Ecological drivers of group living in two populations of the communally rearing rodent, *Octodon degus*

Luis A. Ebensperger,
Centro de Estudios Avanzados en Ecología and Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Raúl Sobrero,
Centro de Estudios Avanzados en Ecología and Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Verónica Quirici,
Centro de Estudios Avanzados en Ecología and Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Rodrigo A. Castro,
Centro de Estudios Avanzados en Ecología and Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Liliana Ortiz Tolhuysen,
Centro de Estudios Avanzados en Ecología and Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Francisco Vargas,
Centro de Estudios Avanzados en Ecología and Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Joseph Robert Burger,
Department of Biology, University of Louisiana at Monroe, Monroe, LA 71203, USA

René Quispe,
Instituto de Ecología y Biodiversidad, and Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile

Department of Behavioural Neurobiology, Max Planck Institute for Ornithology, Seewiesen, Germany

Camila P. Villavicencio,
Instituto de Ecología y Biodiversidad, and Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile

Department of Behavioural Neurobiology, Max Planck Institute for Ornithology, Seewiesen, Germany

Correspondence to: Luis A. Ebensperger, lebensperger@bio.puc.cl.

Rodrigo A. Vásquez, and
Instituto de Ecología y Biodiversidad, and Departamento de Ciencias Ecológicas, Facultad de
Ciencias, Universidad de Chile, Santiago, Chile

Loren D. Hayes
Department of Biology, University of Louisiana at Monroe, Monroe, LA 71203, USA

Luis A. Ebensperger: lebensperger@bio.puc.cl

Abstract

Intraspecific variation in sociality is thought to reflect a trade-off between current fitness benefits
and costs that emerge from individuals' decision to join or leave groups. Since those benefits and
costs may be influenced by ecological conditions, ecological variation remains a major, ultimate
cause of intraspecific variation in sociality. Intraspecific comparisons of mammalian sociality
across populations facing different environmental conditions have not provided a consistent
relationship between ecological variation and group-living. Thus, we studied two populations of
the communally rearing rodent *Octodon degus* to determine how co-variation between sociality
and ecology supports alternative ecological causes of group living. In particular, we examined
how variables linked to predation risk, thermal conditions, burrowing costs, and food availability
predicted temporal and population variation in sociality. Our study revealed population and
temporal variation in total group size and group composition that covaried with population and
yearly differences in ecology. In particular, predation risk and burrowing costs are supported as
drivers of this social variation in degus. Thermal differences, food quantity and quality were not
significant predictors of social group size. In contrast to between populations, social variation
within populations was largely uncoupled from ecological differences.

Keywords

Sociality; Predation risk; Burrowing costs; Food availability; Thermal conditions; Degus

Introduction

Animal social groups range from short-term associations and aggregations (e.g., foraging or
roosting groups) to relatively long-term socially cohesive units (e.g., communally rearing
groups) (Parrish et al. 1997; Krause and Ruxton 2002). Among the vertebrates, considerable
intra- and inter-specific variation in the number and composition of group members
characterizes more socially cohesive groups (Lott 1991; Maher and Burger 2011). Both
sources of variation are the raw material for studies aimed at determining the functional
significance of behavior (Lott 1991; Foster and Endler 1999), including sociality (Travis et
al. 1995; Spinks et al. 2000; Schradin and Pillay 2005).

Intraspecific variation in sociality is thought to reflect a trade-off between current fitness
benefits and costs that emerge from individuals' decision to join or leave groups. Benefits
such as decreased predation risk, decreased burrowing costs, access to resources, and
enhanced thermoregulation are hypothesized to promote the formation and maintenance of
social groups (Alexander 1974; Bertram 1978; Ebensperger 2001; Ebensperger and Cofré
2001; Ebensperger and Blumstein 2006; Table 1). Fitness costs, on the other hand, include
increased parasitism and competition over resources (Hoogland 1995). Since most, if not all,
of these benefits and costs may be influenced by ecological conditions, ecological variation
remains a major, ultimate cause of intraspecific variation in sociality (Slobodchikoff 1984;
Brashares and Arcese 2002).

Intraspecific comparisons of mammalian sociality in populations with different environmental conditions have not revealed a consistent relationship between ecological variation and group living. For example, group size (the most common measure of sociality) of cercopithecoid primates increases in populations under high predation risk (Hill and Lee 1998; see also Hass and Valenzuela 2002). In contrast, the size and composition of mongoose social groups is not different in populations with different predation regimes (Clutton-Brock et al. 1999). Similarly, the size of social groups has been noted to increase with the patchiness of food resources and overall abundance and quality of food across some populations of rodents and ungulates (Travis et al. 1995; Brashares and Arcese 2002), but not others (Spinks et al. 2000). Johnson et al. (2002) found no relationship between the thermal environment (a main determinant of energy expenditure) and the size of social groups across populations of badgers (*Meles meles*) throughout Europe. While these findings contrast with studies of single populations in rodents where the extent of grouping tracks changes in ambient temperature (West 1977; Stapp et al. 1991; Edelman and Koprowski 2007), they support other studies (e.g., Getz and McGuire 1997), suggesting that social group size is not influenced by fluctuations in ambient temperature. Regarding reduced costs of burrow construction, burrow digging has been associated to the evolution of sociality across neotropical (Ebensperger and Cofré 2001; Ebensperger and Blumstein 2006) and African hystricognath rodents (Jarvis et al. 1994). However, it is far from clear whether environmental differences linked to energy expenditure or burrow digging underlies social variety within species.

Model species, hypotheses, and predictions

We first determined how variation in sociality tracks differences in ecological conditions in two populations of the communally rearing rodent *Octodon degus*. We then use this information to examine how this co-variation supports alternate, non-mutually exclusive hypotheses for the causes of group living. Degus are diurnal, medium-sized rodents (ca. 180 g) that feed mostly on the green leaves of grasses and forbs and breed generally once per year (Ebensperger and Hurtado 2005b; Quirici et al. 2010). Degus are plural breeders with communal care of offspring (Brown 1987; Solomon and Getz 1997; Silk 2007), i.e., 1–5 males and 1–8 multiple lactating females share underground nests and rear their litters communally (Ebensperger et al. 2002, 2004, 2007; Hayes et al. 2009).

Single population studies indicate that predation risk influences the size of foraging groups, and that these groups in turn affect the ability of degus to detect approaching predators (Vásquez 1997; Ebensperger and Wallem 2002; Ebensperger et al. 2006). These results suggest that predation risk predisposes degus to live in social groups. Given that in these animals (1) survival increases whenever daytime or crepuscular predators are experimentally excluded (Meserve et al. 1983), and (2) communally nesting individuals (i.e., members of same social group) tend to forage and be active on the same patches during day time (Ebensperger et al. 2004; Soto-Gamboa 2004), we considered predation risk to increase with the frequency of predators active during day time. In addition, shrubs are known to provide overhead, protective cover to degus (Ebensperger and Hurtado 2005a), implying that predation risk would decrease in areas with greater shrub cover (Vásquez et al. 2002). Thirdly, predation risk increases with distance to the nearest burrow opening in degus (Lagos et al. 2009). Thus, we considered predation risk also to decrease with density of burrow openings per burrow system (i.e., abundance of safe havens). Based on these considerations, we conducted between- and within-population comparisons to test five predictions linked to the predation risk hypothesis (Table 1).

Besides an influence of predators, laboratory studies suggest that degus reduce their energy expenditure through huddling (Canals et al. 1989), supporting the hypothesis that thermal conditions influence sociality (Madison 1984; Koprowski 1998). This hypothesis predicts

that (1) group size tracks ambient temperature conditions, with larger groups during cold periods and smaller groups during warmer periods, and that (2) larger groups occur in populations experiencing colder ambient temperatures than in populations experiencing warmer ambient temperatures. We used population contrasts to test the latter prediction (Table 1).

