

Original Article

Absence of kin structure in a population of the group-living rodent *Octodon degus*

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Variation in sociality may have an important impact on population genetic structure. In highly social species, the formation of kin clusters leads to decreasing variation within but increasing genetic variation among social groups. Studies on less social species in which social groups may be more short lived have revealed a greater diversity of consequences on the genetic structure of populations. Thus, studies on populations of less social species can more precisely highlight how social structure and genetic structure covary in wild populations. We explored the relationship between natal dispersal and social structuring (i.e., whether social group are composed of kin) at the local population in a social rodent, *Octodon degus*, using a combination of direct (capture–mark–recapture) and indirect (codominant genetic markers) methods. Previous studies of degus indicated that social groups were characterized by high turnover rate of group members and no sex bias dispersal. As we expected, there was an absence of correlation between social and genetic structure; moreover, social groups were not characterized by high levels of genetic relatedness (R : no different from background population). Direct and indirect (corrected assignment index) methods revealed an absence of sex-biased dispersal. Moreover, this method revealed that our study population was composed of resident and immigrant individuals. Moreover, dispersal distances have no effect on kin structure as revealed by the spatial genetic autocorrelation analysis. Beside some degree of offspring association (R : among juveniles of a same group higher than background population), high turnover rate, dispersal, and perhaps a promiscuous or polyandry mating system seem to avoid a kin genetic structure, thereby limiting the opportunity for the evolution of kin-selected social behavior. **Key words:** offspring associations, relatedness, social groups, spatial genetic autocorrelation analysis. [*Behav Ecol* 22:248–254 (2011)]

Sociality, or the tendency of animal species to live in groups, may have consequences on the genetic structure of their populations (Sugg et al. 1996; Dobson 1998). In particular, the stability or temporal persistence of groups may impact population structure. For example, significant genetic subdivision among small families or social groups within colonies and subpopulations occurs in highly social species in which groups are stable and persist for long periods of time. For these species, the temporal persistence of kin associations at the population level is expected to correlate with decreasing variation within but increasing genetic variation among social groups (Sugg et al. 1996). In contrast, studies on less social species in which social groups may be more short lived have revealed a greater diversity of consequences on the genetic structure of populations. In particular, social groups may (Blundell et al. 2004; Matocq and Lacey 2004; Hare and Murie 2007; Lebigre et al. 2008) or may not (Túnez et al. 2009; Gauffre et al. 2009; Viblanc et al. 2010) represent kin clusters characterized by high levels of genetic relatedness. Thus, studies on populations of less social species can more precisely highlight how social structure and genetic structure covary in wild populations (Dobson 1998).

Quantifying the genetic structure of populations without accounting for social subdivision may lead to higher than

expected levels of homozygosity, or Wahlund effect (Dobson 1998). In theory, genetic subdivision in social populations decreases with natal dispersal but increases with natal philopatry. Relatedness within groups is expected to decrease relative to population levels whenever natal dispersal is frequent but expected to increase whenever dispersal is low. Given that dispersal may be sex biased, stronger correlations are expected between genetic and social subdivision in the more philopatric compared with the more dispersing sex (Dobson 1998). In mammals, females most often represent the philopatric sex, whereas males represent the dispersing sex (Greenwood 1980; Dobson 1982; Pusey 1987; Wolff 1994; Clarke et al. 1997; Dale 2001; Petit et al. 2001). Thus, evidence of kin structure may predict the extent of philopatry and dispersal in highly social species (Sugg et al. 1996).

We explored the relationship between natal dispersal and social structuring (i.e., whether social group are composed of kin) in a social rodent, *Octodon degus*. Degus are small to medium sized (170–300 g) diurnally active rodents (Woods and Boraker 1975) that typically breed once per year during late autumn (May–June, Rojas et al. 1977). After a 3-month pregnancy, females give birth to an average of 6 ± 1 pups in September. Both natal philopatry and dispersal influence the composition of social groups (Ebensperger et al. 2009). Although degus are known to live in social groups (composed of 0–5 males and 1–8 females Ebensperger et al. 2004; Hayes et al. 2009), sociality in these animals seems intermediate between highly social (Pope 1992, 1998; Reeve et al. 1990; Faulkes et al. 1997; Spong and Creel 2004) and solitary living mammals (Cutrera et al. 2005). First, although solitary living does not occur in degus (Hayes et al. 2009), social groups are

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highly unstable in that they are short lived and ruled by an extensive turnover of group members (Ebensperger et al. 2009). Although allonursing seems to occur in captivity (Jesseau et al. 2009), social behavior of these rodents (Ebensperger and Bozinovic 2000; Quirici et al. 2008) does not include forms of cooperative behavior found in other mammals such as coordinated antipredator vigilance (Clutton-Brock et al. 1999) or division of labor (Jarvis 1981; Jarvis and Bennett 1993). Based on these characteristics of degu sociality, we predicted a weak (if any) correlation between social and genetic structuring. Given that neither immigration by adults (Ebensperger et al. 2009) nor offspring dispersal (Quirici et al., forthcoming) are sex biased in degus, we further predicted the correlation between social and genetic structure not to be influenced by sex.

