Journal of Mammalogy, 97(2):361–372, 2016
DOI:10.1093/jmammal/gyv182
Published online November 25, 2015

Octodon degus kin and social structure

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A growing body of evidence showing that individuals of some social species live in non-kin groups suggests kin selection is not required in all species for sociality to evolve. Here, we investigate 2 populations of *Octodon degus*, a widespread South American rodent that has been shown to form kin and non-kin groups. We quantified genetic relatedness among individuals in 23 social groups across 2 populations as well as social network parameters (association, strength, and clustering coefficient) in order to determine if these aspects of sociality were driven by kinship. Additionally, we analyzed social network parameters relative to ecological conditions at burrow systems used by groups, to determine if ecological characteristics within each population could explain variation in sociality. We found that genetic relatedness among individuals within social groups was not significantly higher than genetic relatedness among randomly selected individuals in both populations, suggesting that non-kin structure of groups is common in degus. In both populations, we found significant relationships between the habitat characteristics of burrow systems and the social network characteristics of individuals inhabiting those burrow systems. Our results suggest that degu sociality is non-kin based and that degu social networks are influenced by local conditions.

Es creciente la evidencia que apoya la ocurrencia de especies sociales donde los individuos no están emparentados genéticamente, lo que sugiere que la selección de parentesco no es indispensable para la evolución de la sociabilidad. En este estudio se examinaron dos poblaciones de *Octodon degus*, un roedor sudamericano donde los grupos sociales pueden o no incluir individuos cercanamente emparentados. Se cuantificó el parentesco genético entre individuos en 23 grupos sociales y en redes sociales de dos poblaciones para determinar si estos aspectos de la sociabilidad dependen del grado de parentesco. Además, se examinaron asociaciones entre los parámetros cuantificados de las redes sociales (asociación, fuerza, coeficiente de anidamiento) y las condiciones ecológicas a nivel de los sistemas de madriguera usados por cada grupo. El grado de parentesco genético dentro de los grupos no fue distinto del grado de parentesco entre individuos de la población tomados al azar, lo que apoya que una estructura de grupos no emparentada es la regla en *Octodon degus*. En ambas poblaciones se registró una asociación entre características ecológicas de los sistemas de madriguera y atributos de las redes sociales de los individuos que usan estas estructuras. Nuestros resultados indican que la sociabilidad en *Octodon degus* no está basada en relaciones de parentesco y que las redes sociales de estos animales dependen de las condiciones ecológicas.

Key words: non-kin groups, *Octodon degus*, social networks, sociality

Social structure summarizes the nature and extent to which animals interact with others within a population (Whitehead 2008; Schradin 2013). In social species, the interactions among individuals in a population are the background upon which foraging, mating, and reproductive interactions take place (Wolf et al. 2007). Thus, determining the factors that influence these interactions is crucial to developing a comprehensive understanding of the evolution of sociality. One

well-established model explaining potential conditions leading to and favoring sociality is Emlen's (1995) "integrated theory of family social dynamics." This model incorporates 2 important concepts—ecological constraints (Emlen 1982) and kin selection (Hamilton 1964)—to explain the evolution of animal sociality. The model posits that extended family groups (kin groups) form when juveniles remain philopatric to the natal group under conditions that limit direct reproduction (ecological constraints—Emlen 1982). Under these conditions, kin selection theory predicts that breeders benefit when philopatric individuals assist with offspring care (alloparental care) and philopatric individuals benefit indirectly by providing care to non-descendent offspring produced by closely related kin (Hamilton 1964; Maynard-Smith 1964). Thus, parental care directed toward closely related kin is predicted to increase an individual's inclusive fitness (Hamilton 1964; Maynard-Smith 1964).

The 2 main thrusts of Emlen's model—ecological constraints and kin selection—have been the subject of considerable theoretical and empirical work for decades. The effects of ecological constraints on animal sociality have been demonstrated in several mammals (e.g., Travis et al. 1995; Lucia et al. 2008; Schoepf and Schradin 2012). Consequently, ecological constraints are often viewed as a primary driver for social group formation (but see Arnold and Owens 1998). Regarding the influence of kin selection, decades of research have validated that some mammalian groups typically consist of extended families (Solomon 2003; Kappeler 2008). Taken together, these observations suggest that natal philopatry and inclusive fitness benefits are defining characteristics of groups in many social species (Emlen 1995; Lacey and Sherman 2007; but see Griffin and West 2002).

Emlen's model does not apply universally to social animals and natal philopatry is not the only mechanism underlying the formation of mammal social groups. In some mammals (Faulkes and Bennett 2001; Guichón et al. 2003; Ebensperger et al. 2009), individual or multiple adults move into existing social groups or establish new groups with unrelated conspecifics (Ebensperger and Hayes 2008). Such emigration may be driven by improved breeding opportunities elsewhere (Emlen 1982) or high costs of living with current group members, including competition for resources (Janson 1988), parasitism (Rifkin et al. 2012), or risk of inbreeding (Pusey and Wolf 1996). Consequently, some of these species may live in non-kin social groups with low mean levels of relatedness. Among mammals that live in relatively long-term social groups (i.e., excluding species that form temporal aggregations or herds), non-kin social groups have been reported for relatively few species, including bats (Metheny et al. 2008), cetaceans (Mann et al. 2000; Krützen et al. 2003), and rodents (Túnez et al. 2009; Quirici et al. 2011a). Under these social conditions, individuals do not gain indirect fitness benefits from living in groups and inclusive fitness is based entirely on direct fitness.