Some features of degus suggest that burrows could be another social driver. Members of social groups share a variable number of burrow systems, which include nest sites for rearing their offspring communally (Ebensperger et al. 2004; Soto-Gamboa 2004), and larger social groups use more burrow systems than do smaller groups (Hayes et al. 2009). Degus, which are diurnally active, use these underground burrows to escape and hide from predators (Vásquez et al. 2002; Lagos et al. 2009) and avoid extreme thermal conditions (Kenagy et al. 2002). The observations that degus experience increased energetic costs of digging with increasing soil hardness (Ebensperger and Bozinovic 2000a) and coordinate their digging activity support the hypothesis that digging costs contribute to degu sociality (Ebensperger and Bozinovic 2000b). Thus, two predictions linked to a "nest/refuge building" hypothesis were examined (Table 1).

Food resources are thought to be a major cause of sociality (e.g., Wrangham 1980; Travis et al. 1995; Brashares and Arcese 2002). Groups may form because individuals congregate near more abundant and higher quality food resources or benefit from cooperative foraging in harsh environments (Ebensperger 2001). Although degus occur in a wide range of habitat types with different food conditions, no one has examined the potential effects of food abundance and quality on degu sociality. Thus, we tested two predictions for the potential impact of food abundance and quality at burrow systems used by degus (Table 1).

Methods

Study populations

We examined two degu populations located 400 km apart in two habitats with extreme differences in environmental conditions: Estación Experimental Rinconada de Maipú (33°23 S, 70°31 W, altitude 495 m) (hereafter Rinconada) and at the Bocatoma Los Molles (30°45 S, 70°15 W, altitude 2,600 m) (hereafter Los Molles). While both study areas are characterized by a Mediterranean climate with cold, wet winters and warm, dry summers (di Castri and Hajek 1976), the high altitude area at Los Molles provides degus with a potentially more stressful environment in terms of lower ambient temperature than the low altitude area at Rinconada (Quispe et al. 2009). Given that no empirical data on ambient temperature were available for Los Molles, we used a multiple regression model with latitude and altitude as predictors (R^2=0.74, F=38.2, P<0.001; Houston and Hartley 2003; Houston 2006) and estimated that mean annual temperature for Rinconada and Los Molles were 14.0°C and 9.4°C, respectively. Mean monthly temperatures recorded 5–10 km north of Rinconada (i.e., the Pudahuel weather station, 33°23 S, 70°47 W, 475 m of altitude) indicated a mean annual temperature of 14.3°C at this site, suggesting that our method of estimation was reasonably accurate. The two populations differed in other relevant attributes, including vegetation. A preliminary study conducted in 2006 revealed greater variability in the dry mass of herbs at Los Molles (coefficient of variation, CV=1.30) than at Rinconada (CV=0.83), indicating that vegetative forage used by degus is more patchy at the former site. While the suit of known degu predators was similar in both sites, burrowing owls (*Athene cunicularia*), the lesser grison (*Galictis cuja*), and snakes (*Phylodryas chamissonis*) were seen only at Rinconada. In contrast, mountain caracaras (*Phalcoboenus megalopterus*) and variable hawks (*Buteo polyosoma*) were seen exclusively at Los Molles. Overall, predators were more frequently sighted at Rinconada than at Los Molles. In addition, shrubby vegetation near burrows that can be used by degus as refuge was more

abundant at Los Molles, further implying lower predation risk. The study was conducted in both populations during 2007 and 2008, during the period when females are in late pregnancy or lactating (i.e., September–October at Rinconada; November–December at Los Molles).

Determination of social groups

Degus are diurnally active and remain in underground burrows overnight (Kenagy et al. 2002; Ebensperger et al. 2004). Thus, the main criterion used to assign degus to social groups was the sharing of burrow systems during night time (Ebensperger et al. 2004). The sharing of burrow systems was established by means of (1) night-time telemetry, and (2) burrow trapping in September–October (Rinconada) and in November–December (Los Molles). During burrow trapping, we defined a burrow system as a group of burrow openings surrounding a central location where individuals were repeatedly found during night time telemetry and usually spanning 1–3 m in diameter (Fulk 1976; Hayes et al. 2007). The total number of burrow systems trapped per year at Rinconada was 32 in 2007 and 43 in 2008. These burrows were trapped an average of 31.4 ± 1.2 days in 2007 and 45.3 ± 1.6 days in 2008. The number of traps (model 201 Tomahawk, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) used per day at each burrow system averaged 9.7 ± 0.2 traps in 2007 and 8.0 ± 0.0 traps in 2008. The total number of burrow systems trapped per year at Los Molles was 7 in 2007 and 8 in 2008. These burrows were trapped for 30 days in 2007, and 21 days in 2008. The number of traps used per day at each burrow system averaged 17.1 ± 3.5 traps in 2007 and 19.5 ± 0.3 traps in 2008. The total area examined in Rinconada during 2007 and 2008 reached 0.61 and 2.16 ha, respectively. The area examined at Los Molles reached 0.92 ha in 2007 and 1.10 ha in 2008. Population differences linked to number of burrow systems examined, number of animals radio-collared, and social groups examined reflected major differences in overall abundance of degus.

In both populations, traps were set prior to the emergence of adults during morning hours (06:00 h). After 1.5 h, traps were checked and closed until the next trapping event. We determined the identity, location, sex, body mass (to 0.1 g), and reproductive condition (whether a female had a perforated vagina, was pregnant, or lactating) of all degus. Adults weighing greater than 170 g were fitted with 8 g (BR radio-collars, AVM Instrument Co., Colfax, California, USA) or 7–9 g radio-transmitters (RI-2D, Holohil Systems Limited, Carp, Ontario, Canada and SOM-2190A, Wildlife Materials Incorporated, Murphysboro, Illinois, USA) with unique pulse frequencies.

During night-time telemetry, females were radio-tracked to their burrows. Previous studies at Rinconada confirmed that night time locations represent nest sites where degus remain underground (Ebensperger et al. 2004). Locations were determined once per night approximately 1 h after sunset using an LA 12-Q receiver (for radio collars tuned to 150.000–151.999 MHz frequency; AVM Instrument Co., USA) and a hand held, 3-element Yagi antenna (AVM instrument Co.). Ultimately, there were $n=34$ and $n=21$ radio-collared individuals from Rinconada with sufficient data to assign group membership in 2007 and 2008, respectively. Animals from Rinconada were located on average 18.3 ± 4.2 nights per individual in 2007 and 16.0 ± 0.9 nights per individual in 2008. At Los Molles, there were $n=14$ radio-collared individuals with sufficient data to assign group membership in both years. Degus from Los Molles were located 20.8 ± 0.5 nights per individual in 2007 and 14.6 ± 0.4 nights per individual in 2008. This effort has been shown to be sufficient in determining group membership (Hayes et al. 2009).

The determination of group composition required the compilation of a symmetric similarity matrix of pairwise association of the burrow locations of all adult degus during trapping and telemetry (see Whitehead 2008). We determined the association (overlap) between any two

individuals by dividing the number of evenings that these individuals were captured at or tracked with telemetry to the same burrow system by the number of evenings that both individuals were trapped or tracked with telemetry on the same day (Ebensperger et al. 2004). To determine social group composition, we conducted a hierarchical cluster analysis of the association matrix in SOCPROG software (Whitehead 2009). We confirmed the fit of data with the cophenetic correlation coefficient, a correlation between the actual association indices and the 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.

Ecological variables

To examine the influence of ecological conditions on sociality, we used both between- and within-population comparisons. Ecological conditions included predation risk, abundance, and quality of food resources and soil hardness.

Given that natural predation on small mammals is difficult to measure, we quantified predation risk indirectly. At each population, we conducted scan sampling from fixed vantage points (two per population) located 50–100 m from where degus were active to record sightings of predators known to prey on degus. Every 30 min, the same observer recorded every predator observed over the entire area during a 20-min circular sweep. Observations were conducted during morning (07:30 to 12:00 h) and afternoon hours (17:00–19:30 h), i.e., when degus were observed aboveground. A total of 40 scan samplings were conducted at Rinconada during 2007 and 2008. The number of scan samplings conducted at Los Molles during 2007 and 2008 was 20 and 36, respectively. Data were standardized to predator sightings per hour.