The formation of temporally stable kin groups is thought to be a prerequisite for kin selection (Hamilton 1964; Maynard Smith 1964) to operate (Chesser 1991). In degus, some laboratory studies (Jesseau et al. 2009; Villavicencio et al. 2009, but not others: Ebensperger et al. 2007; Quirici et al. 2008) support that kinship influences social behavior. Although those studies supporting a role for kinship are inconsistent with the instability that characterizes social groups of these animals, kinship may still play some role under natural conditions through the formation of sibling associations during dispersal (i.e., sibling dispersal).

We tested these hypotheses with a combination of direct (capture–mark–recapture) and indirect (codominant genetic markers) methods, a powerful approach to examine the relationship between dispersal, social behavior, and population structure (Clobert et al. 2001; Cano et al. 2008; Sharp et al. 2008).

MATERIALS AND METHODS

Study site and trapping design

The study was conducted between the austral spring (October–November) of 2007 and late autumn (May–June) of 2008 at the Estación Experimental Rinconada de Maipú (lat 33°23'S, long 70°31'W, altitude 495 m), a field station of Universidad de Chile. The study site is characterized by a Mediterranean climate with warm dry summers (December–March) and cold wet winters (June–September) (Yáñez 1976; Meserve et al. 1984). The site consisted of open areas with scattered shrubs (*Proustia pungens*, *Acacia caven*, and *Baccharis* spp.) and annual grasses and forbs (Ebensperger and Hurtado 2005). Therein, we considered a 4–5 ha study area in an area known as the El Litral and in which degus were visually abundant and have been studied (Hayes et al. 2007). In spring 2007, we established a rectangular shaped trapping grid of 100 × 60 m.

We trapped *O. degus* using a combination of Tomahawk (model 201, 14 × 14 × 40 cm, Tomahawk, WI, 300 traps) and locally produced metal live traps (30 × 10 × 9.5 cm, similar to Sherman traps, 100 traps) all baited with rolled oats. We set traps in burrow system entrances for 2 months in spring (32 trapping days) and 2 weeks in autumn (13 trapping days), prior to the emergence of adults. Thus, traps were set before animals emerge to daily activity (spring: 08:00 AM; autumn: 07:00 AM). After 1.5 h, all traps were closed and individual identity, sex, body weight, apparent age (adult vs. juvenile, determined from body weight), and reproductive condition (females only) were recorded for every caught animal. During trapping, we marked degus at the time of first capture by clipping no more than one toe per foot (for further details, see Quirici et al. 2010). Tissue samples were stored in 95% ethanol for genetic analyses of relatedness. All burrow systems were

permanently marked with numbered wooden stakes and coordinates recorded with a GPS. Coordinates were then converted to X–Y (north-east) coordinates with the Locate II software (Pacer Software, Truro, NS, Canada).

Social group determination

Degus remain in underground burrows with conspecifics during the night time (Ebensperger et al. 2004). Therefore, we assigned animals to social groups based on the sharing of burrow systems during night time (Ebensperger et al. 2004). The sharing of burrow systems was established by means of burrow trapping in autumn. We then determined group composition using the SOCPROG 2.3 software (Whitehead 2009) based on a matrix of associations. This symmetric matrix is an estimate of the proportion of times that any 2 individuals were captured in the same burrow system simultaneously. In our case, we determined the association between any 2 individuals by dividing the number of occasions that these 2 animals were captured in the same burrow system simultaneously by the number of trapping days that both individuals were caught (Ebensperger et al. 2004). We performed hierarchical cluster analysis of the association matrix. We confirmed the correlation between the association indices and the level of clustering in the diagram with the cophenetic correlation coefficient (Whitehead 2009): values > 0.8 indicated an effective data representation. We used the maximum modularity criteria (Newman 2004), as implemented in SOCPROG 2.3, to cut off the dendrogram and define social groups. On defining social groups, we determined burrow systems used by each group. For each social group, degus were assigned to 2 alternative categories: residents (i.e., philopatric)—those that were present in the 2007 spring, and immigrants (i.e., dispersers)—those not present during the 2007 spring. Because trapping effort during spring 2007 was more extensive than in previous years (Hayes et al. 2009), we are confident that degus assigned to immigrants were unlikely the result of animals previously present but not trapped.