Cooperation among unrelated individuals may reflect strategies to attract or retain a potential mate (Clutton-Brock 2009) or result from benefits derived from reciprocity among non-kin (Trivers 1971; Clutton-Brock 2009). Among mammals, reciprocal exchanges of resources (Wilkinson 1984), assistance in mating competition (Packer 1977), and allogrooming (Barrett et al. 2002) may be directed to potential mates or unrelated conspecifics (see Clutton-Brock 2009:54, Table 1). Some of these apparently cooperative interactions may be the result of manipulative strategies in which one individual dominates the other (Clutton-Brock 2009). Individuals living with non-kin may also gain direct fitness benefits through group size effects (Krause and Ruxton 2002), such as dilution of predation risk or increased access to resources and access to breeding opportunities (Ebensperger and Cofré 2001).

Intraspecific variation in social systems has been observed in several mammal species (Travis and Slobodchikoff 1993; Brashares and Arcese 2002; Streatfeild et al. 2011). Such variation is expected if the associated costs and benefits of sociality depend on local ecological conditions and result in differential selection on the behaviors influencing group formation (Emlen and Oring 1977; Lott 1991). At the proximate level, intraspecific variation in social structure may arise due to genetic variation and/or varying levels of phenotypic plasticity between populations (Quispe et al. 2009; Schradin 2013). Since groups composed of non-kin are not as well studied, it is critical to investigate the extent to which non-kin social structure is linked to habitat-specific environmental conditions. By identifying the social structure of groups in multiple populations across a species' geographical range, we can determine if non-kin groups are common or the rare product of local conditions acting upon individual populations.

The most commonly used metric of sociality—group size—provides only 1 dimension of an animal's social system. A limitation of group size metrics is that they do not quantify the types of interactions among individuals in a group, limiting our understanding of the evolution of sociality (Wey et al. 2008). A quantifiable method of analysis for such issues is social network analysis (Wey et al. 2008; Whitehead 2008; Sih et al. 2009). Social networks model the ways in which individuals interact with other individuals in the population, allowing researchers to quantify the strength and extent of relationships in ways that traditional methods of social determination cannot (Sih et al. 2009). By analyzing the network dynamics at both the individual and social group level (calculated as means from the values of each group member), it is possible to answer questions about an individual's social connections as well as questions about how the individual associations interact at varying levels to form the social structure of the population as a whole (Wey et al. 2008). For example, social network analysis has provided insights into complex patterns of sociality, including quantifying distinct structural layers within a population's social system (Wolf and Trillmich 2008) and determining how associations predict patterns of cooperation (Croft et al. 2006). Based on kin selection theory, we expect stronger social interactions among kin than non-kin, a prediction that can be tested by comparing within-group relatedness (calculated as a mean from the pairwise relatedness values of group members) with group-level social network parameters (association: proportion

of time individuals are trapped together; strength: sum of an individual's associations), which quantify the frequency in which individuals are recorded in close proximity. Further, ecological characteristics may influence social network parameters by dictating how individuals move through their environment both spatially and temporally, ultimately affecting the extent to which they interact with other individuals in a given area.

An appropriate study species for investigating such questions is the degu (*Octodon degus*), a group living caviomorph rodent endemic to central Chile (Hayes et al. 2011). Degus are widespread, occurring in ecologically distinct habitats throughout their geographic range (Meserve et al. 1984; Quispe et al. 2009; Ebensperger et al. 2012), making them a good model organism for examining how local conditions influence the formation and composition of groups and social associations at the population level. In 1 population (Rinconada de Maipú, Chile; hereafter Rinconada), the immigration and emigration of adults into and out of groups is a more important driver of group formation than natal philopatry by offspring (Ebensperger et al. 2009). Consequently, groups consist of relatives and/or unrelated individuals (Ebensperger et al. 2004; Quirici et al. 2011a) and the genetic relatedness (R) of individuals within groups is similar to that of the background population, indicating an absence of kin structure (Quirici et al. 2011a). A recent study comparing social groups in Rinconada and a 2nd population located 400 km north of Santiago at Bocatoma—Rio Los Molles (hereafter Los Molles)—revealed that groups differ in size between these populations (Ebensperger et al. 2012). This observation suggests some degree of intraspecific variation in degu social organization (also see Quispe et al. 2009). To date, no one has investigated if these differences in social organization and local ecological conditions are linked to differences in kin and social network structure. The objectives of this study were to determine if kin structure differed between 2 degu populations and to use social network analysis to investigate possible links between ecological conditions, kinship, and social associations at both individual- and group-level scales within each population.

While non-kin groups are prevalent at Rinconada, the kin structure of social groups at Los Molles was previously unknown. Ebensperger et al. (2012) also showed that the sites differ in predation risk and distribution of food resources. If group formation at Los Molles follows the expectations of Emlen's model, we predict greater natal philopatry and a greater percentage of kin groups at Los Molles, where resources are more patchily distributed compared to Rinconada. This prediction is based on ecological constraints, since a patchy resource distribution will cause more disparities between natal territory quality and the surrounding territories. Consequently, we also predict that relatedness of group members increases with increasing group size (due to greater natal philopatry) and that genetic relatedness and group size will influence group-level social network parameters at Los Molles.

Alternatively, adult movements may influence social structure more than natal philopatry (Ebensperger and Hayes 2008; Ebensperger et al. 2009), resulting in social groups that primarily comprised non-kin. Under these conditions, we expect a similar percentage of groups to be non-kin groups in Rinconada and Los Molles and a negative relationship between the relatedness of group members and group size due to the addition of more adults at both sites. If social network structure is driven by within-site ecological conditions (e.g., food availability near burrows), regardless of social structure, we predict a positive relationship between the habitat quality at burrows used by an individual and that individual's social network parameters (strength and clustering coefficient, the extent to which an individual's associates interact with each other).