Predation risk was also estimated based on the density of burrow openings and distance of burrow systems to the nearest shrub (Rinconada, 33 in 2008, 38 in 2008; Los Molles, 9 each year). Density of burrow openings (number per square meter) at each burrow system was determined by quantifying the number of burrow openings in the circular area encompassing a 9-m radius from the center of burrow systems. The distance (meter) to nearest tree or shrub (cover) was estimated for each burrow system with a 100-m measuring tape.

To track changes in the abundance of primary food (Quirici et al. 2010), we collected samples of green herbs at 3 and 9 m from the center of each burrow system. In particular, we randomly chose one location at 3 m and 1 at 9 m in the north, east, south, or west directions. At each of these two sampling points, we placed a 250×250-mm quadrant and removed the aboveground parts of all green herbs found. Samples were immediately stored inside 2 kg capacity paper bags. In the laboratory, we oven-dried each plant sample at 60°C for 72 h to determine its dry mass (biomass in grams) (Ebensperger and Hurtado 2005b). Data from 3 to 9 m sampling points were averaged per burrow system and standardized to gram per square meter for subsequent analysis (sample sizes described as above). We used the same sample pattern to record soil penetrability as an index of soil hardness (Lacey and Wieczorek 2003). Soil penetrability was recorded with the use of a hand-held soil compaction meter (Lang Penetrometer Inc., Gulf Shores, AL, USA).

To compare quality of primary foods, we collected samples of green herbaceous vegetation (within 250×250 mm quadrants) at random points throughout the study area where degus were regularly seen foraging. Two indicators of food quality, insoluble and soluble fiber content, were determined by standard chemical analysis at the Instituto de Nutrición y Tecnología de los Alimentos (Universidad de Chile, Santiago, Chile). Dietary fiber represents a barrier to the extraction of soluble nutrients from cells and is difficult to digest

by non-ruminants (Van Soest 1982). Lab studies revealed that degus minimize fiber intake when given a choice of high-fiber and low-fiber foods supporting the hypothesis that dietary fiber is not a preferred dietary component (Veloso and Bozinovic 1993; Bozinovic 1995). The total number of plant samples examined at Rinconada was 4 and 6 during 2007 and 2008, respectively. These numbers were 6 and 7, respectively, at Los Molles.

Degu abundance

We used data from burrow trapping to calculate the abundance of degus with a closed population with heterogeneity in captures model (Keesing 1998; Ribble and Stanley 1998; Cooch and White 2008; Moorhouse and Macdonald 2008), a method that controls for differences in the trappability of individuals in the population. Given that the model used rests on the assumption of closed population (no emigration, immigration, death or birth), we restricted this analysis to the first 11 days of each burrow trapping session at each population and year of study. These analyses were performed using the MARK software, release 5.1 (White and Burnham 1999).

Statistical analysis

Throughout the analysis, social groups determined at each population each year were used as independent replicates. The assumption of temporal independence of these replicates is valid in degus since annual turnover of adult members within groups is extremely high (Ebensperger et al. 2009). We verified the assumptions of normal distribution and homogeneity of variance with the use of Shapiro-Wilks and Cochran tests, respectively.

To examine the effects of population and year of study on sociality measures (total group size, number of females per group, number of males per group) we first tested four possible ANOVA models on each measure: (1) population by year interactive model, (2) population and year main effects model, (3) population only model, and (4) year only model. The best fit model was determined based on Akaike Information Criterion (AIC) (Akaike 1974). In particular, the model selected had the lowest AIC value, delta AIC<2, Akaike weight approaching 0.90 or higher, and evidence ratios close to 1 (Burnham and Anderson 2002; Symonds and Moussalli 2011; for a complete treatment of model selection, see Anderson 2008). We then took the best fit model in each case and reported main and/or interactive effects. We used the same approach to examine population and year of study variation in ecological conditions. In these analyses, the number of females per social group, abundance of food and density of burrow openings were squared root transformed. In contrast, the number of males per social group, predator sightings, and soil hardness could not be normalized.

Within each population and year, we used multiple regressions to determine the extent to which ecological measures (square root transformed density of burrow openings, distance to the nearest shrub, square root transformed abundance of food) predicted total group size and number of females per social. Associations between soil hardness and other ecological measures (density of burrow openings, distance from burrows to the nearest shrub, abundance of food) and the number of males per social group within sites were examined with bivariate, Spearman rank correlations. Soil hardness and the number of males per social group could not be normalized.

We followed Nakagawa and Foster (2004) in reporting the size of statistical effects and P values, instead of reporting post hoc (retrospective) power analysis. We considered equation 1 in Levine and Hullett (2002) to report eta-squared values (η^2) as estimates of size effects. Data are provided as means±SE. Population and ear effects on sociality and ecological variables were conducted using the R 2.4.1 software (R Development Core Team 2006).

Within population and year of study, analyses were conducted using Statistica 9.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Abundance of degus

During both years, the abundance of degus was greater at Rinconada than in Los Molles. In 2007, there were 57±12 and 24±4 adults at Rinconada and Los Molles, respectively. In 2008, there were 61±9 and 33±1 adults at Rinconada and Los Molles, respectively.

Social groups examined

At Rinconada, we monitored 42 females and 14 males, and 30 females and 6 males during 2007 and 2008, respectively. We were able to identify a total of 8 social groups in 2007 and 9 groups in 2008. At Los Molles, we monitored 13 females and 2 males, and 26 females and 6 males in 2007 and 2008, respectively. These animals allowed us to identify a total of four social groups in 2007 and six groups in 2008. Across populations and years, social groups were composed of 4.1±0.4 females and 1.0±0.2 males. Social groups at Rinconada included 4.2±0.5 females and 1.2±0.2 males. At Los Molles, social groups included 3.9±0.6 females and 0.8±0.3 males.

Population and year of study variation in sociality

For total group size, number of females and number of males the best fit model of the four possible models examined with AIC criteria was the population and year interaction model (Table 2). The population and year interaction model was well supported for total group size, but less so for the number of females and males. Thus, groups at Rinconada were larger than those from Los Molles in 2007 but not in 2008 (Fig. 1a). The number of adult females per group tended to be larger at Rinconada than at Los Molles during 2007 but not in 2008 (Fig. 1b). Similarly, groups at Rinconada tended to have more males than social groups at Los Molles during 2007 but not during 2008 (Fig. 1c).

Population and year of study ecological differences

The best fit and well-supported model for variation in the number of predators sighted was the population by year interaction model (Table 3). Predator sightings were more frequent at Rinconada than at Los Molles, but more so in 2007 (Fig. 2a). For distance from burrows to the nearest shrub and density of burrow openings the best fit model of the four possible models examined was the population model (Table 3). The population model was well supported for density of burrow openings, but less so for distance to the nearest shrub. Thus, during both years of study, burrow systems used by degus at Rinconada tended to be farther from the nearest shrub compared with burrow systems used at Los Molles (Fig. 2b). Density of burrow openings at burrows used by degus at Los Molles was greater than that of burrow systems used by degus at Rinconada (Fig. 2c).

A population model was not well supported but provided the best fit to abundance of food (Table 3). Food tended to be more abundant at Rinconada than at Los Molles during both years (Fig. 2d). The best fit and well-supported model for variation in soluble fiber was the population and year interaction model (Table 3). Food had a higher content of soluble fiber at Rinconada than at Los Molles during 2007, but this trend reversed during 2008 (Fig. 2e). A population and year main effects model was not well supported but provided the best fit for variation in insoluble fiber (Table 3). The amount of insoluble fiber in food tended to be greater at Rinconada than in Los Molles (Fig. 2f) and greater in 2008 than in 2007 (Fig. 2f).