Genetic analyses

DNA was extracted from tissue samples using the DNeasy Tissue Extraction Kit (QIAGEN Inc., Valencia, CA). Individuals were genotyped for 4 *Spalacous cyanus* microsatellite loci (Scy1, Scy3, Scy5, and Scy6; Schroeder et al. 2000) and 2 degu microsatellite loci (OCDE1 and OCDE3, Quan et al. 2009), using the conditions recommended by the respective authors. These loci were chosen because they were polymorphic and showed no linkage disequilibrium in our study population. We verified polymerase chain reaction amplification by examining samples on agarose gels. Samples were analyzed on an ABI 310 capillary sequencer (Applied Biosystems, Foster City, CA) in the Laboratory of Molecular Diversity at the Pontificia Universidad Católica de Chile. Fragment sizes were determined and genotypes were assigned using PeakScanner 1.0 (Applied Biosystems).

Quantification of allele frequencies and analyses of linkage disequilibrium were conducted using GENEPOP 3.4 (Raymond and Rousset 1995). Deviations from Hardy–Weinberg equilibrium were evaluated using the Monte–Carlo randomization test of Guo and Thompson (1992) and the *U* statistic of Rousset and Raymond (1995), as implemented in ML-Relate software (Kalinowski et al. 2006). Pairwise coefficient of relatedness (*R*) among individuals was calculated using the ML-Relate software (Kalinowski et al. 2006). The ML-Relate program was chosen because it provides maximum likelihood estimates of relatedness, an accurate approach compared with other estimators available (Milligan 2003). We used *R* to refer to any estimate of genetic relatedness rather than *r*, which denotes the true relatedness based on knowledge of a pedigree (Winters and Waser 2003).

Analyses of kin structure

We first tested the null hypothesis of no association between capture association and genetic relatedness. We evaluated correlations between capture association and R matrices using Dietz (1983) R -test. This test is implemented in SOCPROG 2.3 and differs from the Mantel test in that matrices of ranked values are used instead of raw values. The Dietz R -test is less strongly affected by large (or small) outlying values than the Mantel test. We assessed associations for males and females separately based on 1000 permutations.

We evaluated whether mean R values within groups (calculated for females, males, and all group members) were significantly larger than background levels across social groups in the study population. To calculate background R values, we used bootstrapping using the R 2.4.1 software (R Development Core Team 2006). In particular, we calculated 10 000 values (with replacement) of mean R from N randomly selected R values obtained from nongroup members. The value of N varied according to the total number of adults, males, or females per social group examined. Observed means that fell outside 95% interval confidence intervals for randomly selected individuals were considered different from background.

In addition, we calculated the percentage of pups born to the same burrow systems during spring that stayed in the same natal burrow (i.e., were philopatric: distance moved from spring to autumn was equal to zero) or moved and settle into same or different burrow systems (i.e., dispersed: distance moved from spring to autumn was different from zero). In case of dispersers, we further determined whether offspring from same natal burrows also moved to same burrow systems. Dispersal distance was calculated as the straight-line distance from the burrow system where pup was first captured (i.e., natal burrow) to the burrow system where the same individual was first recaptured in autumn (Quirici et al., forthcoming). We then evaluated whether mean R values between offspring that stayed or moved to same burrow systems were significantly higher than background levels of genetic similarity in the study population.

Analysis of dispersal

An absence of sex-biased dispersal in degus was previously reported based exclusively on capture–mark–recapture (Quirici et al., forthcoming). Given that this approach may lead to problems (Koenig et al. 1996; Dieckmann et al. 1999), we used genetic markers to confirm this pattern. To quantify the extent to which dispersal is sex biased in our local population, we used “assignment index (AI) values” for males and females based on 1000 permutations using FSTAT 2.9.3 (Goudet 1995). The AI measures the probability that an individual genotype would appear in the population from which it was sampled, correcting for differences in population genetic diversity (Farve et al. 1997). AI values are randomly distributed around zero, with negative values indicating that an individual is more likely than average to be a recent immigrant. The variance in AI is expected to be higher in the dispersing sex because of the increased probability that population samples will contain both philopatric and immigrant individuals (Goudet et al. 2002). During these analyses, each of our 7 social groups was treated as a “distinct” population.

To complete our understanding of the impact of dispersal on degu sociality, we performed an autocorrelation spatial analysis. This method employs a multivariate approach to simultaneously assess the spatial signal generated by multiple genetic loci (Peakall et al. 2003), as implemented in GenAlEx 6.3. The autocorrelation coefficient generated (r) is

a correlation coefficient, bounded by $[-1, +1]$ and provides a measure of the genetic similarity between pairs of individuals whose geographic separation falls within the specific distance class. Positive autocorrelation implies that dispersal is limited. Separate analyses were run for males and females. Distance class intervals were set to 10 m, and the total number of distance class used were chosen based on the maximum distance to same sex individuals. Confidence intervals for r values were derived from 1000 bootstrap estimates. Whenever the confidence interval generated does not include the zero, significant spatial genetic structure needs to be inferred.