Materials and Methods

Study populations.—This study was conducted on degu populations at Rinconada de Maipú, Chile (33°23′S, 70°31′W; 495 m altitude) and Bocatoma—Rio Los Molles (30°45′S, 70°15′W; 2,600 m altitude), Chile. Both sites are characterized by a semi-arid, Mediterranean climate with seasonally variable precipitation. The habitat type at Rinconada is a Chilean matorral with a mixture of open areas and shrubs. The habitat type at Los Molles is characterized by a greater density of shrubs (Ebensperger et al. 2012). Rinconada has harder soil, greater food abundance, greater distance from burrows to overhead cover, and lower density of burrow openings than Los Molles (Ebensperger et al. 2012). Predator sightings are more frequent at Rinconada than Los Molles (Ebensperger et al. 2012). The fieldwork was conducted in 2007 and 2008, during the time when females were in late pregnancy or lactating (i.e., September–October at Rinconada and November–December at Los Molles). In the current study, we analyzed tissue samples collected from 23 social groups (17 at Rinconada and 6 at Los Molles) of free-living degus. All applicable international, national, and/or institutional guidelines for the care and use of animals, including those of the American Society of Mammalogists, were followed. The study was covered by IACUC permit no. 0507LH-02 to LDH.

Ecological sampling.—To quantify food availability, a 250 × 250-mm quadrat was placed at 3 and 9 m from the center of each burrow system (defined as a group of burrows surrounding a central location where individuals were repeatedly found during telemetry—Hayes et al. 2007) in one of the cardinal directions (randomly selected for each distance at each burrow system), and all above-ground green herbs were removed, dried, and weighed for biomass. Burrow density (openings per square meter) was quantified by counting the number of burrow openings within a 9-m radius from the center of each burrow system. Soil hardness was sampled similarly to food availability, with a soil penetrability measurement taken at 3 and 9 m from the center of each burrow system in one of the cardinal directions. Distance to overhead cover was measured from the center of each burrow system using a 100-m measuring tape (Ebensperger et al. 2012).

Social group determination.—Degus are diurnal and remain in underground burrows with conspecifics overnight (Ebensperger

et al. 2004). Thus, the main criterion used to assign degus to social groups was the sharing of burrow systems during the nighttime (Ebensperger et al. 2004). To determine social group membership, we used a combination of nighttime telemetry and early morning burrow trapping. Burrow systems were trapped an average of 31.4 ± 1.2 ($\bar{X}$ ± *SE*) days in 2007 and 45.3 ± 1.6 days in 2008 at Rinconada, and for 30 days in 2007 and 21 days in 2008 at Los Molles. Tomahawk live traps (model 201, Tomahawk Live Trap Company, Hazelhurst, Wisconsin) were set prior to the emergence of adults during the early morning hours (0700–0730) and were checked and closed after 1.5 h. The identity, sex, body mass, and reproductive condition of all individuals were determined at 1st capture. Additionally, a small tissue sample was taken from each individual's ear the 1st time it was captured and stored in 99% ethanol at 0°C. Adults weighing more than 170 g were fitted with 8 g BR radiocollars (AVM Instrument Co., Colfax, California) or 7–9 g radiotransmitters (RI-2D; Holohil Systems Limited, Carp, Ontario, Canada) with unique frequencies.

During nighttime telemetry, females were radiotracked to burrow systems. Previous studies at Rinconada have demonstrated that telemetry locations represent sites where degus remain underground throughout the night (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., Colfax, California) and a hand held, 3-element Yagi antenna (AVM instrument Co., Colfax, California).

To determine social group membership, we created a similarity matrix of pairwise associations of the burrow locations of all adult degus during trapping and telemetry (see Whitehead 2009). Associations were determined using the "simple ratio" association index (Ginsberg and Young 1992), i.e., the number of times that 2 individuals are captured or tracked via telemetry at the same burrow system on the same day divided by the total number of times each is captured/tracked on the same day regardless of burrow system. For example, 2 individuals who were always trapped together would receive an association value of 1, while 2 individuals who were never trapped together would receive a value of 0. Social groups were determined using a hierarchical cluster analysis in SOCPROG 2.0 software (Whitehead 2009). Only associations with a value greater than 0.1 (i.e., 10% overlap of trapping/telemetry locations) were considered to be part of the same social group (Hayes et al. 2009). We consider individuals with 10–50% overlap as "associates" of groups (Hayes et al. 2009). We include these individuals because they likely have sufficient interactions with other more closely associating group members to potentially impact reproductive success of group members and/or stability of groups.

Since social network parameters are calculated based on trapping data, only degus that were trapped for at least 5 days were included in analyses to exclude poorly sampled individuals (Wey et al. 2013). Thus, some individuals and social groups previously used in Ebensperger et al. (2012) were excluded from our study to avoid biasing the network data. For example, Ebensperger et al. (2012) reported 4 social units at Los Molles in 2007; however, one of these units consisted of a solitary individual, and several individuals within 2 other groups were trapped infrequently. Thus, we use only 1 social group from this year in this study.