A well-supported population by year interaction model provided the best fit to examine soil hardness (Table 3). Soil was harder at Rinconada than at Los Molles and more so in 2008 compared with 2007 (Fig. 2g).

Within-population predictors of social variation: Rinconada

At Rinconada, multiple regression revealed that distance from burrows used to the nearest shrub cover ($F_{1,12}=0.07$, $P=0.794$, $^2=0.01$), density of burrow openings ($F_{1,12}=0.12$, $P=0.739$, $^2=0.01$) and abundance of food ($F_{1,12}=2.06$, $P=0.176$, $^2=0.14$) were not significant predictors of total group size. Similarly, the number of females did not vary with the square root transformed distance from burrows used to the nearest shrub cover ($F_{1,12}=0.82$, $P=0.383$, $^2=0.05$), density of burrow openings ($F_{1,12}=0.06$, $P=0.808$, $^2<0.01$), or with abundance of food ($F_{1,12}=2.77$, $P=0.122$, $^2=0.18$).

No association was detected between the number of males per social group and distance from burrows used to the nearest shrub cover (Spearman rank correlation, $r_s=-0.09$, $n=16$, $P=0.752$), density of burrow openings ($r_s=0.26$, $n=16$, $P=0.335$), or with food abundance ($r_s=-0.05$, $n=16$, $P=0.866$). There was a statistically significant association between soil hardness and the number of males ($r_s=0.54$, $n=16$, $P=0.032$), but not with the number of females ($r_s=0.29$, $n=16$, $P=0.282$), or total group size ($r_s=0.48$, $n=16$, $P=0.057$) at Rinconada.

Within-population predictors of social variation: Los Molles

Total group size did not vary with distance from burrows used to the nearest shrub cover ($F_{1,6}=0.46$, $P=0.521$, $^2=0.05$), density of burrow openings ($F_{1,6}=1.96$, $P=0.211$, $^2=0.20$), and abundance of food ($F_{1,6}=1.51$, $P=0.266$, $^2=0.15$). Likewise, the number of females did not vary with distance from burrows used to the nearest shrub cover ($F_{1,6}=0.21$, $P=0.663$, $^2=0.02$), density of burrow openings ($F_{1,6}=0.57$, $P=0.480$, $^2=0.08$) and with abundance of food ($F_{1,6}=1.64$, $P=0.247$, $^2=0.19$). No association was detected between the number of males per social group and the distance from burrows used to the nearest shrub cover (Spearman rank correlation, $r_s=-0.18$, $n=10$, $P=0.626$), density of burrow openings ($r_s=0.54$, $n=10$, $P=0.105$), or with food abundance ($r_s=-0.33$, $n=10$, $P=0.359$).

There was not a statistically significant association between soil hardness and the number of males ($r_s=-0.14$, $n=10$, $P=0.698$), number of females ($r_s=0.44$, $n=10$, $P=0.203$), or total group size ($r_s=0.29$, $n=10$, $P=0.412$).

Within-population predictors of social variation: year of study

Neither total group size nor the square root transformed number of females were influenced by density of burrow openings in 2007 (both $F_{1,8}$ values<2.13, both P values>0.183, both ^{2} values<0.21) or 2008 (both $F_{1,10}$ values<2.32, both P values>0.159, both ^{2} values=0.16), distance from burrows used to the nearest shrub cover in 2007 (both $F_{1,10}$ values<2.94, both P values>0.125, both ^{2} values<0.24) or 2008 (both $F_{1,10}$ values=0.28, $P=0.610$, $^2<0.02$), or by abundance of food in 2007 (both $F_{1,8}$ values=0.43, both P values=0.529, both ^{2} values<0.03) or 2008 (both $F_{1,10}$ values<2.22, both P values<0.167, both ^{2} values<0.15).

The number of males increased with soil hardness in 2007 ($r_s=0.81$, $n=12$, $P=0.001$), but not in 2008 ($r_s=-0.19$, $n=14$, $P=0.505$). There were no statistically significant associations between soil hardness and total group size ($r_s=0.45$, $n=12$, $P=0.143$) or the number of females ($r_s=0.17$, $n=12$, $P=0.600$) in 2007. Likewise, no relationships were found between soil hardness and total group size ($r_s=-0.14$, $n=14$, $P=0.633$), or the number of females ($r_s=-0.04$, $n=14$, $P=0.901$) in 2008.

Discussion

General findings

Our study revealed population and temporal variation in total group size and possibly, on the number of males per social group in degus. These population and yearly differences covaried with population and yearly differences in predation risk and soil hardness. While the size and composition of social groups was variable within population and year of study, we found little evidence of covariation between ecology and degu sociality at this scale. The only ecological variable to influence group size within populations was soil hardness, which was linked to the number of males per group during 1 year of the study and in only one population (Rinconada).

Sociality and predation risk

Abundant evidence from single population studies on vertebrates and invertebrates generally supports that individuals in groups experience decreased predation risk by means of several mechanisms (Ebensperger 2001; Krause and Ruxton 2002; Ebensperger and Blumstein 2006). Together, this evidence suggests that decreasing predation risk is one major factor that maintains group living in some species. Our study revealed that both total group size and possibly the number of males per social group were larger at Rinconada compared to Los Molles in 2007 but not in 2008. Qualitatively, this population by year interaction mirrored variation in predation risk. The observation that (1) predators were more frequently sighted (in 2007), (2) burrow systems of social groups tended to be far from overhead cover, and (3) there was a lower density of openings at Rinconada indicated that this site represented a riskier habitat to degus compared with Los Molles. We note that population and year of study variation in sociality seemed less fine tuned to population and year differences in distance from burrow systems to the nearest shrub cover and density of burrow openings than to the frequency of predators sighted. However, yearly variation in social groups might be expected to reflect relatively short-term variation in response to predators per se. The temporal scale to which burrow density and distance to the nearest shrub cover varies is probably longer compared with fluctuations in predator abundance. Both burrow construction (or expansion) and reproduction and growth of native shrubs takes years (Ebensperger and Hurtado 2005b).

While long-term data sets are needed to examine other, long-term adjustments in degu social groups, previous evidence further supports a role for predators influencing degu sociality. Degus forage in larger groups when in more exposed patches (without overhead cover), and larger groups are more efficient in detecting an approaching predator (Ebensperger and Wallem 2002; Vásquez et al. 2002; Ebensperger et al. 2006). Regarding a broader context, variation in sociality observed in this study is also consistent with predation playing a role during the evolution of sociality across neotropical caviomorphs (Ebensperger and Blumstein 2006) and other mammals (Hill and Lee 1998; Brashares et al. 2000; Gygax 2002; Caro et al. 2004).

We cannot completely rule out that predators tracked degu abundance. The greater frequency of predator sightings at Rinconada may have resulted from predators visiting more areas with more abundant prey. Larger social groups at Rinconada could in turn be the result of higher degu abundance, as has been reported in numerous vertebrates, including social rodents (e.g., Wolff 1994; Lucia et al. 2008). However, several observations suggest that degu sociality is not density dependent. First, while degu abundance was similarly high in 2008 compared with 2007 at Rinconada, the number of predators sighted increased 2.9 times in the area, implying that more frequent predator visits were not simply the direct consequence of more abundant degu prey. Secondly, there is no evidence so far that density

influences the size and composition of degu social groups in Rinconada (Ebensperger et al. 2011). Finally, degu groups form not only as a result of delayed dispersal of offspring and adult fidelity, but also as the consequence of offspring dispersal and immigration of adults (Ebensperger et al. 2009) resulting in groups that lack kin structure (Quirici et al. 2011). These observations are in contrast to the expected mechanisms of group formation (delayed dispersal) and group composition (extended families) expected when groups form as a result of high population density (Emlen 1995; Ebensperger and Hayes 2008).