RESULTS

Microsatellite variation

No evidence of linkage disequilibrium was detected among the loci screened (all $P > 0.05$). Number of alleles per locus range from 2 to 10 (6.67 ± 2.66); observed heterozygosity range from 0.26 to 0.77 (0.54 ± 0.17) (Table 1). Significant departures from Hardy–Weinberg expectations, however, were detected for 4 loci ($P < 0.001$, Table 1). Calculations of R were performed adjusting relatedness to accommodate the possible presence of null alleles with the ML-Relate software. In addition, AI analyses are robust enough to departures from Hardy–Weinberg equilibrium (Paetkau et al. 1995). Thus, data from all 6 loci screened were included in our analyses of kinship.

Social groups and kin structure

Based on the maximum modularity criteria (Newman 2004), 7 social groups were identified and monitored in autumn 2008. There were 3.8 ± 2.3 (range: 1–6) residents females and 1 ± 0 residents males per group. There were 3 ± 2.9 (range: 1–8) immigrant females and 1.6 ± 0.9 (range: 1–3) immigrant males per group (Table 2). In total, 55.9% of 34 females present in autumn were residents and the remaining 44.1% were immigrants. In contrast, 14.3% of 14 males present in autumn were residents and the remaining 85.7% were immigrants. Thus, males were less likely than females to become residents (Yates corrected $\chi^2 = 5.38$, $P = 0.02$). There was a nonstatistically significant trend for males (mAI = 0.529) to exhibit higher mean AI compared with females (mAI = -0.249) (mAI: $P = 0.93$). The variance linked to AI did not statistically differ between females (vAI = 3.827) and males (vAI = 2.187) (vAI: $P = 0.711$). Altogether, this method revealed that our study population was composed of resident and immigrant individuals.

The spatial genetic autocorrelation analysis did not detect fine-scale genetic structure for females (Figure 1a) or males (Figure 1b). Thus, genetic structure is not influenced by

Table 1
Diversity of the microsatellite loci used to estimate relatedness in *Octodon degus*

Locus	No. of alleles	H_o	H_e	P value
Scy1	6	0.26	0.65	<0.001
Scy3	7	0.60	0.82	<0.001
Scy5	2	0.50	0.48	0.54
Scy6	8	0.54	0.85	<0.001
OCDE1	7	0.77	0.84	0.38
OCDE3	10	0.56	0.83	<0.001

P value indicates significance of differences between observed (H_o) and expected (H_e) heterozygosity.

Table 2
Number of resident and immigrant female and male degus per social group

Social group ID	Female (res)	Female (imm)	Mean $R (\pm SD)$	95% CI	Male (res)	Male (imm)	Mean $R (\pm SD)$	95% CI	Total	Mean $R (\pm SD)$	95% CI	Offs (dist)	Mean $R (\pm SD)$	95% CI
G1	—	2	0.08	0–0.5	—	1	—	—	3	0.03 (0.04)	0–0.35	—	—	—
G2	2	8	0.11 (0.23)	0.02–0.26	—	3	0.25 (0.23)	0–0.35	13	0.15 (0.26)	0.03–0.23	—	—	—
G3	1	1	0	0–0.5	—	1	—	—	3	0.16 (0.24)	0–0.35	—	—	—
G4	4	3	0.16 (0.23)	0–0.29	1	1	0	0–0.43	9	0.16 (0.22)	0.02–0.25	3 (25 m)	0.16 (0.29)	0–0.35
G5	6	—	0.15 (0.16)	0–0.31	1	1	0.2	0–0.43	8	0.17 (0.16)	0.01–0.26	3 (20 m)	0.32 (0.25)	0–0.35
G6	—	1	—	—	—	3	0.27 (0.29)	0–0.35	4	0.17 (0.23)	0–0.32	3 (0 m)	0.27 (0.26)	0–0.35
G7	6	—	0.22 (0.29)	0–0.31	—	2	0.3	0–0.43	8	0.19 (0.29)	0.01–0.26	3 (30 m)	0.56 (0.11)	*0–0.35

Mean (\pm standard deviation, SD) pairwise R values and its confidence interval (CI) for total group, female group, male group, and siblings. Abbreviations: res, residents, imm, immigrant, offs, offspring, dist, distance. See text for details.

* R values that fell outside the 95% confidence interval.

distance among individuals. Only in 3 of 35 distance classes, the calculated confidence interval around r did not include the zero. Relatedness tended to be directly correlated with spatial distance in females that were within 10 m or less. In contrast, relatedness and spatial distance were inversely related in females and males that were within 110 and 120 m, respectively.