Social network analysis.—Social network analysis was used to look for patterns of sociality at the individual level, including pairwise relationships between group members and non-group members. For each individual, we calculated the strength—the sum of associations (Whitehead 2008)—calculated from the pairwise association networks. High strength indicates a high total amount of spatial and temporal overlap with other individuals, resulting from strong associations, many associations, or a combination of both (Wey et al. 2013). For each individual, we also calculated the clustering coefficient, a measure of how connected an individual's associates are to each other (e.g., an individual with a high clustering coefficient has close associations with individuals who also associate closely with each other, forming a "cluster"). For each social group, we calculated the mean association (from each pair of group members, based on the "simple ratio" explained above) and the mean strength, based on the individual values for each group member. Network parameters were calculated from pairwise similarity matrices in SOCPROG 2.0.

Genetic analysis.—Genetic analyses to determine relatedness (R—following Quirici et al. 2011a) were conducted in the Molecular Ecology lab at the Universidad de Chile in Santiago, Chile. Analyses were conducted on tissue samples collected from $n = 14$ and $n = 26$ individuals at Los Molles and $n = 21$ and $n = 29$ individuals at Rinconada in 2007 and 2008, respectively. Genomic DNA was extracted from tissue using a standard salt extraction protocol (Aljanabi and Martinez 1997). Amplification of DNA was achieved using polymerase chain reaction of 60 ng of DNA from each individual using the conditions recommended by Quan et al. (2009). Amplification was confirmed with agarose gel electrophoresis. Individuals were genotyped using 5 degu microsatellite loci (OCDE3, OCDE6, OCDE11, OCDE12, OCDE13—Quan et al. 2009). There was no evidence of linkage disequilibrium across all 5 loci screened ($P > 0.05$ for each loci). The number of alleles per locus ranged from 5 to 12. The observed heterozygosity of loci ranged from 0.36 to 0.79 for Rinconada and 0.48 to 0.91 for Los Molles. These loci were used because they were polymorphic and showed no linkage disequilibrium during previous studies (Quan et al. 2009; Quirici et al. 2011a). Allele quantification and testing for linkage disequilibrium were performed in GENEPOP 4.2 (Raymond and Rousset 1995). Microsatellite sequencing was performed by Macrogen, Inc. (Seoul, South Korea). Allele sizes were determined and genotypes assigned using Peak Scanner version 1.0 (Applied Biosystems, Foster City, California). Deviations from Hardy–Weinberg equilibrium and the pairwise coefficient of relatedness (R) among individuals were calculated using the ML-Relate software (Kalinowski et al. 2006). In both populations, deviations from Hardy–Weinberg equilibrium were detected for 2 loci (OCDE6 and OCDE12, $P < 0.01$). Therefore, estimations of pairwise

relatedness were adjusted to account for potential null alleles using the ML-Relate software (Quirici et al. 2011a).

Statistical analysis.—To determine if social groups consisted of closely related kin, mean pairwise relatedness across group members was compared to the relatedness of the background population consisting of all individuals in the same population for which there was genetic data. To determine the relatedness of the background population, bootstrapping analysis (n = 1,000 permutations, with replacement) was performed on randomly selected pairs of individuals irrespective of social group, with sample sizes dependent on the number of individuals in each social group (e.g., 3 randomly selected pairs for group size = 3) using R 3.1.1 software (R Development Core Team 2014). Groups with mean pairwise relatedness that fell outside of the 95% confidence interval (*CI*) for the randomly selected background population were considered statistically different from the background population.

To determine if there was a relationship between population, group size, genetic relatedness, and group-level social network parameters (mean association and mean strength), we used Akaike Information Criterion (AIC—Akaike 1974) to determine the best-fit model for both mean association and mean strength. Each possible combination of factors and interactions was tested and models with ΔAIC < 7 were considered to be well supported (Burnham et al. 2011).

To evaluate the relationship between an individual's social network parameters (strength and clustering coefficient) and the ecology (food biomass, burrow density, and soil hardness) of its burrow systems within both populations, we conducted multiple regressions with all weighted (based on proportion of captures at burrow systems) ecological characteristics as independent variables and each network parameter as the dependent variable. Ecological characteristics were weighted so that estimates were not biased by conditions at infrequently used burrow systems. To test the assumption that the model was linear, we visually inspected a plot of standardized residuals. Data were not considered to be autocorrelated if the Durbin–Watson statistic (d) was between 1.5 and 2.5. To test for homoscedasticity, we visually inspected the data point spread showing the regression standardized residual versus the regression standardized predicted value. Variables were considered collinear if the variability inflation factor (VIF) was greater than 4.0. Multiple regressions were conducted with SPSS version 22.0 (IBM 2013). For all analyses, we set the alpha level to $P = 0.05$. Throughout, we report means with standard errors (*SE*).

Results

Descriptive data.—The mean (*SE*) group size at Rinconada was 3.58 ± 0.37 (range: 2–7). The mean (*SE*) group size at Los Molles was 4.67 ± 0.80 (range: 2–7). The pairwise relatedness between individuals ranged from 0.00 to 0.52 and 0.00 to 0.58 for Rinconada and Los Molles, respectively. The mean group-level relatedness ranged from 0.07 to 0.21 at Rinconada and from 0.09 to 0.25 at Los Molles. The mean relatedness of all sampled individuals in each population was 0.12 and 0.16 at Rinconada and Los Molles, respectively.

Individual network strength (the sum of associations an individual has in the network) ranged from 0.07 to 4.13 (1.92 ± 0.81) and 1.01 to 8.00 (4.55 ± 1.44) for Rinconada and Los Molles, respectively. The clustering coefficient for individuals ranged from 0.01 to 0.94 (0.34 ± 0.17) for Rinconada and 0.41 to 1.00 (0.81 ± 0.37) for Los Molles. At the group level, mean strength ranged from 0.09 to 3.48 (2.23 ± 0.67) at Rinconada and 1.00 to 6.79 (3.36 ± 1.40) at Los Molles. Mean association ranged from 0.17 to 0.96 (0.44 ± 0.51) at Rinconada and 0.45 to 1.00 (0.88 ± 0.46) at Los Molles.