Sociality and social thermoregulation

Degus at Los Molles faced generally cooler thermal conditions compared with degus at Rinconada, implying that individuals were subjected to greater maintenance costs at Los Molles. Our observation that social groups were larger at Rinconada than Los Molles suggests that social group formation and maintenance is not driven by social thermoregulation. These findings depart from studies of single populations or comparisons of multiple populations in mammals (mostly rodents) where the extent of grouping tracks changes in ambient temperature (West 1977; Madison 1984; Stapp et al. 1991; Edelman and Koprowski 2007; Taraborelli and Moreno 2009). However, our results are in agreement with studies on voles (Getz and McGuire 1997) and badgers (Johnson et al. 2002) in which group size is uncoupled from ambient temperatures. Understanding why some social mammals respond differently to ambient temperature conditions will be crucial to predicting how major environmental perturbations such as climate change will affect social species.

Sociality and nest/refuge building

Group living has been linked to life in long-lasting, expandable nests (Alexander 1991). Since constructing and maintaining these structures, including burrows, is energetically costly (Lovegrove 1989; Ebensperger and Bozinovic 2000a), animals may be forced to live in groups to share their use or minimize such energetic cost (Arnold 1990; Powell and Fried 1992). Indeed, active burrow digging has been linked to the evolution of group-living of New World histricognath rodents (Ebensperger and Cofré 2001; Ebensperger and Blumstein 2006). Evidence of a functional connection between group-living and nest/refuge construction in degus remains equivocal. On the one hand, our observations that soil was harder and groups were larger at Rinconada than Los Molles are consistent with this hypothesis. These findings add to previous studies in which degus in groups coordinate their digging and remove more soil per capita than solitary degus (Ebensperger and Bozinovic 2000b). In contrast, within-population analyses did not lend strong support to a functional connection between group-living and nest/refuge construction. Soil hardness was not correlated with the number of females and total group size in both populations. There was only a weak link between soil hardness and the number of males per group. In degus, care provided by males has no immediate fitness effects to offspring (Ebensperger et al. 2010). Our results suggest the possibility that males play a more important role in the maintenance of burrows, a hypothesis worthy of further testing.

Sociality and food resources

Feeding habits may predispose some organisms to adopt social life (Rolland et al. 1998; Beauchamp 2002) through several mechanisms (Ebensperger 2001; Krause and Ruxton 2002), most of which predict the size of social groups to increase with increasing abundance, quality and patchiness of food resources (Wrangham 1980; Travis et al. 1995; Brashares and Arcese 2002; Verdolin 2007). While groups were larger at Rinconada, the possibility that preferred foods tracked this social trend and were more abundant at Rinconada than at Los Molles was not well supported. These results provide weak (if any) support to a link between food abundance and sociality in degus. Likewise, our observation that the content of soluble fiber was greater at Rinconada during 2007 but not 2008 and the

content of insoluble fiber was higher at Rinconada during both years, did not lend complete support to this possibility. Similarly to food quality, patchiness of food does not seem to be a contributing factor either. Based on 16 randomly sampled quadrants (250×250 mm) at Los Molles and 36 quadrants at Rinconada in 2006, we noted that variation (CV) of preferred food resources was higher at Los Molles than at Rinconada (Ebensperger and Hayes, unpublished results). This pattern is the opposite of that expected if sociality results from food patchiness (Travis et al. 1995). Taken together, our data provide negligible support to variation in food conditions as drivers of variation in degu social groups between populations.

Within-population variation in ecology

In contrast to between-populations variation, within-population variation in ecology scarcely predicted any variation in the size or composition of degu social groups. The generally small effect sizes detected, coupled with non-statistically significant comparisons suggests a general lack of ecologically meaningful differences instead of a lack of statistical power to detect such effects. More generally, however, these data suggest that social variation in degus is uncoupled from ecological differences when quantified within local populations.

Concluding remarks

Our study revealed (1) moderate between- and within-population variation in the size and composition of degu social groups and (2) extensive between- and moderate within-population variation in ecological conditions. Variation in ecology between populations supported the hypotheses that predation risk, food abundance, and the costs of burrow digging, but not thermal conditions and food quality, are drivers of social variation in degus. Within-population variation in ecology supported in part only one hypothesis—costs of nest/refuge building—and thus, was a not a strong predictor of variation in degu sociality. Overall, the between- and within-population comparisons of this study provided a test of multiple hypotheses for the ecological causes of degu sociality. However, comparisons of more populations and across more years are needed to determine the impact of intraspecific variation in ecology and that of periodic (interannual) disturbances (e.g., El Nino) on degu sociality. As suggested previously (Ebensperger 2001), these future studies need to consider that no single factor seems responsible for driving sociality in present day populations.

Acknowledgments

References

Akaike H. A new look at the statistical model identification. IEEE T Automat Contr. 1974; 19:716–723.

Alexander RD. The evolution of social behavior. Annu Rev Ecol Syst. 1974; 5:325–383.

Alexander, RD. Some unanswered questions about naked molerats. In: Sherman, PW.; Jarvis, JUM.; Alexander, RD., editors. The biology of the naked mole-rat. Princeton: Princeton University Press; 1991. p. 446-465.

Anderson, DR. Model based inference in the life sciences: a primer on evidence. USA: Springer; 2008.

Arnold W. The evolution of marmot sociality: I. Why disperse late? Behav Ecol Sociobiol. 1990; 27:229–237.

Beauchamp G. Higher-level evolution of intraspecific flock-feeding in birds. Behav Ecol Sociobiol. 2002; 51:480–487.

Bertram, BCR. Living in groups: predators and prey. In: Krebs, JR.; Davies, NB., editors. Behavioural ecology: and evolutionary approach. Oxford: Blackwell Scientific Publications; 1978. p. 64-96.

Bozinovic F. Nutritional energetics and digestive responses of an herbivorous rodent (*Octodon degus*) to different levels of dietary fiber. J Mammal. 1995; 76:627–637.

Brashares JS, Arcese P. Role of forage, habitat and predation in the behavioral plasticity of a small African antelope. J Anim Ecol. 2002; 71:626–638.

Brashares JS, Garland T Jr, Arcese P. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behav Ecol. 2000; 11:452–463.

Brown, JL. Helping and communal breeding in birds: ecology and evolution. USA: Princeton University Press; 1987.

Burnham, KP.; Anderson, DR. Model selection and multimodel inference. 2nd edn.. New York: Springer; 2002.

Canals M, Rosenmann M, Bozinovic F. Energetics and geometry of huddling in small mammals. J Theor Biol. 1989; 141:181–189. [PubMed: 2632987]

Caro TM, Graham CM, Stoner CJ, Vargas JK. Adaptive significance of antipredator behaviour in artiodactyls. Anim Behav. 2004; 67:205–228.

Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll AD, Kansky R, Chadwick P, Manser M, Skinner JD, Brotherton PNM. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. J Anim Ecol. 1999; 68:672–683.

Cooch E, White G. Program Mark: a gentle introduction. 2008 http://www.phidot.org/software/mark/index.html.

di Castri, F.; Hajek, E. Bioclimatología de Chile. Santiago: Pontificia Universidad Católica de Chile; 1976.

Ebensperger LA. A review of the evolutionary causes of rodent group-living. Acta Theriol. 2001; 46:115–144.

Ebensperger LA, Blumstein DT. Sociality in New World hystricognath rodents is linked to predators and burrow digging. Behav Ecol. 2006; 17:410–418.

Ebensperger LA, Bozinovic F. Energetics and burrowing behaviour in the semifossorial degu, *Octodon degus* (Rodentia: Octodontidae). J Zool (Lond). 2000a; 252:179–186.

Ebensperger LA, Bozinovic F. Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality? Behav Ecol Sociobiol. 2000b; 47:365–369.

Ebensperger LA, Cofré H. On the evolution of group-living in the New World cursorial hystricognath rodents. Behav Ecol. 2001; 12:227–236.

Ebensperger LA, Hayes LD. On the dynamics of rodent social groups. Behav Process. 2008; 79:85–92.