Mean R of entire social groups ranged from 0.03 to 0.19 (0.15 ± 0.05). These values range from 0.08 to 0.19 (0.14 ± 0.05) for females and 0 to 0.27 (0.21 ± 0.12) for males. When each social group was examined separately, R values within groups were not different from the total (0.13 ± 0.2), females (0.13 ± 0.19), and males (0.12 ± 0.18) background levels of genetic similarity in the study population (Table 2).

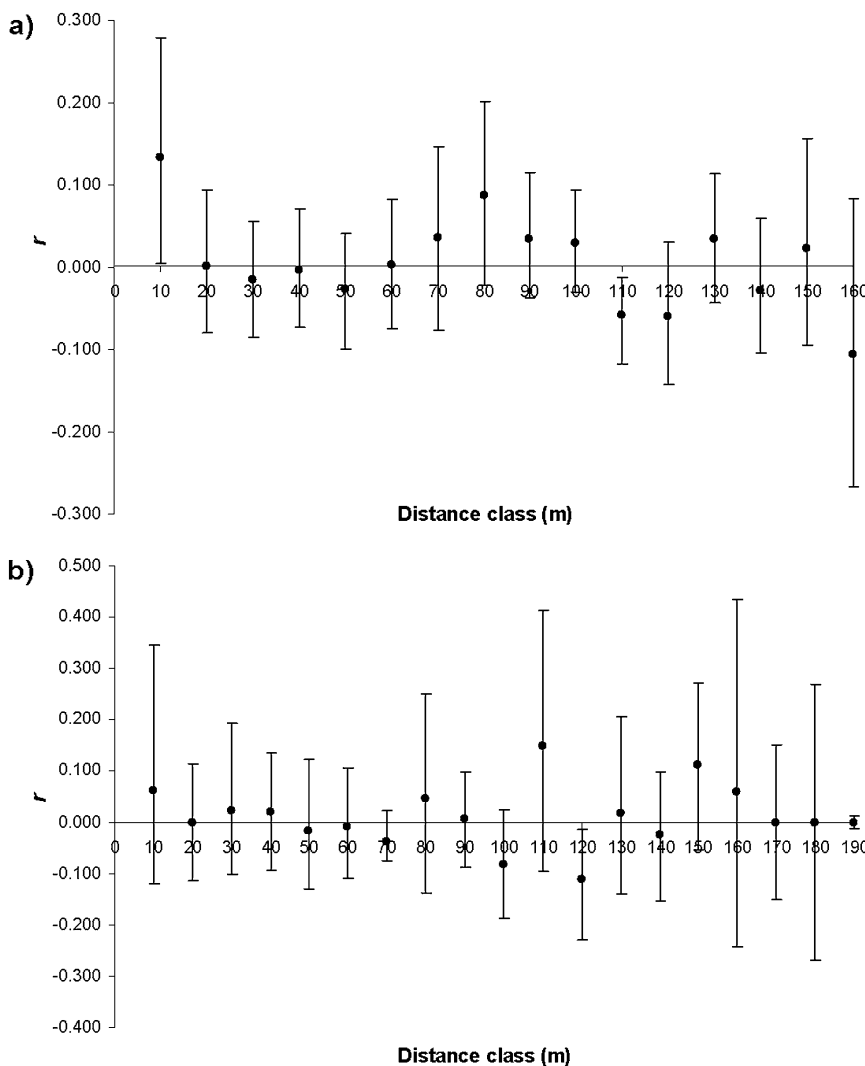


Figure 1
 Spatial genetic autocorrelation estimated over cumulative distance class for females a) and males b).

Based on 1000 permutations, we detected no correlation between genetic and social associations based on burrow trapping neither for males ($N = 14$, Dietz R -test: $R_D = 0.014$, $P = 0.41$) nor females ($N = 34$, Dietz R -test: $R_D = 0.031$, $P = 0.21$). Thus, social groups determined from trapping were independent of genetic similarity of individuals.

Relatedness of offspring

Of the 175 pups marked in spring 2007 (103 females and 72 males), 16 (9.14%) were recaptured subsequently in autumn 2008 (15 females and 1 male). The mean body mass of these pups at first capture in spring 2007 (59.03 ± 13.21 g) was lower than expected for juveniles exhibiting exploratory behavior (Fulk 1976), implying that natal burrows for these animals were estimated accurately. Twelve of these 16 pups (75%) were recaptured in 4 associations of 3 animals each and 4 (25%) were recaptured alone. Of these 4 associations, 3 represented cases of individuals that moved at least 20 m from natal burrow system (Table 2). The R value in one of these associations departed from background expectations was marginally significant in another and not significantly different in the remaining association (Table 2). Only one association represented a case of animals staying at their natal burrow system and calculated R did not depart from background expectations (Table 2).

