Sociality of *Octodontomys gliroides* and other octodontid rodents reflects the influence of phylogeny

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Multiple ecological factors are known to drive variation in social behavior. However, group-living in some species appears to be highly conserved, suggesting a phylogenetic influence. In this study, we evaluated both scenarios using intraspecific and interspecific comparisons across octodontid rodents. We first examined 2 different populations of Andean degu (*Octodontomys gliroides*), representing 2 extremes of a climate vegetation gradient across the Andes range. We evaluated how ecological variation in terms of abundance and distribution of food resources, predation risk, and burrowing costs predicted interpopulation variation in group size and range-area overlap (2 proxies of sociality). We estimated these measures of sociality from livetrapping and radiotelemetry. We then used phylogenetic methods to determine whether sociality exhibits a phylogenetic signal and reconstructed the ancestral state of sociality across the family Octodontidae. Overall activity of females and males of *O. gliroides* was greater during nighttime than daytime. Across populations we found significant differences in ecology, including abundance and distribution of food, predation risk, and burrowing costs. However, populations were similar in terms of group size and range-area overlap. The phylogenetic approach revealed a strong and significant phylogenetic signal associated with sociality, where this behavior was present early during the evolution of octodontid rodents. Together, these findings imply that sociality of *O. gliroides* is not linked to current population differences in ecology.

Key words: ecological factors, group-living, group size, Octodontidae, *Octodontomys gliroides*, phylogenetic signal, range-area overlap

Intraspecific variation in the number and composition of group members characterizes not only socially flexible, but also socially cohesive groups in vertebrates (Lott 1991; Maher and Burger 2011; Schradin et al. 2012). Within and between population differences in sociality are generally consistent with differences driven by variation in ecological conditions (e.g., weather, predation pressure, density, nest site availability, and quality, quantity, or distribution of food—Lott 1991), which in turn determine several fitness benefits and costs associated with an individual's decision to join or leave groups (Ebensperger 2001; Krause and Ruxton 2002; but see Schradin [2013] for alternative explanations for this variation).

The hypothesis that differences in vertebrate sociality are driven by ecological conditions is supported by species comparisons in a phylogenetic context. For instance, exposure to predation has been a driver of colonial nesting (Rolland et al. 1998), and bird flocking (or social foraging) seems linked to the use of clumped food items (Beauchamp 2002). In mammals, the importance of ecological conditions is suggested in ungulates and dolphins where group size is associated with differences in predation risk as measured from habitat openness (Brashares et al. 2000; Gygax 2002; Caro et al. 2004). In primates, both food availability (and its effect on within-group competition) and predation risk are connected to group size

(Janson and Goldsmith 1995; Majolo et al. 2008). Thus, evidence supports the idea that ecological conditions play an important role in driving bird and mammal sociality.

Other comparative studies indicate additional factors might be relevant, including ancestor–descendant relationships. Under this scenario, the social trait in contemporary populations may have been inherited from ancestral forms and then remained invariant despite potential ecological differences between environments of ancestral and extant forms (i.e., "phylogenetic inertia"). In support of this hypothesis, Linklater (2000) found that social and spatial organization in feral horses (family Equidae) was invariant despite different environmental and demographic contexts in which these animals live. Similarly, species variation in social organization (based on asymmetry of social interactions) in macaques (Thierry et al. 2000) and sociality in cavies (Rowe and Honeycutt 2002) are predicted by phylogeny. Moreover, the observation that sociality is the most likely ancestral state in several bird families implies this trait may be more closely associated with past than current ecological conditions in some lineages (Arnold and Owens 1998, 1999; Covas and Griesser 2007). Taken together, the extent to which population variation in sociality of extant species reflects current differences in ecological conditions or the legacy of ancestral forms remains far from clear.

In this study we combine species and population comparisons, 2 complementary approaches, to infer the relative importance of current ecological conditions and ancestor–descendant relationships on the microevolutionary history of an octodontid rodent and its closest relatives. New World hystricognath (or caviomorph) rodents are appropriate model organisms to this end (Ebensperger 1998, 2001; Lacey and Sherman 2007; Maher and Burger 2011). Caviomorph rodents exhibit within- and across-population differences in social behavior and ecology (Lacey and Ebensperger 2007; Maher and Burger 2011; Ebensperger et al. 2012). Across species, ecological factors (predation risk and distribution of critical resources) have been supported to drive caviomorph sociality (Ebensperger and Blumstein 2006). However, other comparative studies across cavioids (i.e., a lineage of caviomorphs that includes cavies, maras, agoutis, and capybaras) did not support the hypothesis that the use of patchy and risky habitat conditions promotes greater sociality (Rowe and Honeycutt 2002). Thus, sociality across cavioids would have been inherited from an already social ancestor, implying a strong influence of phylogeny (Rowe and Honeycutt 2002; but see Trillmich et al. 2004).

Within caviomorphs, the social behavior of the Andean degu (*Octodontomys gliroides*) remains scarcely known, yet this knowledge is critical to determine the extent to which social behavior in octodontids (degus, cururos, and viscacha rats) is linked to current ecological conditions (Ebensperger et al. 2008). According to phylogenetic reconstructions (Honeycutt et al. 2003; Gallardo et al. 2004; Opazo 2005; Rowe et al. 2010), *O. gliroides* is basal to the clade composed of more-social octodontids, that is, the Chilean clade (Ebensperger et al. 2004; Gallardo et al. 2007; Lacey and Ebensperger 2007). Solitary-living in *O. gliroides* would imply that sociality in octodontids is a relatively recent trait and more likely to be more associated with current habitat conditions. In contrast, group-living in *O. gliroides* would support that sociality in octodontids evolved relatively early in this lineage and is less likely to be associated with current ecological conditions. Studies based on social and ecological variation across populations of octodontids are consistent with a role of ecological conditions as predictors of social differences. Group size in degus (*Octodon degus*) is larger in populations and years with more abundant predators, lower density of burrow openings (i.e., refuges), and in groups whose burrows are far from overhead cover, observations that support an influence of predation risk (Ebensperger et al. 2012). Subterranean cururos (*Spalacopus cyanus*) are more social in mesic montane habitats than at arid coastal sites, a finding consistent with the importance of habitat conditions (Lacey and Sherman 2007). Thus, different ecological factors have been associated with population differences in sociality of octodontids.