Ebensperger LA, Hurtado MJ. On the relationship between herbaceous cover and vigilance activity of degus (*Octodon degus*). Ethology. 2005a; 111:593–608.

Ebensperger LA, Hurtado MJ. Seasonal changes in the time budget of degus, *Octodon degus*. Behaviour. 2005b; 142:91–112.

Ebensperger LA, Wallem PK. Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. Oikos. 2002; 98:491–497.

Ebensperger LA, Veloso C, Wallem PK. Do female degus communally nest and nurse their pups? J Ethol. 2002; 20:143–146.

Ebensperger LA, Hurtado MJ, Soto-Gamboa M, Lacey EA, Chang AT. Communal nesting and kinship in degus (*Octodon degus*). Naturwissenschaften. 2004; 91:391–395. [PubMed: 15309311]

Ebensperger LA, Hurtado MJ, Ramos-Jiliberto R. Vigilance and collective detection of predators in degus (*Octodon degus*). Ethology. 2006; 112:879–887.

Ebensperger LA, Hurtado MJ, León C. An experimental examination of the consequences of communal versus solitary breeding on maternal condition and the early postnatal growth and survival of degu, *Octodon degus*, pups. Anim Behav. 2007; 73:185–194.

Ebensperger LA, Chesh AS, Castro RA, Ortiz Tolhuysen L, Quirici V, Burger JR, Hayes LD. Instability rules social groups in the communal breeder rodent *Octodon degus*. Ethology. 2009; 15:540–554.

Ebensperger LA, Ramírez-Otarola N, León C, Ortiz ME, Croxatto HB. Early fitness consequences and hormonal correlates of parental behaviour in the social rodent, *Octodon degus*. Physiol Behav. 2010; 101:509–517. [PubMed: 20688088]

Ebensperger LA, Chesh AS, Castro RA, Ortiz Tolhuysen L, Quirici V, Burger JR, Sobrero R, Hayes LD. Burrow limitations and group living in the communally rearing rodent, *Octodon degus*. J Mammal. 2011; 92:21–30. [PubMed: 22328789]

Edelman AJ, Koprowski JL. Communal nesting in asocial Abert's squirrels: the role of social thermoregulation and breeding strategy. Ethology. 2007; 113:147–154.

Emlen ST. An evolutionary theory of the family. Proc Natl Acad Sci USA. 1995; 92:8092–8099. [PubMed: 7667250]

Foster, SA.; Endler, JA. Geographic variation in behavior: perspectives on evolutionary mechanisms. New York: Oxford University Press; 1999.

Fulk GW. Notes on the activity, reproduction, and social behavior of *Octodon degus*. J Mammal. 1976; 57:495–505.

Getz LL, McGuire B. Communal nesting in prairie voles (*Microtus ochrogaster*): formation, composition, and persistence of communal groups. Can J Zool. 1997; 75:525–534.

Gygax L. Evolution of group size in the superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae): a quantitative comparative analysis. Mammal Rev. 2002; 32:295–314.

Hass CC, Valenzuela D. Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). Behav Ecol Sociobiol. 2002; 51:570–578.

Hayes LD, Chesh AS, Ebensperger LA. Ecological predictors of range areas and use of burrow systems in the diurnal rodent, *Octodon degus*. Ethology. 2007; 113:155–165.

Hayes LD, Chesh AS, Castro RA, Ortiz Tolhuysen L, Burger JR, Bhattacharjee J, Ebensperger LA. Fitness consequences of group living in the degu *Octodon degus*, a plural breeder rodent with communal care. Anim Behav. 2009; 78:131–139.

Hill RA, Lee PC. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. J Zool (Lond). 1998; 245:447–456.

Hoogland, JL. The black-tailed prairie dog: social life of a burrowing mammal. Chicago: University of Chicago Press; 1995.

Houston J. Variability of precipitation in the Atacama desert: its causes and hydrological impact. Int J Climatol. 2006; 26:2181–2198.

Houston J, Hartley AJ. The central Andean west-slope rainshadow and its potential contribution to the origin of hyper-aridity in the Atacama desert. Int J Climatol. 2003; 23:1453–1464.

Jarvis JUM, O'Riain MJ, Bennett NC, Sherman PW. Mammalian eusociality: a family affair. Trends Ecol Evol. 1994; 9:47–51. [PubMed: 21236765]

Johnson DDP, Jetz W, Macdonald DW. Environmental correlates of badger social spacing across Europe. J Biogeogr. 2002; 29:411–425.

Keesing F. Ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. J Mammal. 1998; 79:919–931.

Kenagy GJ, Nespolo RF, Vásquez RA, Bozinovic F. Daily and seasonal limits of time and temperature to activity of degus. Rev Chil Hist Nat. 2002; 75:567–581.

Koprowski, JL. Conflict between the sexes: a review of social and mating systems of the tree squirrels. In: Steele, MA.; Merritt, JF.; Zegers, DA., editors. Ecology and evolutionary biology of tree squirrels. Vol. 6. Virginia Museum of Natural History, Special Publication; 1998. p. 33-41.

Krause, J.; Ruxton, GD. Living in groups. Oxford: Oxford University Press; 2002.

Lacey EA, Wieczorek JR. Ecology of sociality in rodents: a ctenomyid perspective. J Mammal. 2003; 84:1198–1211.

Lagos PA, Meier A, Ortiz Tolhuysen L, Castro RA, Bozinovic F, Ebensperger LA. Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. Can J Zool. 2009; 87:1016–1023.

Levine TR, Hullett CR. Eta squared, partial eta squared, and misreporting of effect size in communication research. Hum Commun Res. 2002; 28:612–625.

Lott, DF. Intraspecific variation in the social systems of wild vertebrates. Cambridge: Cambridge University Press; 1991.

Lovegrove BG. The cost of burrowing by the social mole rats (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture. Physiol Zool. 1989; 62:449–469.

Lucia KE, Keane B, Hayes LD, Lin YK, Schaefer RF, Solomon NG. Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. Behav Ecol. 2008; 19:774–783.

Madison, DM. Group nesting and its ecological and evolutionary significance in overwintering microtine rodents. In: Merritt, JF., editor. Winter ecology of small mammals. Vol. 10. Carnegie Museum of Natural History, Special Publication; 1984. p. 267-274.

Maher C, Burger JR. Intraspecific variation in space use, group size, and mating systems of caviomorph rodents. J Mammal. 2011; 92:54–64. [PubMed: 22328790]

Meserve PL, Martin RE, Rodriguez J. Feeding ecology of two Chilean caviomorphs in a central Mediterranean savanna. J Mammal. 1983; 64:322–325.

Moorhouse TP, Macdonald DW. What limits male range sizes at different population densities? Evidence from three populations of water voles. J Zool (Lond). 2008; 274:395–402.

Nakagawa S, Foster TM. The case against retrospective statistical power analyses with an introduction to power analysis. Acta Ethol. 2004; 7:103–108.

Newman MEJ. Analysis of weighted networks. Phys Rev E. 2004; 70 056131.

Parrish, JK.; Hamner, WM.; Prewitt, CT. Introduction—from individuals to aggregations: unifying properties, global framework, and the holy grails of congregation. In: Parrish, JK.; Hamner, WM., editors. Animal groups in three dimensions. Cambridge: Cambridge University Press; 1997. p. 1-13.

Powell RA, Fried JJ. Helping by juvenile pine voles (*Microtus pinetorum*), growth and survival of younger siblings, and the evolution of pine vole sociality. Behav Ecol. 1992; 3:325–333.

Quirici V, Castro RA, Ortiz Tolhuysen L, Chesh AS, Burger JR, Miranda E, Cortés A, Hayes LD, Ebensperger LA. Seasonal variation in the range areas of the diurnal rodent *Octodon degus*. J Mammal. 2010; 91:458–466. [PubMed: 22328788]

Quirici V, Faugeron S, Hayes LD, Ebensperger LA. The influence of group size on natal dispersal in the communally rearing and semifossorial rodent, *Octodon degus*. Behav Ecol Sociobiol. 2011; 65:787–798.