Relatedness and social structure.—Bootstrapping analysis indicated that social group members were not significantly more related to each other compared to randomly selected individuals from the background population, with mean pairwise relatedness of all groups falling within the 95% *CI*s of the background population (Appendix I). Additionally, there was not a statistically significant relationship between group size and relatedness at either Los Molles ($\beta = -0.79$, $R^2 = 0.63$, $P = 0.06$) or Rinconada ($\beta = -0.27$, $R^2 = 0.07$, $P = 0.30$).

Model selection using the AIC suggested that some combination of population, group size, and/or genetic relatedness were the best predictors of group-level strength, with a model including all 3 parameters, a model including just population and group size, and a model including population and relatedness all having ΔAIC values less than 7 (Table 1). For group-level association, several models met the criteria for support, suggesting that no single model was a particularly good fit for the data (Table 1).

Ecology and network structure.—Multiple regression analyses adhered to the model assumptions for linearity, homoscedasticity, and autocorrelation. For the strength analysis, model-level significance was detected at both Los Molles ($F_{3,29} = 47.47$, $R^2 = 0.85$, $P < 0.01$) and Rinconada ($F_{3,79} = 6.45$, $R^2 = 0.20$, $P < 0.01$). Similarly, the model for clustering coefficient was significant at both Los Molles ($F_{3,27} = 11.64$, $R^2 = 0.59$, $P < 0.01$) and Rinconada ($F_{3,75} = 15.10$, $R^2 = 0.39$, $P < 0.01$). At both sites, analyses revealed statistically significant relationships between the ecological characteristics of burrow systems used by individuals and the individuals' network parameters. At Rinconada, as soil hardness increased, individuals' network strength decreased, whereas when food availability increased, individuals' clustering coefficient also increased (Table 2; Fig. 1). At Los Molles, individuals' network strength increased with increasing food availability, increasing soil hardness, and increasing burrow density. However, individuals' clustering coefficient decreased with increasing food availability and increasing burrow density (Table 2; Fig. 2).

Discussion

Social structure and kinship.—In our study, mean relatedness within social groups was not significantly greater than would be expected from random pairwise comparisons of individuals selected from the background population in both Rinconada and Los Molles. These observations, and those made previously in Rinconada (Quirici et al. 2011a), suggest that non-kin group structure is typical of degu sociality and

Table 1.—AIC values for the 7 possible best-fit models explaining the influence of population, group size, and genetic relatedness on group-level strength and association. GS = group size.

Variable examined and model	AIC	ΔAIC	AIC weight	Evidence ratio
Strength				
Population GS relatedness	2.59	0	0.83	1
Population GS	6.96	4.37	0.09	0.11
Population relatedness	8.67	6.09	0.04	0.05
GS	9.96	7.38	0.02	0.03
GS relatedness	11.95	9.36	0.01	0.01
Population	11.99	9.41	0.01	0.01
Relatedness	33.72	31.13	1.44E-07	1.74E-07
Association				
Population	−61.60	0	0.46	1
Population GS	−60.48	1.12	0.26	0.57
Population relatedness	−59.66	1.94	0.17	0.38
Population GS relatedness	−58.58	3.02	0.10	0.22
GS relatedness	−46.30	15.30	2.19E-04	4.77E-04
Relatedness	−43.65	17.95	5.83E-05	1.27E-04
GS	−42.04	19.56	2.61E-05	5.66E-05

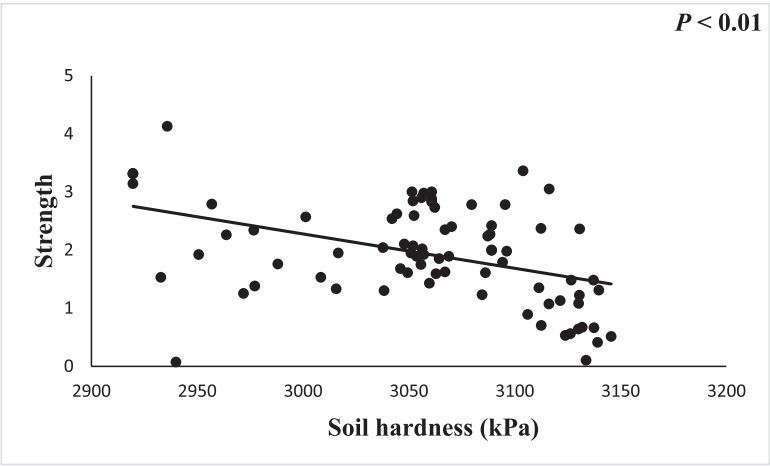
Table 2.—Multiple regression statistics for individuals' network parameters versus weighted habitat characteristics at Rinconada and Rio Los Molles, 2007–2008.