The influence of ecological conditions on sociality of *O. gliroides* is not well known. However, the habitat of these animals suggests differences in social behavior. *O. gliroides* inhabits relatively open habitats that include patches of shrubs, cacti, and rocks (Mann 1978). Therein, these rodents burrow in patches of columnar and ground-level cacti or shrubs where they feed on vegetation, hide from terrestrial and aerial predators, and rear offspring (Rivera 2013). Interestingly, *O. gliroides* is found on both sides of the Andes (i.e., northern Chile and Bolivia–northern Argentina), a distribution marked by an east to west gradient of decreasing precipitation that results in east and west (from the Andes) populations with contrasting differences in the abundance and patchiness of vegetation cover (Sala and Aguiar 1996; Aguiar and Sala 1999). Differences in abundance and patchiness of vegetation cover may translate into differences in critical resources (e.g., food and shelter), which in turn contribute to differences in sociality. Thus, greater sociality is expected in populations with patchily distributed resources (food, shelter) where these resources can be monopolized compared to populations where food resources are uniformly distributed (Travis and Slobodchikoff 1993; Travis et al. 1995). Greater sociality also is expected in habitats with relatively low shrub cover, longer distance to the nearest refuge, and low density of burrow openings, all conditions that increase predation risk (Vásquez et al. 2002; Ebensperger and Hurtado 2005; Hayes et al. 2007; Taraborelli 2009; Ebensperger et al. 2012). Greater sociality is expected in populations experiencing harder soils due to costs of digging and burrowing (Ebensperger and Bozinovic 2000; Ebensperger et al. 2012).

In the current study, we examined 2 populations of *O. gliroides* representing 2 extremes of an east to west climate–vegetation gradient to determine how differences in ecological conditions (food, shelter, and soil conditions) translate into differences in sociality. If current ecological conditions linked to food and refuge against predators drive group-living

variation, we predicted greater sociality in populations of *O. gliroides* where plant cover, food, and shelter are more patchily distributed. Greater sociality in the population with harder soil conditions would support the hypothesis that burrowing costs are relevant to Andean degu sociality. In contrast, an absence of differences in sociality in spite of ecological variation would indicate that sociality is not a response to current ecological conditions.

MATERIALS AND METHODS

Interspecific comparisons.—We used the available literature to collect information on sociality of extant species of octodontids. Maximum-likelihood reconstruction of ancestral states of sociality was undertaken using topology as well as branch lengths obtained from Bayesian analyses of 2 nuclear DNA markers (Opazo 2005). These data allowed us to associate the origin of group-living with an estimated time of the molecular clock in which the character appeared. To detect the direction of change in sociality, species were categorized as being either group-living (1) or not (0). The ancestral state of each node was estimated by maximum likelihood in the program Mesquite version 2.75 (Maddison and Maddison 2011). A likelihood-ratio test was previously performed to compare the goodness of fit of a 2-parameter model (allowing unequal forward and backward transitions rates) with a 1-parameter model (allowing equal forward and backward rates—Pagel 1999). The 1-parameter model was selected because it did not lead to a significant reduction in likelihood. Phylogenetic signal in group-living was estimated using the ancestor-states method of Maddison and Slatkin (1991) implemented in the program Mesquite version 2.75 (Maddison and Maddison 2011). The number of evolutionary transitions in sociality was estimated using maximum parsimony. The observed number of transitions in sociality was compared with a null distribution using 10,000 permutations. A *P*-value was calculated as the percentage of values of the null distribution that were less than or equal to the observed percentage. If group-living evolves fewer times than expected at random, then we can conclude that the trait has evolved sufficiently slowly to retain phylogenetic information and thus has been influenced by ancestor–descendant relationships.

Study populations of Octodontomys gliroides.—We examined 2 Andean degu populations located 400 km apart in 2 habitats with extreme differences in ecology. The Oploca population (hereafter Eastern population) was located in southwestern Bolivia (21°20′S, 65°50′W; 3,121 m above sea level); the Chusmiza population (hereafter Western population) was located in the high Andean plateau of northern Chile (19°40′S, 69°10′W; 3,460 m above sea level). The Eastern population is characterized by dry climate with rainfall ranging from 200 to 650 mm; most rain falls during summer (November–February), and mean temperature ranges from 14°C to 19°C (López 2003; Servicio Nacional de Meteorología e Hidrología 2012). The study area of this population included

xerophytic vegetation, where the succulents *Trichocereus tacaquirensis*, *Oreocereus celsianus*, and *Opuntia boliviensis*, and the thorn scrubs *Acacia feddeana*, *Cercidium andicola*, and *Prosopis ferox* were the most common species (López 2000; Ibisch et al. 2003; López et al. 2010). In contrast, the climate of the Western population is more arid than that of the Eastern population, with a mean annual precipitation of 101 mm (Ministerio de Obras Públicas 2012) that concentrates during austral summer (January–March; invierno boliviano—Garreaud et al. 2009). Mean ambient temperature of Western population ranged from −0.2°C to 6.8°C (Ministerio de Obras Públicas 2012), and vegetation was dominated by small bushes and cacti, including *Atriplex* sp., *Baccharis boliviensis*, *Senna birostris*, *Lophopappus tarapacanus*, *Corryocactus brevistylus*, *Oreocereus leucotrichus*, *Trichocereus atacamensis*, *Opuntia soehrensii*, and *Opuntia camachoi* (Philippi 1941; Villagrán et al. 1999; Moreira-Muñoz 2011).

Ecological differences at the level of populations.—At the level of population, availability of food resources was estimated based on abundance of ground-level cacti biomass. We previously determined that *O. gliroides* feeds principally on ground-level cacti in the Western population but on cacti and shrubs (*P. ferox*) in the Eastern population (Villanueva 2014). One 100-m transect was established randomly in each study population. Then, each transect was divided into ten 10 × 2-m plots. Within each plot we used 0.25-m² quadrats to quantify the abundance of cacti leaves. From each 0.25-m² quadrat we randomly removed 5 leaves, stored them inside paper bags, and transported them to the laboratory. All cacti leaf samples were oven-dried at 60°C for 10 consecutive days to determine dry mass (biomass in grams).

