed effort to evaluate interactions among ecology, demography, and social organization in tuco-tucos. Future studies will build upon these comparisons to generate a more comprehensive assessment of the causes of variation in social behavior among members of the *opimus* clade and, more generally, the genus *Ctenomys*.

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Supplementary Data

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

Supplementary Data SD1.—Summary of spatial data obtained for 10 (two male, eight females) adult tuco-tucos monitored via radiotelemetry at Antofagasta de la Sierra during 8–25 December 2019. The sex, reproductive status, and body weight for each animal monitored are given, as are the number days of monitored, the number of radio fixes recorded, and the associated home range size. Home range size was estimated based on 95% minimum convex polygons (MCPs) constructed from all radio fixes collected per individual. Additionally, reproductive status and body weight are shown for two females (K, L) captured on the study site for which telemetry data were not obtained. Letters correspond to the animal IDs used in Fig. 1 and Supplementary Data SD2–SD5.

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 two adult male (A and B) and eight adult female tuco-tucos from Antofagasta de la Sierra. Home ranges were estimated using 95% minimum convex polygons (MCPs). The x-axis depicts the percentage of the total number of fixes per individual used to construct each MCP. The y-axis depicts home range size, as determined from 95% MCPs generated in the adehabitatHR package in R (Calenge 2015). The inflection point for each graph indicates the percentage of the total number of fixes required to obtain a robust estimate of home range size. Letters correspond to the animal IDs used in Fig. 1 and Supplementary Data SD1 and SD3–SD5.

Supplementary Data SD3.—Daily home range sizes and percentage of home range overlap on successive days for eight adult (one male, seven females) tuco-tucos from Antofagasta de la Sierra that were monitored from 21 to 23 December 2019. Home ranges were calculated using 100% minimum convex polygons (MCPs); daily samples size (number of radio fixes) was 24 fixes per individual. Letters correspond to the animal IDs used in Fig. 1 and Supplementary Data SD1, SD2, SD4, and SD5.

Supplementary Data SD4.—Percent overlap of home ranges for pairs of adult tuco-tucos monitored at Antofagasta de la Sierra. Overlapping home ranges were identified based on 95% minimum convex polygons (MCPs) generated from all radio fixes obtained per animal. Data for both male–female and female–female pairs are shown. Because the overlap between pairs of individuals was not symmetric, estimates of percent overlap were calculated from the perspective of each member of a pair; the resulting mean ± 1 *SD* percent overlap is shown for each pair. Letters correspond to the animal IDs used in Fig. 1 and Supplementary Data SD1–SD3 and SD5.

Supplementary Data SD5.—Percent overlap of daily home ranges for pairs of adult tuco-tucos monitored at Antofagasta de la Sierra. Individuals with overlapping home ranges were identified based on 100% minimum convex polygons (MCPs) generated using radio fixes obtained during hourly monitoring conducted for 72 consecutive hours during 21 to 23 December 2019. Data for both male–female and female–female pairs are shown. Because the overlap between pairs of individuals was not symmetric, estimates of percent overlap were calculated from the perspective of each member of a pair; the resulting mean ± 1 *SD* percent overlap is shown for each pair. Letters correspond to the animal IDs used in Fig. 1 and Supplementary Data SD1–SD4.

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Appendix I

List of mitochondrial cytochrome-b sequences included in analyses of the phylogenetic placement of tuco-tucos (*Ctenomys* sp.) captured at Antofagasta de la Sierra, Catamarca Province, Argentina. Sequences are organized by current taxonomic identity. For each sequence, the collection locality and GenBank accession number are given.

Sequences generated during this study:		
Taxon	Locality	GenBank accession #
Ctenomys 1 (rocky habitat)	ARGENTINA	
	Catamarca Province	MZ540021
	Antofagasta de la Sierra (−26.09627, −67.39727, 3,323 msl)	MZ540022
Ctenomys 2 (saltgrass habitat)	ARGENTINA	
	Catamarca Province	MZ540025
	Antofagasta de la Sierra (−26.09627, −67.39727, 3,323 msl)	MZ540026
Ctenomys opimus	ARGENTINA	
	Jujuy Province	MZ540023
	Laguna de los Pozuelos (−22.46943, −65.99456, 3,600 msl)	MZ540024
Sequences obtained from GenBank:		
Taxon	Locality	GenBank accession #
Ctenomys		
australis	ARGENTINA	
	Buenos Aires Province, Necochea	AF370697
fulvus	CHILE	
	Salar de Atacama, Antofagasta	AF370685
	Vegas de Turi, Antofagasta	AF370686, AF370687
	San Pedro de Atacama, El Loa	AF370688
haigi	ARGENTINA	
	Neuquen Province, Nahuel Huapi	AF370697
	Neuquen Province, Bariloche	AF007063
leucodon	BOLIVIA	
	San Andrés de Machaca	AF007056
mendocinus	ARGENTINA	
	Mendoza Province, Cerro de la Gloria	HM777480
	Mendoza Province, Las Heras	AF007062
opimus	ARGENTINA	
	Jujuy Province, Tres Cruces	AF370700
	BOLIVIA	
	Oruro, Huancaroma	AF007041, AF007042
rionegrensis	URUGUAY	
	Las Cañas	AF119103
saltarius	ARGENTINA	
	Salta Province, Tolombón	HM777493
scagliai	ARGENTINA	
	Tucumán Province, Valle del Tafí	HM777494
sociabilis	ARGENTINA	
	Neuquén Province, Nahuel Huapi	HM777495
	Chubut Province, Nahuelquir	KU659601
steinbachi	BOLIVIA	
	Buen Retiro	AF007044
talarum	ARGENTINA	
	Buenos Aires Province, Buenos Aires	AF370698
	Buenos Aires Province, Saladillo	HM777498
Octodon		
degus	CHILE	AF007058
Tympanoctomys		
barrerae	ARGENTINA	AF007060