Predictor Variable	Rinconada				Rio Los Molles			
	Partial *r*	Beta	*t*	*P*	Partial *r*	Beta	*t*	*P*
Soil hardness								
Strength	−0.41	−0.41	−3.97	< 0.01	0.77	0.64	6.11	< 0.01
Clustering coefficient	−0.16	−0.13	−1.38	0.17	−0.33	−0.36	−1.69	0.10
Burrow density								
Strength	0.07	0.07	0.65	0.52	0.90	1.27	10.69	< 0.01
Clustering coefficient	−0.19	−0.16	−1.6	0.11	−0.44	−0.60	−2.39	0.03
Food biomass								
Strength	0.18	0.17	1.6	0.11	0.43	0.24	2.44	0.02
Clustering coefficient	0.54	0.53	5.49	< 0.01	−0.74	−1.04	−5.40	< 0.01

not just a characteristic of 1 population (Fig. 3). However, the best-fit model for group-level network strength included genetic relatedness, suggesting that kinship does have some influence on social group dynamics. Our observations that group size is not a significant predictor of group relatedness for Rinconada are also consistent with previous findings regarding the mechanisms of group formation in degus at Rinconada. Although natal philopatry plays a minor role in the formation of degu groups at Rinconada, non-sex-biased dispersal and the movement of adults between groups are the most important drivers of group formation (Ebensperger et al. 2009; Quirici et al. 2011a). Under these conditions, a negative relationship between group size and relatedness is not expected, as the composition of groups varies based on the relative influence of each mechanism on group formation. The negative, albeit statistically non-significant, relationship between group size and relatedness at Los Molles ($P = 0.06$) suggests the possibility that natal philopatry is not common at this site. Further analysis is needed to determine the extent to which each mechanism influences group composition, particularly at Los Molles.

Some authors have questioned the validity of kin selection as the ultimate driver of sociality across taxa (Griffin and West 2002; Wilson 2005). Although natal philopatry (and the resultant kin groups) remains a common mechanism of group formation in many species, other mechanisms of group formation, including the immigration and emigration of adults, influence group structure in some mammals (e.g., Solomon 2003; Ebensperger and Hayes 2008; Kappeler 2008). At Rinconada, the dispersal of degu offspring is not sex biased, with both sexes dispersing at roughly the same rate (Ebensperger et al. 2009; Quirici et al. 2011b). Further, the primary determinant of group formation and composition at Rinconada is the disappearance of adults and the movement of adults between social groups. As a result, annual turnover of adults comprising social groups is typically high (Ebensperger et al. 2009), likely explaining low kin structure in this population. Although we did not monitor these behaviors at Los Molles, we expect similar mechanisms to have evolved to maintain non-kin structure in this population. A test of this hypothesis would require a multi-year study to track individuals and their social affiliations between and within seasons (Ebensperger et al. 2009).

a



b

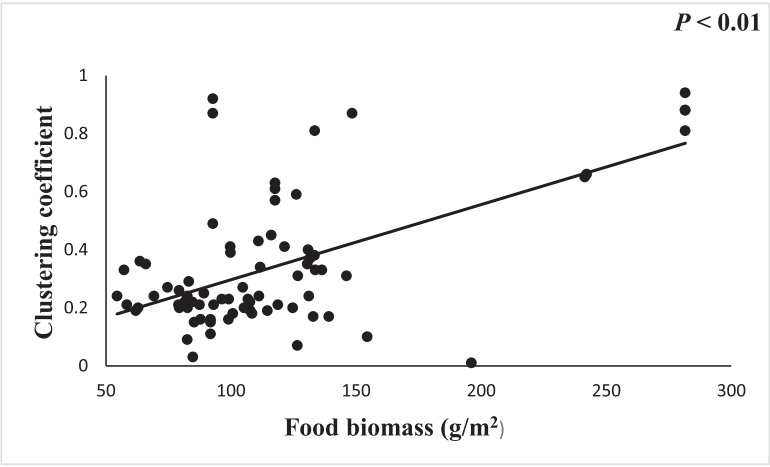


Fig. 1.—Statistically significant relationship between (a) soil hardness and individuals' network strength and (b) food biomass and individuals' clustering coefficient at Rinconada in 2007–2008. Data points represent individual degus.

Life history may explain the evolution of non-kin groups in some cases where kin selection does not provide an adequate explanation for group living. For example, kin structure is expected in long-lived species in which social groups experience low turnover rates. Evidence for this hypothesis comes from studies showing kin structure in long-lived species such as African elephants (*Loxodonta africana*—Archie et al. 2006), coypus (*Myocastor coypus*—Túnez et al. 2009), and several primate species (Silk 2002). In contrast, due to high turnover rates, social structure in species with short lifespans often lacks kin structure, as has been seen in woodrats (*Neotoma macrotis*—Matocq and Lacey 2004). In terms of life history, degus have low survival (Ebensperger et al. 2009, 2013) and high turnover rates from year to year (Ebensperger et al. 2009), possibly explaining non-kin social structure.

Given the potential survival and reproductive costs of dispersal (Bonte et al. 2012), 2 important evolutionary questions are 1) why do adult degus regularly leave social groups? and 2) why do degu offspring of both sexes regularly disperse from their natal groups? One explanation for the movement of adults away from social groups is that competition among individuals for critical resources increases with increasing group size and/or tenure of particular individuals in groups. For example, Dittus (1988) found that group fission in toque macaques (*Macaca sinica*) was driven by increased intragroup competition as group size increased and available food resources decreased due to environmental stress. Alternatively, adults may leave groups as increasing group size leads to an increased risk of parasites and disease (Rifkin et al. 2012). Equal rates of dispersal of both male and female offspring, uncommon in mammals (Lawson Handley and Perrin 2007), may have evolved in degus as a means to maximize lifetime direct fitness. Female degus may disperse from groups in search of available breeding opportunities to avoid reproductive suppression commonly observed in cooperatively breeding mammals (Solomon and Getz 1997). Previous research has demonstrated that the probability of offspring dispersal increases with the number of degus per burrow system, suggesting that increased competition as group size increases may be driving dispersal (Quirici et al. 2011b).