A 2nd measure of food availability was vegetation cover (Reus et al. 2013). We estimated vegetation cover based on ground-level cacti, columnar cacti, and shrubs. To do so, we established fifteen 50 × 2-m randomly located transects at each population. Vegetation cover was recorded every 10 m using the line point intercept method (Bonham 1989). Percent cover was calculated as the number of hits for each plant species or ground cover class divided by the total number of points per transect.

We used Poisson variance to mean ratios of distance between patches with ground-level cacti, columnar cacti, and shrubs to estimate the distribution of resources within each population. To do this, all patches in the total area (11 ha) were georeferenced in each population. We then divided the variance of distance between patches by its mean. Values < 1 indicated a relatively uniform distribution; values > 1 were taken to represent a relatively clumped distribution (Travis and Slobodchikoff 1993; Krebs 1999).

At the level of population, predation risk was recorded first from the active burrow entrances at each burrow system. Active burrow entrances were identified from the presence of fresh droppings, urine marks, signs of recent soil digging, or remains of recently consumed cacti leaves. Number of active burrow entrances per square meter at each burrow system was calculated as the number of active burrow openings divided by

the area covered by the burrow system (hereafter density of burrow openings—Ebensperger and Wallem 2002; Ebensperger and Hurtado 2005). A 2nd measure of predation risk was distance (m) from each burrow system to the nearest shrub or a cactus (distance to cover). Finally, predation risk was recorded from vegetation overhead cover, as suggested by previous studies (Hill and Dunbar 1998; Jensen et al. 2003; Ebensperger and Hurtado 2005). Vegetation overhead cover was estimated from the same transects used to estimate food availability. However, ground-level cacti at the Western population were too small to provide *O. gliroides* with hiding places and were excluded from these estimates. Instead, ground-level cacti at the Eastern population were large enough to provide coverage against predators and were part of these estimates.

We estimated soil penetrability as an index of soil hardness and, therefore, energy costs associated with building burrows (Lacey and Wieczorek 2003; Ebensperger et al. 2012). At the level of the population we established 15 randomly located transects (50 × 2 m). Soil penetrability was recorded twice every 10 m using a handheld soil penetrometer (Lang Penetrometer Inc., Gulf Shores, Alabama).

Trapping and marking of animals.—The study was conducted in both populations during the spring–summer transition (i.e., before the rainy season), which is part of the breeding season (Anderson 1997; Díaz and Barquez 2007). Thus, the Eastern population was examined during October through December 2011, and the Western population during November 2012 through January 2013. We trapped *Octodontomys* using a combination of Tomahawk (model 201, dimensions: 41 × 14 × 14 cm; Tomahawk Live Trap Co., Hazelhurst, Wisconsin) and locally produced medium- and large-sized Sherman traps (23 × 9 × 8 cm and 38 × 12 × 11 cm, respectively) all baited with a mixture of tuna's fruit (*Opuntia ficus-indica*) and grated apple. We set traps at previously identified burrow systems. Occupancy of burrows was established based on the presence of tracks, "paths," fresh droppings, or fresh traces of consumption of cacti leaves or seedpods in the vicinity of burrows. We placed a total of 220 traps in the Eastern population and 160 traps in the Western population. The total area examined in both populations was similar and reached 11 ha. A similar combination of Sherman and Tomahawk traps was used in each burrow system. The number of traps used per day at each burrow system averaged 8 ± 0.2 for the Eastern population, and 6 ± 0.0 for the Western population. The total number of burrow systems trapped was 45 and 40 in the Eastern and Western populations, respectively. These burrows were found primarily at the base of shrubs, columnar cacti, and ground-level cacti in the Eastern population, but they were associated only with columnar cacti in the Western population.

We first trapped *O. gliroides* during 26 consecutive days in the Eastern population and 18 consecutive days in the Western population. Traps were opened during most daylight hours and were checked approximately every 2 h. Traps were closed from 1100 h until 1630 h to prevent deaths through overheating. The sex, body mass, and reproductive condition (e.g., whether females were perforated, pregnant, or lactating and males had descended testes) were recorded for all animals captured. Upon 1st capture, individuals were given a unique identification with the use of metal ear tags coded with numbers (National Band and Tag Co., Newport, Kentucky). In addition, a small sample of ear tissue was taken from first-caught subjects for subsequent genetic analyses. To characterize spatial relationships among individuals, all adult-sized subjects (≥ 140 g) caught during this trapping period were fitted with 6-7 g radiocollars (AVM Instrument Co., Colfax, California). Mass of radiocollars represented 4–5% of study subjects' body mass. At the end of data collection (see below) all radiocollared animals were recaptured and transmitters were removed.

All procedures that involved handling of animal subjects followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and adhered to Bolivian and Chilean laws (permit MMAyA-VMA-DGBAP N 0937/11 by the Dirección General de Biodiversidad y Áreas Protegidas and permit 1-62-2012 [2373] by the Servicio Agrícola y Ganadero). All procedures were approved by the Faculty of Biological Sciences at Pontificia Universidad Católica de Chile (CBB-040-2011).

Temporal activity and range areas.—The Andean degu has been presumed to be active at night by some researchers (Ipinza et al. 1971; Nowak 1999; Pedreros and Valenzuela 2009) but diurnally active by other authorities (Mann 1978). Therefore, we first examined patterns of temporal activity to resolve this discrepancy. We used the homing technique (Kenward 2001) to follow all radiocollared animals with the use of LA 12-Q receivers and handheld, 3-element yagi antennas (tuned to 150.000–151.999 MHz; AVM Instrument Co.). In particular, 2 observers, each holding a receiver and an antenna, tracked all radiocollared animals every 2 h during nighttime and daytime. Once located, the position of each animal was marked with coded flags. Each fixing location was then georeferenced with a Garmin portable global positioning system unit (Garmin International Inc., Olathe, Kansas). The rugged microtopography of both study populations caused frequent signal bounce and precluded the use of long-range radiofixes (i.e., triangulation—Kenward 2001). To prevent observers affecting the movements of animals and disrupting their behavior, each observer was trained to avoid stepping loudly when near each radiocollared subject and to leave swiftly once its location was confirmed. Daily patterns of activity were then characterized from variation in inactivity during night and day in both populations.