DISCUSSION

Kin structure: turnover rates and mating system

We found no correlation between pairwise relatedness (R) and the composition of social groups inferred from trapping (or spatial association) (Dietz correlation by ranks not different from random expectations), suggesting that composition of social groups in degus is not influenced by genetic relatedness. Although mean genetic relatedness within groups was not very different from that reported during one previous analysis (Ebensperger et al. 2004), social groups were not characterized by genetic relatedness higher than background levels in our study population. On the contrary, it seems that groups of individuals sharing burrows rather constitute a single global population at the spatial scale of this study (100×60 m). Two factors, namely short life span coupled to high rates of turnover within groups and a potentially promiscuous or polyandry mating system may explain these patterns.

Life span is known to affect turnover rate of group members in social species (McShea 1990; Kokko and Lundberg 2001), which in turn impact dispersal, philopatry, and kin structure (Branch 1993; Solomon 2003; Randall et al. 2005; Nunes 2007). For example, strong evidence of kin structure characterizes relatively long-lived social species such as Columbian ground squirrels (*Uroctellus columbianus*) (Viblanco et al. 2010) and coypus (*Myocastor coypus*) (Túnez et al. 2009). As expected, no evidence of kin structure characterizes some short-lived species with relatively high turnover rates of group members, including black grouse (Lebigre et al. 2008), woodrats (*Neotoma macrotis*) (Matocq and Lacey 2004) and degus (this study). Besides life span, dispersal distance seems to have a major impact on the observed patterns of kin structure in solitary living species, including the banner-tailed kangaroo rats (*Dipodomys spectabilis*) (Winters and Waser 2003; Busch et al. 2009) and tuco-tucos (*Ctenomys talarum*) (Cutrer et al. 2005). Based on the minimum genetic autocorrelation observed, our study did not support an influence of dispersal distance in social degus. However, studies on other social species are needed to confirm these findings.

Mating system strongly influences genetic relatedness within groups of social species (Ross 2001). High relatedness is expected in groups in which 2 or a few group members breed,

that is, in species with high breeding skew. In contrast, relatively low genetic relatedness is expected in groups of species in which plural breeding is the norm, that is, breeding is shared more equally among group members (Ross 2001). In addition, genetic relatedness may increase in polygynous species characterized by female choice over few males (Chesser 1991). Social rodents seem to fit to these expectations. Whereas high relatedness characterizes colonies of highly skewed naked mole-rats (*Heterocephalus glaber*) (Reeve et al. 1990), more intermediate relatedness characterizes the social group of polygynous coypus (*M. coypus*) (Túnez et al. 2009). Thus, if mating system is a major determinant of relatedness within groups in rodents, we predict degus to exhibit a rather polygynous to promiscuous mating system. Although Soto-Gamboa (2004) reported degus to exhibit a socially polygynous mating system, subsequent paternity analyses may reveal a more promiscuous system. However, based on absence of sex bias dispersal (Quirici et al., forthcoming)—implying that the cost of dispersal and benefits of philopatry did not vary in relation to sex (Greenwood 1980; Gardner 2010)—we predict promiscuous mating system.

Offspring associations

Dispersal may dilute kinship within groups and reduces the potential influence of kin selection on social behavior (Emlen 1997; Perrin and Goudet 2001; Ross 2001; Gardner and West 2006). Sibling dispersal could be a mechanism to reduce such dilution (Johnson and Gaines 1990; Ross 2001; Gardner and West 2006). Sibling dispersal has been documented in several social birds (Heinsohn et al. 2000; Koenig et al. 2000; Williams and Rabenold 2005; Sharp et al. 2008) but in only a few social mammals (Lambin et al. 2001; Bradley et al. 2007). In degus, most offspring (75%) exhibited joint dispersal, that is, animals were recaptured after dispersal jointly with previous natal burrow mates. However, data on 4 such associations revealed that relatedness may or may not be high. Preliminarily therefore, “sibling” associations may not be strong mechanism to reduce the effect of kinship dilution by dispersal in the local population under study. The low recovery of juveniles from spring to autumn are consistent with the hypothesis that most disappearances were due to high predation in the population under study (Ebensperger and Wallem 2002; Lagos et al. 2009) rather than long-distance dispersal from the grid (Quirici et al., forthcoming). If so, high juvenile mortality might prevent sibling association from reducing the any possible effect of kinship dilution by dispersal. A comparative study among degu populations facing different regimes of predation risk will bring light into this topic. If predation risk dilutes sibling association, we expect to find higher level of sibling associations, which could result in stronger kin structure, in those populations facing lower risk of predation.