Our observation that degus do not live with kin suggests that the inclusive fitness of individuals is derived mostly from direct

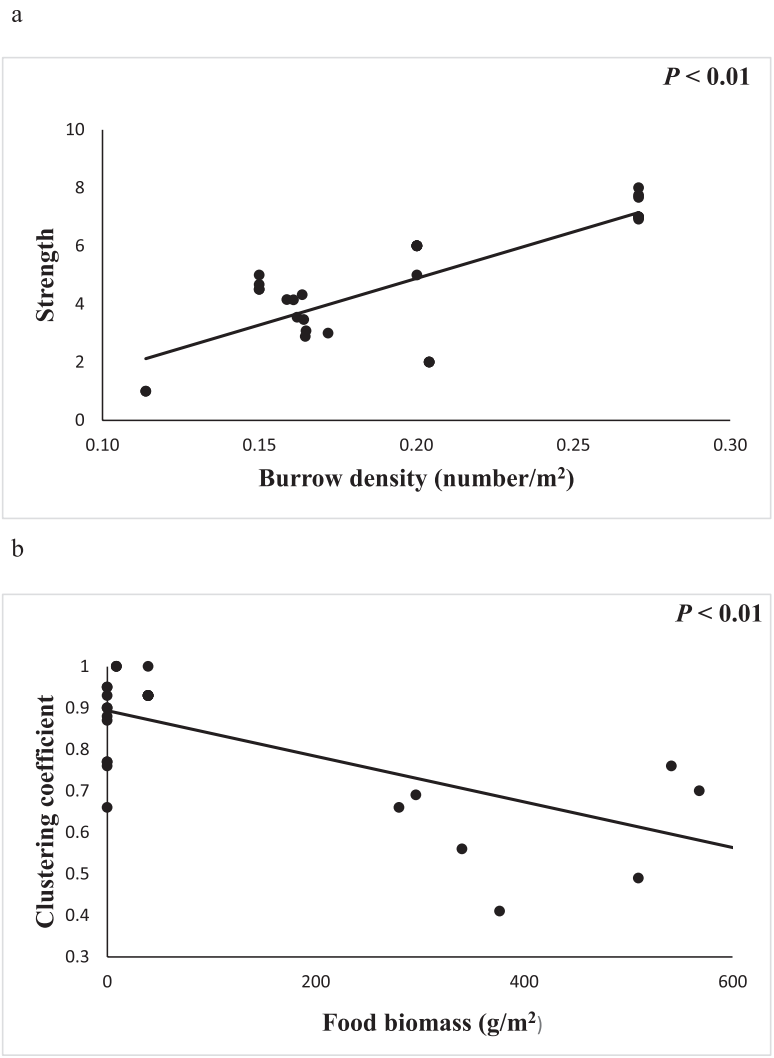


Fig. 2.—Statistically significant relationship between (a) burrow density and individuals' network strength and (b) food biomass and individuals' network clustering coefficient at Rio Los Molles in 2007–2008. Data points represent individual degus.

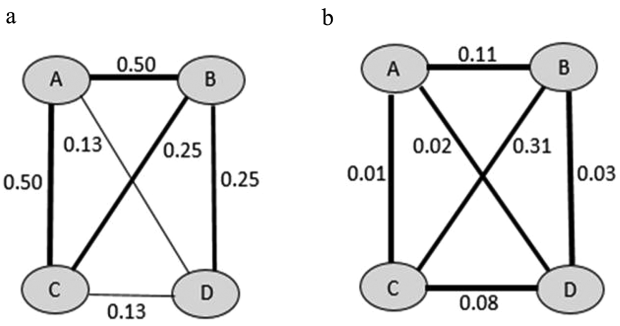


Fig. 3.—Social network structure of (a) a theoretical social group exhibiting kin structure and (b) an actual social group from the Rio Los Molles 2007 population. Ovals represent group members (A–D), lines represent pairwise social associations between group members, and numeric values represent the pairwise genetic relatedness of group members. In (a) associations are stronger between individuals with high relatedness, whereas in (b) associations vary irrespective of relatedness.

fitness. Sociality confers group size benefits to degus, including reduced digging costs (Ebensperger and Bozinovic 2000a) and reduced risk of predation (Ebensperger et al. 2006). However, laboratory and field studies have not revealed tangible benefits from the communal rearing of offspring (Ebensperger et al. 2007, 2014) or that group living reduces the costs of ectoparasitism (Burger et al. 2012) or the trade-offs between current and future reproduction (Ebensperger et al. 2013). This indicates that reciprocal benefits are limited. Short-term field studies suggest that increasing sociality has direct fitness costs to females (Hayes et al. 2009; Ebensperger et al. 2011). In contrast, in a study covering 8 years, Ebensperger et al. (2014) showed that the relationship between the number of females (an indicator of communal care) and per capita offspring produced was most positive in years with low mean food availability. This observation suggests that degu sociality—and non-kin social structure—may have evolved as a means to ensure direct fitness under the harshest environmental conditions.

Social networks and habitat conditions.—Contrary to previous work in which local ecological conditions had little predictive power for group sizes (Hayes et al. 2009; Ebensperger et al. 2012), we observed that social network structure was influenced by local ecological conditions in both populations (see Figs. 1 and 2; Table 2). At Rinconada, the negative relationship

between strength and soil hardness suggests that individuals inhabiting burrow systems with softer soil experience stronger and/or more social associations. This observation is consistent with a study in which social tuco-tucos (*Ctenomys sociabilis*) were found in areas with softer soils than solitary tuco-tucos (*C. haigi*—Lacey and Wieczorek 2003). However, previous studies on degus found that the energetic cost of digging in hard soil is greater than digging in soft soils (Ebensperger and Bozinovic 2000a) and that degus digging in groups remove more soil per capita than solitary individuals (Ebensperger and Bozinovic 2000b). Further, while softer soil may provide better habitat and result in a greater degree of sociality, a previous study of degus at Rinconada and Los Molles does not support this relationship (Ebensperger et al. 2012). The positive relationship between food biomass and clustering coefficient suggests that individuals may be clustering together around burrows where food resources are abundant. Our observation is in agreement with previous studies on invertebrates (Tanner et al. 2011) and vertebrates (Foster et al. 2012) showing that food availability influences a population's social network structure.