Population differences in sociality.—The main criterion used to assign Andean degus to social groups was the sharing of resting locations (i.e., putative nest places—Ebensperger et al. 2004). Given that *O. gliroides* concentrated its activity mostly during nighttime (see "Results"), we established the sharing of burrow systems by means of daytime telemetry. During a total of 10 days we determined resting locations at burrow systems 3 times per day: in the morning (0930–1130 h), afternoon (1230–1430 h), and before sunset (1530–1730 h). This effort adequately determined group membership in other
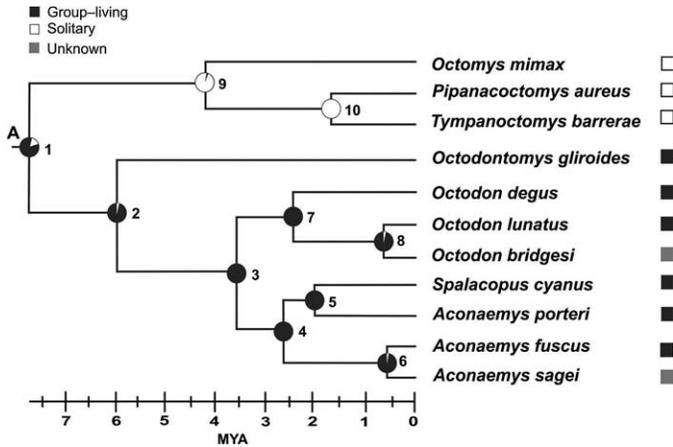
FIG. 1.—Reconstruction of the ancestral state of group-living of current octodontid rodents based on the topology and branch lengths proposed by Opazo (2005). Circles next to tips of the phylogeny indicate group-living (black), solitary (white), and unknown data (gray). The pie chart in the nodes of phylogeny shows the proportional likelihood of each state estimated. For nodes 8 and 6, we recalculated the probability that these nodes were group-living. To do so, we considered the alternative options that *Octodon bridgesi* and *Aconaemys sagei* (2 unknown tips) were solitary (0) and group-living (1). The calculated probabilities represent averages between these alternatives (for node 8: 0 = 0.087 and 1 = 0.913; for node 6: 0 = 0.086 and 1 = 0.914). The letter A indicates the calibration point (7.79 million years ago—Opazo 2005). Data on group-living of extant species of octodontids were obtained from Reise and Gallardo (1989), Mares et al. (1997), Begall and Gallardo (2000), Ebensperger et al. (2008), Hayes et al. (2009), Rivera (2013), Frugone (2012), and Sobrero et al. (2014).

octodontid rodents (Ebensperger et al. 2004). Determination of group composition required compilation of a symmetrical similarity matrix of pairwise associations of the burrow locations of all adult Andean degus during daytime telemetry (Whitehead 2008). We determined the association (overlap) between any 2 individuals by dividing the number of days that these 2 animals were tracked with telemetry to the same burrow system by the number of days that both individuals were tracked with telemetry on the same day (Ebensperger et al. 2004). We determined group composition using SOCPROG software (Whitehead 2009). We performed hierarchical cluster analysis of the association matrix. We confirmed the fit of data with the cophenetic correlation coefficient, a correlation between actual association indexes and levels of clustering in the diagram. Under this procedure, values above 0.8 indicate that hierarchical cluster analysis has provided an effective representation of the data (Whitehead 2008). We chose maximum modularity criteria (Newman 2004) to cut off the dendrogram and define social groups. Group size was then calculated as the number of adult Andean degus assigned to the same social group.

Range areas and overlap.—To determine whether Andean degus assigned to the social unit formed a socially cohesive group when active aboveground, we used night radiolocations to monitor patterns of space use. Locations of radiofixes for
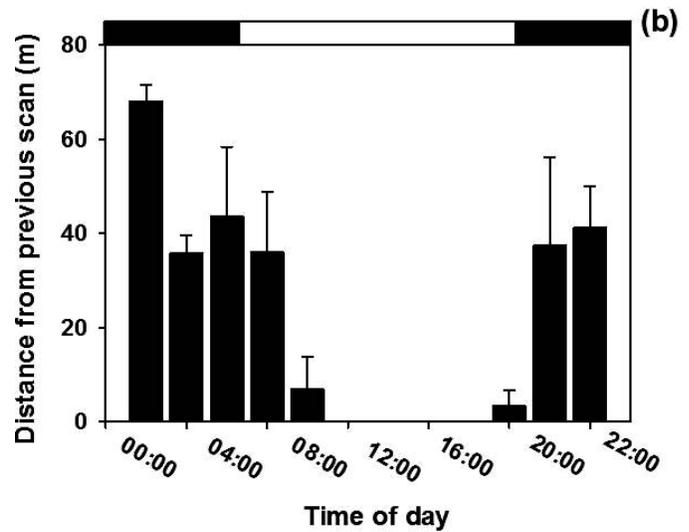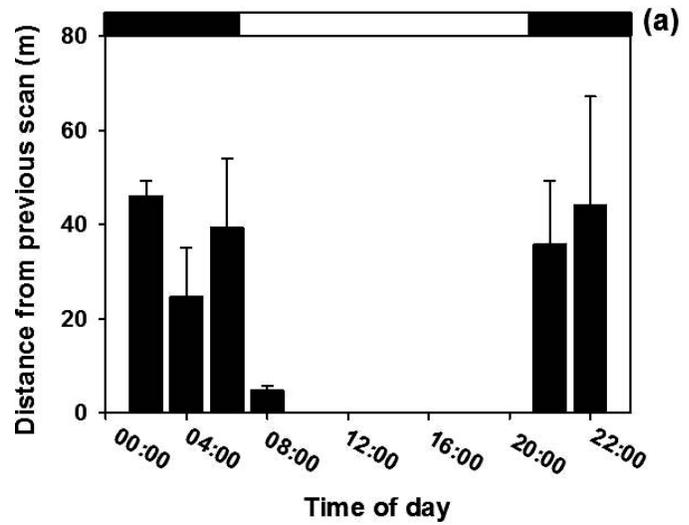
FIG. 2.—Mean (± *SE*) distance moved (m) since previous scan of Andean degus (*Octodontomys gliroides*) monitored every 2 h for 3 days and 3 nights from a) Eastern population (*n* = 14 adult degus) and b) Western population (*n* = 15 adult degus). Black bars at the top of graphs indicate night hours.