High to moderate levels of kinship are thought to be required for kin-selected behavior (Chesser 1991). Whereas some laboratory studies suggest a relationship between kinship and social behavior in degus, others do not (Ebensperger et al. 2006, 2007; Quirici et al. 2008). Instead, social familiarity, that is, animals born and raised together, may be more important. Villavicencio et al. (2009) demonstrated that social familiarity instead of phenotypic similarity determines kin discrimination in degus. Our field data revealing that offspring disperse together are consistent with a greater role of social familiarity reported by Villavicencio et al. (2009). As it has been suggested in social birds (Sharp et al. 2008; Sonsthagen et al. 2010) and rodents (Mateo 2007), offspring associations may be the result of rearing together. This mechanism conducting to sibling associations is likely to operate in degus in which offspring are reared communally in underground burrow systems for at least 3 weeks (Ebensperger et al. 2004; Hayes et al. 2009). However, this result should be taken with caution, due to low recapture of juveniles.

To summarize, our study revealed no evidence of kin structure in the population of social degus studied. High turnover rates of group members and dispersal are likely contributors to the lack of kin structure in degu groups. Therefore, opportunities for the evolution of kin-selected social behavior (e.g., cooperative care of young) appear to be limited in this local population. Subsequent studies are needed to better quantify the extent to which sibling associations may promote kin selected or other forms of cooperation, in which individuals with kin or familiar mates should have enhanced fitness compared with individuals without kin or familiar companions (e.g., Viblanc et al. 2010).