Quispe R, Villavicencio CP, Cortés A, Vásquez RA. Inter-population variation in hoarding behaviour in degus, *Octodon degus*. Ethology. 2009; 115:465–474.

R Development Core Team. R Foundation for Statistical Computing. Vienna: 2006. R: a language and environment for statistical computing.

Ribble DO, Stanley S. Home ranges and social organization of syntopic *Peromyscus boylli* and *P. truei*. J Mammal. 1998; 79:932–941.

Rolland C, Danchin E, de Fraipont M. The evolution of coloniality in birds in relation to food, habitat, predation, and life history traits: a comparative analysis. Am Nat. 1998; 151:514–529. [PubMed: 18811373]

Schradin C, Pillay N. Intraspecific variation in the spatial and social organization of the African striped mouse. J Mammal. 2005; 86:99–107.

Silk JB. The adaptive value of sociality in mammalian groups. Phil Trans R Soc Lond B. 2007; 362:539–559. [PubMed: 17363359]

Slobodchikoff, CN. The ecology of social behaviour. San Diego: Academic Press, Inc; 1984.

Solomon, NG.; Getz, LL. Examination of alternative hypotheses for cooperative breeding in rodents. In: Solomon, NG.; French, JA., editors. Cooperative breeding in mammals. Cambridge: Cambridge University Press; 1997. p. 199-230.

Soto-Gamboa, M. Ph.D. Dissertation. Pontificia Universidad Católica de Chile; 2004. formación y estabilidad de estructuras sociales en micromamíferos, su regulación hormonal y la importancia de las interacciones entre machos.

Spinks AC, Bennett NC, Jarvis JUM. Comparative patterns of philopatry and dispersal in two common mole-rat populations: implications for the evolution of mole-rat sociality. J Anim Ecol. 2000; 69:224–234.

Stapp P, Pekins PJ, Mautz WW. Winter energy expenditure and the distribution of southern flying squirrels. Can J Zool. 1991; 69:2548–2555.

Symonds MRE, Moussalli A. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol. 2011; 65:13–21.

Taraborelli P, Moreno P. Comparing composition of social groups, mating system and social behaviour in two populations of *Microcavia australis*. Mamm Biol. 2009; 74:15–24.

Travis SE, Slobodchikoff CN, Keim P. Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. Ecology. 1995; 76:1794–1803.

Van Soeste, IJ. Nutritional ecology of the ruminant. Ithaca: Cornell University Press; 1982.

Vásquez RA. Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile. Rev Chil Hist Nat. 1997; 70:557–563.

Vásquez RA, Ebensperger LA, Bozinovic F. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. Behav Ecol. 2002; 13:182–187.

Veloso C, Bozinovic F. Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. Ecology. 1993; 74:2003–2010.

Verdolin JL. Resources, not male mating strategies, are a determinant of social structure in Gunnison's prairie dogs (*Cynomys gunnisoni*). Behaviour. 2007; 144:1361–1382.

West SD. Midwinter aggregation in the red-backed vole, *Clethrionomys rutilus*. Can J Zool. 1977; 55:1404–1409.

White GC, Burnham KP. Program MARK: survival estimation from populations of marked animals. Bird Stud. 1999; 46(Suppl):120–138.

Whitehead, H. Analyzing animal societies: quantitative methods for vertebrate social analysis. Chicago: Chicago University Press; 2008.

Whitehead H. SOCPROG programs: analyzing animal social structures. Behav Ecol Sociobiol. 2009; 63:765–778.

Wolff JO. Reproductive success of solitarily and communally nesting white-footed and deer mice. Behav Ecol. 1994; 5:206–209.

Wrangham RW. An ecological model of female-bonded primate groups. Behaviour. 1980; 75:262–300.
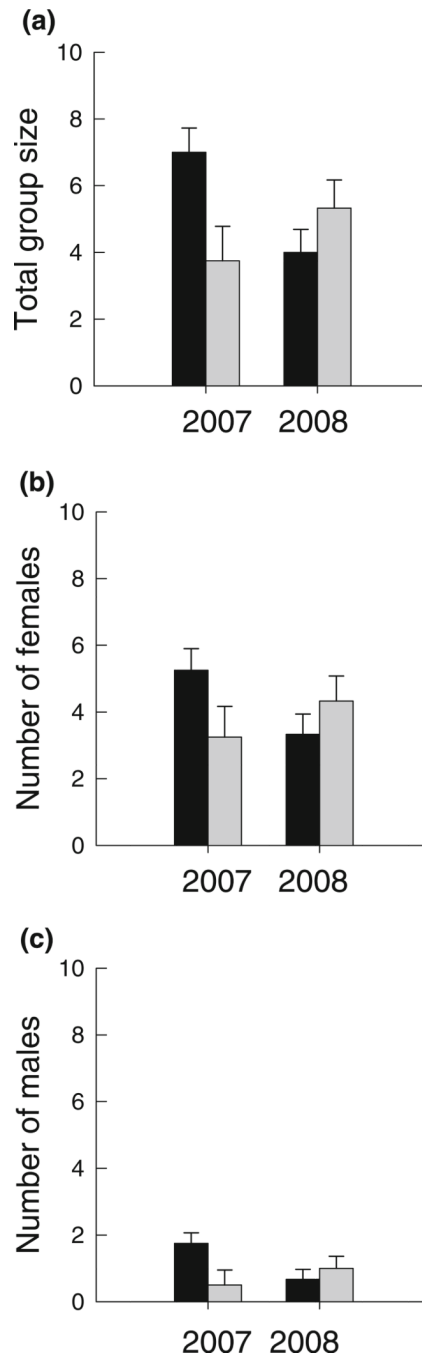
Fig. 1.
Mean (±SE) total group size (**a**), number of female group members (**b**), and number of male group members (**c**) at Rinconada (*black square*) and Los Molles (*white square*). *Lines* and *asterisks* on top of the bars are used to indicate differences between sites when the best-fit AIC model that explained these differences was also well supported. A best fit model that was well supported had the lowest AIC value, delta AIC<2, Akaike weight approaching 0.90 or higher, and evidence ratios close to 1 (Burnham and Anderson 2002; Symonds and Moussalli 2011). A total of 27 social groups were used as replicates
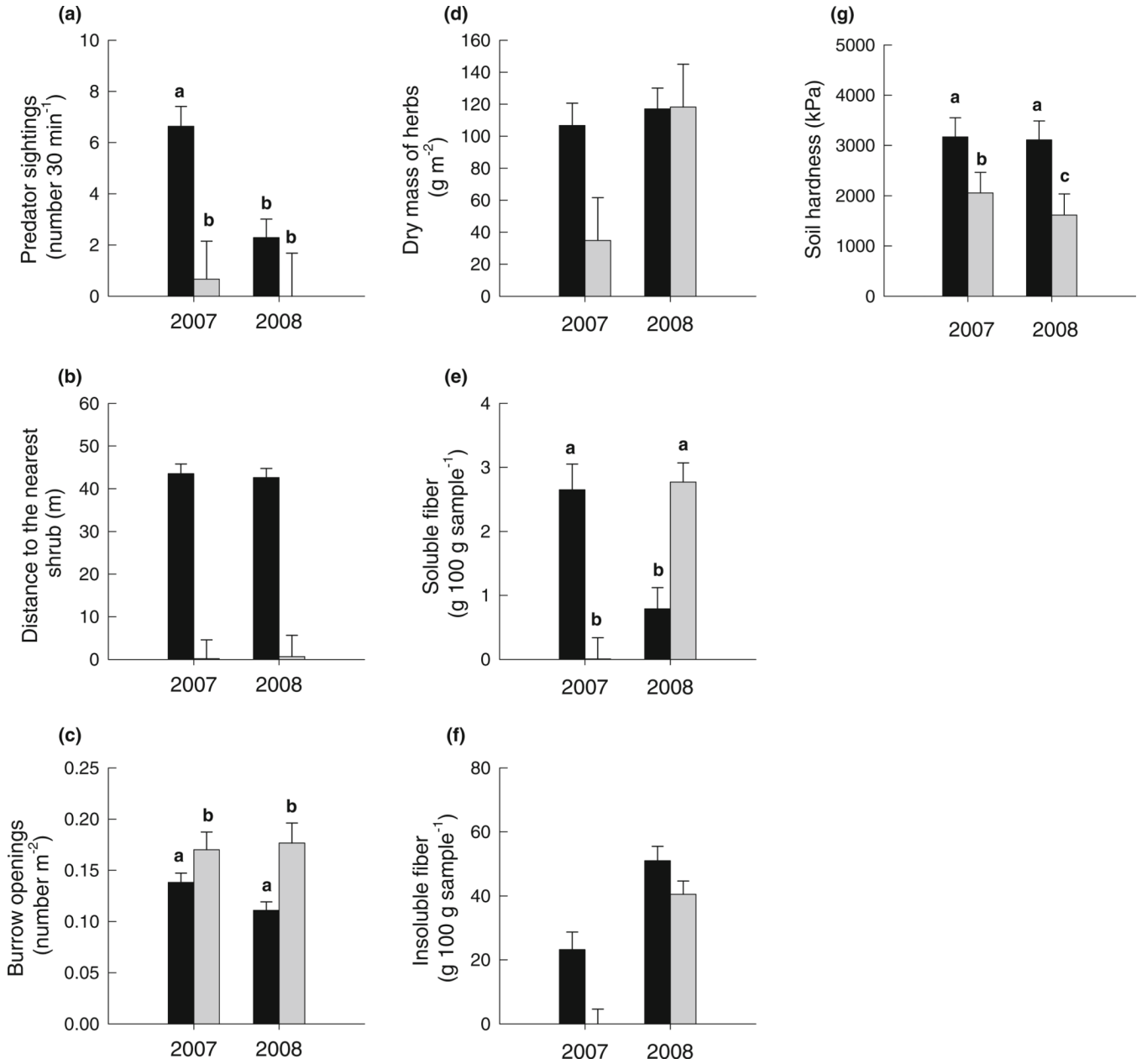
Fig. 2.
Mean (±SE) population (*black square* Rinconada; *white square* Los Molles) and year of study differences in terms of **a** number of predator sightings, **b** distance of main burrow systems used to the nearest shrub, **c** density of burrow openings, **d** abundance of food, **e** amount of soluble fiber, **f** amount of insoluble fiber, and **g** soil hardness. *Different letters on top of the bars* are used to indicate population or year differences when the best-fit AIC model that explained these differences was also well supported. A best fit model that was well supported had the lowest AIC value, delta AIC<2, Akaike weight approaching 0.90 or higher, and evidence ratios close to 1 (Burnham and Anderson 2002; Symonds and Moussalli 2011). For abundance of food and density of burrow openings differences were examined on squared root transformed values