each individual were first transferred to an x–y system of coordinates and then mapped using the 95% minimum convex polygon algorithm (MCP) with the software Ranges VI (Kenward et al. 2003). Pairwise estimates of percentage of home-range overlap among individuals and nesting associations were also calculated using Ranges VI (Kenward et al. 2003; Ebensperger et al. 2006).

Ecological predictors at the level of social groups.—At the level of burrow systems used by social group members, distribution of food resources was measured as distance between patches with shrubs or ground-level and columnar cacti and density of vegetation patches. Both distance between patches and density of vegetation patches were calculated as distance and number of locations with shrubs or ground-level or columnar cacti on an area of 1 ha around each burrow system used by these rodents. We measured food availability as

vegetation cover around burrow systems based on ground-level cacti, columnar cacti, and shrubs. We randomly located transects on the perimeter of each burrow system to quantify vegetation cover. This variable was recorded using the line point intercept method (Bonham 1989, see above). Percent cover was calculated as the number of hits for each plant species or ground cover class divided by the total number of points per transect.

To examine predation risk, we considered density of burrow openings (number of active burrow entrances/m^2), overhead vegetation cover, and distance (m) from each burrow system used to the nearest overhead shrub or cactus. In the context of energy costs associated with burrow digging, we recorded soil penetrability around burrow systems of social groups. Soil penetrability was recorded 5 times in each of 4 points located in north, east, west, and south orientation and on the perimeter of each burrow system used by Andean degus. The 5 measures per point were averaged for subsequent analyses.

Andean degu abundance.—We used data from burrow trapping to calculate abundance of adult-sized Andean degu assuming a closed population (no emigration, immigration, death, or birth). We restricted this analysis to the first 18 days of burrow trapping at each population. These analyses were performed using CAPTURE software (Otis et al. 1978; Rexstad and Burnham 1991).

Statistical analysis.—Unless stated differently, statistical analyses were performed using Statistica 9.0 (StatSoft, Inc. 2009). We used general linear models (GLMs) when data did not violate the assumptions of normal distribution and homogeneity of variances, or they could be transformed to meet these assumptions. Percentage values were arcsine square-root transformed (Zar 1996). Alternatively, we used generalized linear model (GLZ) assuming a Poisson distribution and a log-link function. Within each population, measures of daytime and nighttime activity were compared using the Wilcoxon signed-rank test, with individuals as blocks and day and night as treatments (Sokal and Rohlf 1995).

We used GLZs assuming a Poisson distribution and a log-link function to determine how ecological conditions differed across populations. During this analysis population was entered as a categorical factor and ecological predictors (i.e., measures of food availability, Poisson variance to mean ratio, predation risk, and soil hardness) represented dependent variables. Similarly, we used GLZs to examine how group size (a measure of sociality) varied between populations. For this analysis population was entered as a categorical factor (Eastern versus Western), and group size was entered as the dependent variable. To analyze within-group range-area overlap (a measure of social cohesion during activity), we used a GLM where population was entered as a categorical factor (Eastern versus Western populations), group size was entered as a covariate, and range-area overlap was the dependent variable. For descriptive purposes, we also used a GLM approach to examine effects of population (Eastern versus Western), sex (males versus females), and population by sex interaction on the size of range areas.

We used generalized linear mixed model (GLMM) approaches to examine how ecological variables within populations predict variation in sociality. Because our experimental design included data from 2 unreplicated Andean degu populations, these tools allowed population to be included in the analysis as a grouping, random component in the models. Two approaches were employed to model the relationship between ecological predictors and sociality measures using GLMM: hypothesis-oriented testing, and multimodel variable selection. During the 1st approach we performed separate GLMM analyses for group size and range-area overlap as dependent variables, but we used the same ecological predictors: distance between patches, density of vegetation patches, and vegetation cover as measures of resource distribution and availability; density of burrow openings, overhead vegetation cover, and distance to cover as measures of predation risk; and soil hardness as a measure of burrowing costs. We modeled predictors without interactions to avoid overfitting given our low sample size. Additionally, we tested for random intercepts and slopes using population as a factor.

During multimodel variable selection we used an algorithm for GLMM where all predictor variables were used as inputs and examined how all possible variable combinations predicted sociality measures. Given that no specific variable combination resulted in statistically significant effects we decided not to report all the models examined during this last approach. Analyses based on GLMMs were conducted in R (R Development Core Team 2012) using library 'lme4' (Bates 2007). Visual inspection of residual plots revealed deviations from homoscedasticity; however, no improvements were obtained after incorporating heterogeneity of variances into the model. Model significance was tested by contrasting against the intercept-only null model, and *P*-values were obtained by likelihood-ratio tests. Data are reported as mean ± *SE*. Statistical significance was determined at $P < 0.05$.

RESULTS

Interspecific comparisons.—The ancestral character reconstructions for the phylogeny nodes indicated that the most likely common ancestor of all extant octodontids was likely group-living (log-link $= -3.46$, proportional likelihood = 64%; node 1 in Fig. 1). Similarly, the common ancestor of extant group-living octodontids was probably social (proportional likelihood = 92%; node 2 in Fig. 1). Group-living exhibited a strong and statistically significant phylogenetic signal across Octodontidae; the number of character transitions in sociality was lower than that expected by chance (observed 1 versus expected 3, $P < 0.001$; Fig. 1).