At Los Molles, the positive relationships between network strength and both food biomass and burrow density suggest a similar trend that individuals inhabiting high-quality habitats have stronger and/or more social associations. In contrast to the observed trend at Rinconada, the relationship between network strength and soil hardness at Los Molles was positive. This difference may be explained by site-level differences in ecological conditions (Ebensperger et al. 2012). Overall, the soil at Los Molles is softer than Rinconada. Since some level of soil hardness is necessary to maintain the structure of burrows, it is possible that harder soil provides better habitat quality at Los Molles, as softer soil may not maintain the burrow structures. Other relationships between ecological conditions and social network structure observed at Los Molles, but not at Rinconada, are more difficult to interpret. The negative relationships between clustering coefficient and both food biomass and burrow density suggest that individuals are not clustering more strongly in areas with abundant food and burrows. It is possible that differences in predation risk (Ebensperger et al. 2012) influence the distribution of degus and thus social network structure at Los Molles. Examinations of the relationship between spatial and temporal variation in predator abundance and social network structure are needed to test this hypothesis.

Regardless, our results (including the difference in R^2 values between the models for the 2 populations) suggest that local ecological conditions influence social interactions and help shape social structure in degu populations. Intraspecific social variation in response to local ecological conditions has also been demonstrated in numerous taxa (Lott 1991; Schradin 2013), including reptiles (Shine and Fitzgerald 1995), birds (Davies and Lundberg 1984), and mammals (MacDonald 1979; Streatfeild et al. 2011). Regarding social networks, Henzi et al. (2009) found that female associations of chacma baboons (*Papio hamadryas ursinus*) varied cyclically in relation to temporal variation in food abundance. In this sense, degu social structure seems to fit within a common theme, that local ecological conditions are a significant driver of social variation across species. Future work should aim to determine if the processes (e.g., phenotypic plasticity) underlying intraspecfic variation in social structure (Schradin 2013) differ between sites. Such work could have important implications for fully explaining the drivers of social variation.

Concluding remarks.—The major take-home point of this study is that degu social groups are consistently non-kin based across 2 populations and that this social structure is not influenced by local ecological conditions or social network structure. Thus, the results of this and previous studies on degus (Ebensperger et al. 2009; Quirici et al. 2011a) suggest that the degu social system is characterized by non-kin structure. However, our findings also demonstrate that degu social network structure is influenced by local ecological conditions, and that these influences may result in population-specific social structure. To fully understand these relationships, future work should investigate how degu social networks vary in relation to temporal changes in ecological conditions among populations. At the broader scale, researchers need to further examine the complex relationships between life history, ecological conditions, and social/kin structure. To accomplish this, future research should make use of large comparative databases (e.g., PanTHERIA—Jones et al. 2009; Lukas and Clutton-Brock 2012) to determine if the relationships between these factors are consistent across taxa.

Acknowledgments

We thank M. Kovach, H. Klug, and J. Bhattacharjee for help with genetic and statistical analyses. We also thank F. Peña for help with genetic techniques in the Molecular Ecology lab at Universidad de Chile. GTD received funding from the UTC Provost Student Research Award and the Animal Behavior Society. LDH was funded by National Science Foundation IRES (International Research Experiences for Students) grant no. 0553910 and 0853719. LAE was funded by Fondo Nacional de Ciencia y Tecnología (FONDECYT) grants no. 1060499 and 1130091. RAV was funded by Fondo Nacional de Ciencia y Tecnología (FONDECYT) grant no. 1140548 and RAV and EP were funded by the Institute of Ecology and Biodiversity grants ICM-P05-002 and PFB-23-CONICYT-Chile.

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Submitted 11 March 2015. Accepted 30 October 2015.

Associate Editor was Marcus V. Vieira.

APPENDIX I

Group size and within-group relatedness of social groups at Rinconada and Rio Los Molles, 2007–2008.

Year	Social group	Group size	Genetic relatedness	95% *CI*
Rinconada				
2007	1	3	0.19	0–0.31
2007	2	7	0.08	0–0.21
2007	3	6	0.15	0–0.22
2007	4	4	0.17	0–0.25
2007	5	3	0.14	0–0.31
2007	6	3	0.11	0–0.31
2007	7	6	0.09	0–0.22
2008	8	5	0.11	0–0.24
2008	9	2	0.07	0–0.41
2008	10	2	0.21	0–0.41
2008	11	3	0.16	0–0.31
2008	12	3	0.09	0–0.31
2008	13	3	0.11	0–0.31
2008	14	2	0.12	0–0.41
2008	15	2	0.14	0–0.41
2008	16	3	0.09	0–0.31
2008	17	4	0.07	0–0.25
Rio Los Molles				
2007	1	4	0.09	0–0.23
2008	2	6	0.09	0–0.23
2008	3	2	0.21	0–0.46
2008	4	3	0.25	0–0.33
2008	5	6	0.09	0–0.23
2008	6	7	0.10	0–0.23

CI = confidence interval.