Table 1

Functional hypotheses for group living that were examined in *Octodon degus* (for a discussion of specific mechanisms associated to each hypothesis, see Ebensperger (2001))

Functional hypothesis	Predictions	
	Between population	**Within population**
Group living decreases predation risk	Larger social groups in the population with more frequent predator sightings	
	Larger social groups in the population where distance from burrows used by social groups to the nearest shrub (protective cover) is greater	Group size increases with distance from burrows used to the nearest shrub cover
	Greater density of burrow openings in burrows used by larger social groups	Density of burrow openings increases with group size
Group living decreases thermoregulation cost	Larger social groups in the population facing lower ambient temperature	
Group living decreases costs of nest/refuge building	Larger social groups in the population facing harder soil conditions (i.e., higher digging costs)	Group size increases with increasing soil hardness
Group living enhances foraging efficiency	Larger social groups in the population holding a greater abundance or quality of food	Group size increases with increasing abundance of food

Table 2

AIC values of the four possible best-fit models explaining between-site differences in total group size, number of females per group, and number of males per group

Variable examined and model	Number of parameters	AIC	Delta AIC	AIC weight	Evidence ratio
Total group size					
Population × year	3	*121.45*	*0.00*	*0.81*	*1.00*
Population + year	2	127.11	5.66	0.05	0.06
Population	1	127.48	6.03	0.04	0.05
Year	1	125.60	4.15	0.12	0.13
Number of females					
Population × year	3	**115.12**	**0.00**	**0.40**	**1.00**
Population + year	2	117.54	2.42	0.12	0.30
Population	1	116.86	1.74	0.17	0.42
Year	1	115.68	0.56	0.31	0.76
Number of males					
Population × year	3	**76.41**	**0.00**	**0.56**	**1.00**
Population + year	2	79.51	3.10	0.12	0.21
Population	1	79.52	3.11	0.12	0.21
Year	1	78.37	1.96	0.21	0.38

Italicized values indicate the best-fit and well supported model for each variable. Values in bold indicate the best-fit yet not well supported model for each variable. A best fit model that was well supported had the lowest AIC value, delta AIC<2, Akaike weight approaching 0.90 or higher, and evidence ratios close to 1 (Burnham and Anderson 2002; Symonds and Moussalli 2011)

Table 3

AIC values of the four possible best-fit models explaining between-site differences in predator sightings, distance from burrows to nearest shrub, density of burrow openings, abundance of food, soluble and insoluble fiber in food, and soil hardness (see text for all units)

Variable examined and model	Number of parameters	AIC	Delta AIC	AIC weight	Evidence ratio
Predator sightings					
Population × year	3	*744.14*	*0.00*	*0.98*	*1.00*
Population + year	2	751.45	7.31	0.03	0.03
Population	1	765.87	21.73	0.00	0.00
Year	1	777.51	33.37	0.00	0.00
Distance from burrows to nearest shrub					
Population × year	3	701.57	3.91	0.09	0.14
Population + year	2	699.61	1.95	0.25	0.38
Population	1	**697.66**	**0.00**	**0.66**	**1.00**
Year	1	782.04	84.38	0.00	0.00
Density of burrow openings					
Population × year	3	394.27	7.74	0.0194	0.0209
Population + year	2	394.78	8.25	0.02	0.02
Population	1	*386.53*	*0.00*	*0.93*	*1.00*
Year	1	393.18	6.65	0.03	0.04
Food abundance					
Population × year	3	490.93	0.56	0.31	0.76
Population + year	2	491.23	0.86	0.27	0.65
Population	1	**490.37**	**0.00**	**0.42**	**1.00**
Year	1	508.93	18.56	0.00	0.00
Soluble fiber					
Population × year	3	*60.99*	*0.00*	*1.00*	*1.00*
Population + year	2	87.08	26.09	0.00	0.00
Population	1	86.95	25.96	0.00	0.00
Year	1	85.08	24.09	0.00	0.00
Insoluble fiber					
Population × year	3	129.33	1.02	0.37	0.60
Population + year	2	**128.31**	**0.00**	**0.61**	**1.00**

Variable examined and model	Number of parameters	AIC	Delta AIC	AIC weight	Evidence ratio
Population	1	154.36	26.05	0.00	0.00
Year	1	135.45	7.14	0.02	0.03
Soil hardness					
Population × year	3	*277.01*	*0.00*	*0.99*	*1.00*
Population + year	2	289.75	12.74	0.00	0.00
Population	1	297.81	20.80	0.00	0.00
Year	1	471.84	194.83	0.00	0.00

Italicized values indicate the best-fit and well supported model for each variable. Values in bold indicate the best-fit yet not well supported model for each variable. A best fit model that was well supported had the lowest AIC value, delta AIC<2, Akaike weight approaching 0.90 or higher, and evidence ratios close to 1 (Burnham and Anderson 2002; Symonds and Moussalli 2011)