Ecological differences at the level of populations.—Two measures of food availability, abundance of ground-level cacti biomass (GLZ: $\chi^2_1 = 358.27$, $P < 0.001$) and vegetation cover (GLM: $F_{1,28} = 5.19$, $P = 0.030$), were higher in the Eastern population than in the Western population (Table 1). The Poisson variance to mean ratio of distance between patches was higher in the Western population compared with the Eastern

TABLE 1.—Mean ($\pm$ *SE*) estimates and statistical comparisons of ecological conditions between Eastern and Western populations of *Octodontomys gliroides*. Values in boldface type indicate statistically significant differences at $P < 0.05$.

Ecological condition and variables	Populations		*P*-value
	Eastern (Oploca)	Western (Chusmiza)	
Food abundance			
Abundance of food biomass (g/m^2)	141.19 $\pm$ 42.48	77.64 $\pm$ 5.82	**< 0.001**
Vegetation cover (%)	46.67	36.67	**0.03**
Distribution of resources			
Poisson variance to mean ratio of distance between patches	31.44 $\pm$ 0.44	39.21 $\pm$ 1.21	**< 0.001**
Predation risk			
Overhead vegetation cover (%)	46.67	24.67	**< 0.001**
Distance to cover (m)	27.93 $\pm$ 0.43	37.77 $\pm$ 0.57	**< 0.001**
Density of burrow openings (no./m^2)	0.1 $\pm$ 0.02	0.14 $\pm$ 0.03	0.749
Burrowing costs			
Soil hardness (kg/cm^2)[a]	29.42 $\pm$ 0.22	24.36 $\pm$ 0.25	**< 0.001**

[a] To convert pound-force per square inch (lbf/in^2) into kg/cm^2 we used 1 lbf/in^2 = 0.07031 kg/cm^2 (Pennycuick 1988).

population (GLZ: $\chi^2_1 = 314.8$, $P < 0.001$; Table 1), implying a more clumped distribution of food resources in the Western population.

Two of the 3 measures of predation risk differed between populations. Distance to overhead cover (GLZ: $\chi^2_1 = 18.2$, $P < 0.001$) was greater in the Western population than in the Eastern population. In contrast, overhead vegetation cover was higher in the Eastern compared with the Western population (GLM: $F_{1,28} = 21.71$, $P < 0.001$; Table 1). Even though the absolute number of active burrow entrances per burrow system was greater in the Eastern (5.4 $\pm$ 0.89) compared with the Western population (1.62 $\pm$ 0.14), density of burrow openings (number of burrow entrances/m^2) did not differ between populations (GLZ: $\chi^2_1 = 0.1$, $P = 0.749$; Table 1). Soil was significantly harder in the Eastern population compared with the Western population (GLZ: $\chi^2_1 = 7.11$, $P < 0.001$; Table 1).

FIG. 3.—Mean ($\pm$ *SE*) for total group size (black bars), and number of female (white bars) and male group (gray bars) members at Eastern and Western populations of *Octodontomy gliroides* examined.
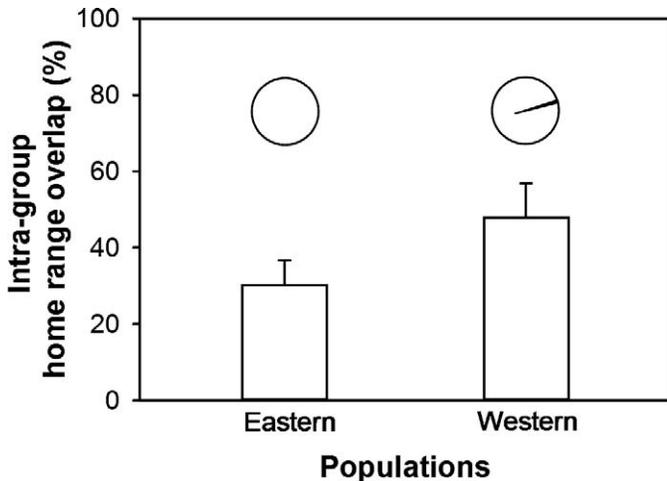
Temporal activity and range areas.—Aboveground activity recorded as distance moved between radioscans varied through time of day or night in both populations. Andean degu activity was markedly higher after sunset, and decreased after sunrise (Fig. 2). In the Eastern population, female and male activity recorded during nighttime (26 $\pm$ 10 m, range: 15–56 m, $n = 4$ and 88 $\pm$ 1 m, range: 14–379 m, $n = 10$, respectively) was greater than activity recorded during daytime (1 $\pm$ 1 m, range: 0–4 m, $n = 4$ and 1 $\pm$ 1 m, range: 0–5 m, $n = 10$, respectively) and this difference was statistically significant (Wilcoxon signed-rank test, $Z = 3.29$, $n = 14$, $P < 0.001$). The distance moved between any 2 consecutive radiofixes during the night in the Western population in females and males averaged 33 $\pm$ 5 m (range: 13–56 m, $n = 7$) and 53 $\pm$ 10 m (range: 15–106 m, $n = 8$), respectively, and was larger than distance moved during the day (4 $\pm$ 1 m, range: 0–11 m, $n = 7$ and 7 $\pm$ 2 m, range: 0–16 m, $n = 8$; Wilcoxon signed-rank test, $Z = 3.41$, $n = 15$, $P < 0.001$).

Population differences in sociality.—In the Eastern population, we monitored 6 females and 9 males, and we identified a total of 5 social groups. In the Western population, we monitored 5 females and 6 males, representing 5 social groups. Group sizes of Eastern and Western populations did not differ statistically (GLZ: $\chi^2_1 = 0.61$, $P = 0.435$; Fig. 3). Group size ranged from 2 to 4 adults in the Eastern population and from 2 to 3 adults in the Western population. Social groups in the Eastern population consisted of 2 males and 1 female ($n = 3$), 2 males and 2 females ($n = 1$), and a male–female pair ($n = 1$). Social groups in the Western population consisted of male–female pairs ($n = 4$), and 2 males and 1 female ($n = 1$). In both populations, Andean degus from the same social group always used 1 burrow system as a resting and hiding place.

Individual range areas of *O. gliroides* in the Western population (0.37 $\pm$ 0.07 ha) were significantly larger than range areas in the Eastern population (0.12 $\pm$ 0.03 ha; GLM: $F_{1,22} = 20.652$, $P < 0.001$). Range areas varied significantly with sex (GLM: $F_{1,22} = 7.62$, $P = 0.011$), and range areas of males (0.29 $\pm$ 0.06 ha) were larger than those of females (0.14
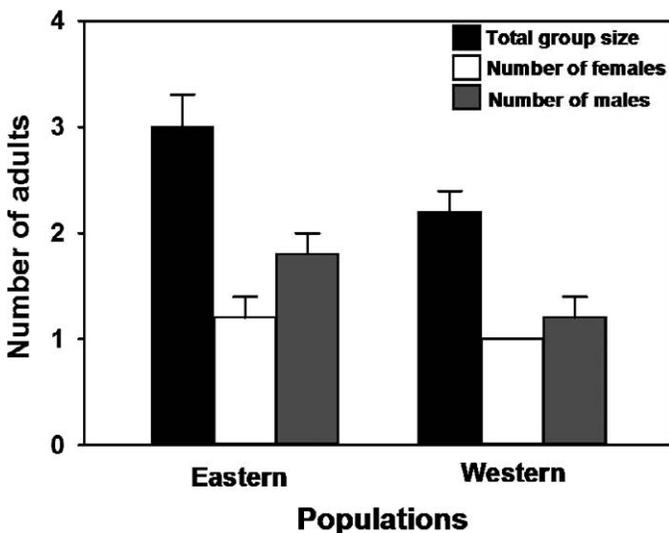
FIG. 4.—Mean ($\pm$ *SE*) range-area overlap among individuals of same social groups in Eastern and Western populations of *Octodontomys gliroides* examined. Pie graphs on top of the bars are used to compare range-area overlap among individuals from same social groups (white portion) and overlap among individuals from different social groups (black portion). There was no overlap in range areas among individuals from different social groups in the Eastern population.

$\pm$ 0.03 ha). The population by sex interaction on range areas was not statistically significant (GLM: $F_{1,22} = 0.25$, $P = 0.620$).

Range-area overlap among same group members (50.9% $\pm$ 6.9%) was greater than overlap among individuals from different social groups (0.6% $\pm$ 0.4%) in the Western population (GLZ: $\chi^2_1 = 56.96$, $P < 0.001$; Fig. 4). Likewise, overlap among same-group members (32.8% $\pm$ 8.9%) was greater than overlap among individuals from different social groups (0%) in the Eastern population (Fig. 4). Overlap of range areas among same-group members in the Eastern and Western populations did not differ when group size was controlled (GLM: $F_{1,7} = 1.64$, $P = 0.242$ and $F_{1,7} = 0.02$, $P = 0.896$, respectively; Fig. 4).

Andean degu abundance.—The abundance of Andean degus estimated in an area of 11 ha in the Western population (23 $\pm$ 4 adults) tended to be greater than abundance of degus in a similar area in the the Eastern population (19 $\pm$ 4 adults).

Ecological predictors at the level of social groups.—After adding population as a random, grouping factor in the models we found no evidence for any ecological predictors of group size (GLMMs: distribution and availability of food resources: all $Z < 0.5$, all $P > 0.05$; predation risk: all $Z < 0.3$, all $P > 0.05$; burrowing costs: all $Z < 0.4$, all $P > 0.05$; see Supporting Information S1, DOI: 10.1644/14-MAMM-A-057. S1). For range-area overlap, no ecological conditions predicted variation in this response variable (GLMMs: distribution and availability of food resources: all $Z < 0.7$, all $P > 0.05$; predation risk: all $Z < 0.3$, all $P > 0.05$; burrowing costs: all $Z < 1.3$, all $P > 0.05$; Supporting Information S2, DOI: 10.1644/14-MAMM-A-057.S2). For both sociality measures (group size and range-area overlap), the best model always included

"population" as a grouping factor; however, estimates did not reach statistical significance (all $\chi^2 < 0.9$, all $P > 0.05$ and all $\chi^2 < 2.7$, all $P > 0.05$, respectively; Supporting Information S1 and S2).

DISCUSSION

Our study revealed ecological differences between populations. First, preferred food resources (as assessed from ground-level cacti biomass and vegetation cover) were more abundant in the Eastern than in the Western population. Second, preferred food and other resources (e.g., hiding or resting places) were patchier (as estimated from Poisson variance to mean ratios) in the Western population. Third, distance to cover was longer and overhead vegetation cover lower in the Western population, implying that refuge against predators was less abundant and more patchily distributed. Fourth, soil was harder in the Eastern population, suggesting higher burrowing costs. Fifth, abundance of Andean degus tended to be higher in the Western population. Taken together, ecological conditions in terms of resource abundance, distribution, and predation risk were more challenging in the Western population, but the opposite was true in terms of burrowing costs.

These population differences did not translate into social differences in terms of group size and range-area overlap within a group, 2 measures of group-living and social cohesion during activity. This lack of covariation between population differences in ecology and social behavior in *O. gliroides* suggests a minor role of ecological conditions in current-day populations. Results from these population-level comparisons were further supported by our phylogenetic approach based on species contrasts. Ancestral character reconstruction indicated that the ancestor of *O. gliroides* and that of all extant octodontids was likely social. These findings imply that sociality of octodontids, including *O. gliroides*, had an ancient origin and likely is the consequence of past ecological conditions. In addition, group-living exhibited a strong phylogenetic signal, implying an influence of ancestral relationships.

Covariation between ecological conditions (e.g., food abundance and distribution, predation risk, and population density) and group size and composition characterizes socially cohesive groups in vertebrates (Lott 1991; Maher and Burger 2011). Such variation is predicted to reflect trade-offs between current fitness benefits and costs that emerge from individuals' decisions to join or leave groups (Ebensperger et al. 2012). Thus, variation in sociality should mirror population differences in ecology. Our study on *O. gliroides* revealed that group size and range-area overlap within groups did not vary with population differences in food abundance and distribution, predation risk, or burrowing costs. Thus, costs and benefits linked to sociality in *O. gliroides* are not fine-tuned to current differences in ecology. Subsequent studies are needed to examine how this lack of social variation holds across breeding and nonbreeding conditions. Costs associated with reproduc-

tive competition may change with breeding activity and result in social differences (Schradin et al. 2010).

The lack of population-level differences in sociality of *O. gliroides* departs from previous results in other social octodontids (Ebensperger et al. 2012), other social rodents (Travis et al. 1995; Schradin and Pillay 2005), and other social mammals (e.g., ungulates—Rowe-Rowe et al. 1992; Brashares and Arcese 2002). However, a lack of differences in sociality despite differences in ecological conditions has been documented in several other social species. For example, size and composition of meerkat (*Suricata suricatta*) social groups did not differ across 2 populations with different predation regimens (Clutton-Brock et al. 1999). Colony size of the common mole-rat (*Cryptomys hottentotus hottentotus*) did not differ across 2 populations with significant differences in mass, density, quality (water and energy content), and distribution of food (geophyte) resources (Spinks et al. 2000). Furthermore, differences in thermal conditions are not related to the size of social groups across populations of European badgers (*Meles meles*—Johnson et al. 2002), and population differences in density are not associated with social variation in Brants whistling rats (*Parotomys brantsii*—Jackson 1999) and African lions (e.g., *Panthera leo*—Bothma and Walker 1999). Overall, reasons for ecologically driven social flexibility across species remain poorly understood. Subsequent studies are needed to explore how factors such as habitat conditions or phylogeny explain the evolution of species variation in environmentally driven social flexibility (Clutton-Brock and Sheldon 2010; Maher and Burger 2011).

Our phylogenetic approach indicated that sociality across octodontid rodents has been influenced by ancestor–descendent relationships. In particular, our results support the hypothesis that the ancestor of octodontids was social, and that group-living has been retained in some species (*Aconaemys*, *Octodon*, and *Spalacopus*), but lost in other species (*Octomys*, *Pipanacoctomys*, and *Tympanoctomys*). The origin and subsequent retention of group-living may in part reflect historical changes in environmental conditions. According to the molecular clock calibration proposed by Opazo (2005), the split of octodontid rodents into 2 major clades, the social genera and solitary species, would have occurred in the middle to late Miocene around 8 million years ago. This period was matched with physical and vegetation changes associated with uplifting of the Andes and concomitant changes in rainfall regimes (Solbrig 1976; Reig 1986; Contreras et al. 1987; Vucetich et al. 1999). Thus, social octodontids, including *O. gliroides*, may have responded to increasing aridity and greater patchiness of habitat (Honeycutt et al. 2003; Galewski et al. 2005; Patterson and Velazco 2008). However, the shift to solitary-living is not easily accounted for by these historical changes in environmental conditions. Extant solitary octodontids are desert specialists with relatively narrow geographic distributions, they use highly patchy and open xeric habitats, and some feed on hypersaline food resources (Mares et al. 1997; Gallardo et al. 2007; Ojeda 2010). Whether the extremely low ambient productivity that characterizes desert conditions contributed to these changes in social behavior needs to be examined.

Intriguingly, social groups in the Eastern population were composed mostly of 1 female and 1 or 2 males, whereas the Western population consisted mostly of male–female pairs, implying the possibility that these groups represent short-term male–female mating associations. However, the observation that male–female pairs involved pregnant females and their potential weaned offspring suggest a more permanent form of sociality. On the other hand, social groups composed of 1 female and 1 or 2 males raises the possibility of a socially monogamous or polyandrous mating system. Future studies using molecular markers are needed to confirm these unusual mating systems in a mammal species (Eisenberg 1966; Orians 1969; Clutton-Brock and Harvey 1978).

In summary, population-level comparisons of *O. gliroides* conducted in a phylogenetic framework were consistent with the hypothesis that group-living in *O. gliroides* represents the historical legacy from ancestors already exhibiting social behavior (i.e., phylogenetic inertia). The lack of differences in sociality across populations of *O. gliroides* despite differences in ecology suggests an association with past but not current ecological conditions. Thus, our study highlights the relevance of integrating the action of current ecological conditions with phylogenetic information to understand social behavior in extant species.

RESUMEN

La variación en la conducta social ha sido atribuida a múltiples factores ecológicos. Sin embargo, la vida en grupo en algunas especies es un rasgo altamente conservado, sugiriendo una influencia filogenética. En este estudio, se evaluó ambos escenarios usando comparaciones intraespecíficas e interespecíficas a través de roedores octodóntidos. En primer lugar se evaluaron 2 poblaciones de degu Andino (*Octodontomys gliroides*) que representan 2 extremos de un gradiente climático y de vegetación a través de la Cordillera de los Andes. Se evaluó como la variación en términos de abundancia y distribución de recursos alimenticios, riesgo de depredación, y costos asociados a cavar madrigueras podrían predecir la variación interpoblacional en tamaño de grupo y solapamiento del ámbito de hogar (2 medidas de sociabilidad). Estas medidas fueron estimadas con datos de trampeo y radiotelemetría. Además, se utilizaron métodos filogenéticos para determinar si el rasgo social presenta señal filogenética, y de esta manera reconstruir el estado ancestral de la sociabilidad a través de la familia Octodontidae. Se encontraron diferencias estadísticamente significativas entre las poblaciones en términos de ecología, incluyendo abundancia y distribución de recursos alimenticios, riesgo de depredación, costos asociados a cavar madrigueras. Sin embargo, el tamaño de grupo y solapamiento del ámbito de hogar fueron similares entre ambas poblaciones. El análisis filogenético reveló una fuerte y significativa señal filogenética asociada a la sociabilidad, y que esta conducta estuvo presente temprano en la evolución de los roedores octodóntidos. En conjunto, estos resultados implican que la

vida en grupo en *O. gliroides* no está relacionada a las diferencias en ecología en las poblaciones actuales.

SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Ecological predictors of group size
Found at DOI: 10.1644/14-MAMM-A-057.S1
SUPPORTING INFORMATION S2.—Ecological predictors of range area overlap
Found at DOI: 10.1644/14-MAMM-A-057.S2

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