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REFERENCES

- Blundell GM, Ben-David M, Groves P, Bowyer RT, Geffen E. 2004. Kinship and sociality in coastal river otters: are they related? *Behav Ecol*. 15:705–714.
- Bradley BJ, Doran-Sheehy DM, Vigilant L. 2007. Potential for female kin associations in wild western gorillas despite female dispersal. *Proc R Soc B Biol Sci*. 274:2179–2185.
- Branch LC. 1993. Social organization and mating system of the plains viscacha (*Lagostomus maximus*). *J Zool Lond*. 229:473–491.
- Busch JD, Waser PM, DeWoody JA. 2009. The influence of density and sex on patterns of fine-scale genetic structure. *Evolution*. 63:2302–2314.
- Cano JM, Mäkinen HS, Merilä J. 2008. Genetic evidence for male-biased dispersal in the three-spined stickleback (*Gasterosteus aculeatus*). *Mol Ecol*. 17:3234–3242.
- Chesser RK. 1991. Influence of gene flow and breeding tactics on gene diversity within populations. *Genetics*. 129:573–583.
- Clarke A, Saether B, Roskaft E. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos*. 79:429–438.
- Clobert J, Danchin E, Dhondt AA, Nichols JD. 2001. *Dispersal*. New York: Oxford University Press. 452 pp.
- Clutton-Brock TH, O’Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS, Manser M. 1999. Selfish sentinels in cooperative mammals. *Science*. 84:1640–1644.
- Cutrerera AP, Lacey EA, Busch C. 2005. Genetic structure in a solitary rodent (*Ctenomys talarum*): implications for kinship and dispersal. *Mol Ecol*. 14:2511–2523.
- Dale S. 2001. Female biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos*. 92:344–356.
- Dieckmann U, OñHara B, Weisser W. 1999. The evolutionary ecology of dispersal. *Trends Ecol Evol*. 14:88–90.
- Dietz EJ. 1983. Permutation tests for association between two distance matrices. *Syst Zool*. 32:21–26.
- Dobson FS. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav*. 38:205–214.
- Dobson FS. 1998. Social structure and gene dynamics in mammals. *J Mammal*. 79:667–670.
- Ebensperger LA, Bozinovic F. 2000. Communal burrowing in the hystri-cognath rodent, *Octodon degus*: a benefit of sociality? *Behav Ecol Sociobiol*. 47:365–369.
- Ebensperger LA, Chesh AS, Castro RA, Ortiz-Tolhuysen L, Quirici V, Burger R, Hayes LD. 2009. Instability rules social groups in the communal breeder rodent *Octodon degus*. *Ethology*. 115:540–554.
- Ebensperger LA, Hurtado MJ. 2005. Seasonal changes in the time budget of degus, *Octodon degus*. *Behaviour*. 142:91–112.
- Ebensperger LA, Hurtado MJ, León C. 2007. An experimental examination of the consequences of comunitaria versus solitary breeding on maternal condition and the early postnatal growth and survival of degus, *Octodon degus*, pups. *Anim Behav*. 73:185–194.
- Ebensperger LA, Hurtado MJ, Soto-Gamboa M, Lacey EA, Chang AT. 2004. Communal nesting and kinship in degus (*Octodon degus*). *Naturwissenschaften*. 91:391–395.
- Ebensperger LA, Hurtado MJ, Valdivia I. 2006. Lactating females do not discriminate between their own young and unrelated pups in the communally breeding rodent, *Octodon degus*. *Ethology*. 112:921–929.
- Ebensperger LA, Wallem PK. 2002. Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. *Oikos*. 98:491–497.
- Emlen ST. 1997. Predicting family dynamics in social vertebrates. In: Krebs JR, Davis NB, editors. *Behavioural ecology: an evolutionary approach*. 4th ed. Oxford: Blackwell Science. p. 228–253.
- Farve L, Balloux F, Goudet J, Perrin N. 1997. Female-biased dispersal in the monogamous mammal *Crocodyura russula*: evidence from field data and microsatellite patterns. *Proc R Soc Lond B Biol Sci*. 264:127–132.
- Faulkes CG, Abbott DH, O’Brien HP, et al. 1997. Micro- and macro-geographic genetic structure of colonies of naked mole-rats, *Heterocephalus glaber*. *Mol Ecol*. 6:615–628.
- Fulk GM. 1976. Notes on the activity, reproduction and social behavior of *Octodon degus*. *J Mammal*. 57:495–505.
- Gardner A. 2010. Sex-biased dispersal of adults mediates the evolution of altruism among juveniles. *J Theor Biol*. 262:339–345.
- Gardner A, West SA. 2006. Demography, altruism, and the benefits of budding. *J Evol Biol*. 19:1707–1716.
- Gauffre B, Petit E, Brodier S, Bretagnolle V, Cosson JF. 2009. Sex-biased dispersal patterns depend on the spatial scale in a social rodent. *Proc R Soc B Biol Sci*. 276:3487–3494.
- Goudet J. 1995. Fstat: a computer program to calculate F-statistics. *J Heredity*. 86:485–486.
- Goudet J, Perrin N, Waser P. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Mol Ecol*. 11:1103–1114.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav*. 28:1140–1162.
- Guo SW, Thompson EA. 1992. Performing the exact test of Hardy-Weinberg proportions for multiple alleles. *Biometrics*. 48:361–372.
- Hamilton WD. 1964. The genetical evolution of social behavior. *J Theor Biol*. 7:1–52.
- Hare JF, Murie JO. 2007. Ecology, kinship, and ground squirrel sociality: insights from comparative analysis. In: Wolff JO, Sherman PW, editors. *Rodent societies: an ecological and evolutionary perspective*. Chicago: University of Chicago Press. p. 345–355.
- Hayes LD, Chesh AS, Castro RA, Ortiz-Tolhuysen L, Burger JR, Bhattacharjee J, Ebensperger LA. 2009. Fitness consequences of group living in the degu *Octodon degus*, a plural breeder rodent with communal care. *Anim Behav*. 78:131–139.
- Hayes LD, Chesh AS, Ebensperger LA. 2007. Ecological predictors of range areas and use of burrow systems in the diurnal rodent, *Octodon degus*. *Ethology*. 113:155–165.
- Heinsohn R, Dunn P, Legge S, Double M. 2000. Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proc R Soc B Biol Sci*. 267:243–249.
- Jarvis JUM. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science*. 212:571–573.
- Jarvis JUM, Bennett NC. 1993. Eusociality has evolved independently in two genera of bathyergid mole-rats - but occurs in no other subterranean mammal. *Behav Ecol Sociobiol*. 33:253–260.
- Jesseau SA, Holmes WG, Lee TM. 2009. Communal nesting and discriminative nursing by captive degus *Octodon degus*. *Anim Behav*. 78:1183–1188.

- Johnson ML, Gaines MS. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu Rev Ecol Syst.* 21:449–480.
- Kalinowski ST, Wagner AP, Taper ML. 2006. ML-Relate: a computer program for maximum likelihood estimation of relatedness and relationship. *Mol Ecol Notes.* 6:576–579.
- Koenig WD, Hooge PN, Stanback MT, Haydock J. 2000. Natal dispersal in the cooperatively breeding acorn woodpecker. *Condor.* 102:492–502.
- Koenig WD, van Vuren D, Hooge PN. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol Evol.* 11:514–517.
- Kokko H, Lundberg P. 2001. Dispersal, migration and offspring retention in saturated habitats. *Am Nat.* 157:188–202.
- Lagos PA, Meier A, Ortiz-Tollhuysen L, Castro RA, Bozinovic F, Ebensperger LA. 2009. Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small mammal prey. *Can J Zool.* 87:1016–1023.
- Lambin X, Aars J, Pieltney SB. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal.* Oxford: Oxford University Press. p. 110–122.
- Lebigre C, Alatalo RV, Fross HE, Siitari H. 2008. Low levels of relatedness on black grouse leks despite male philopatry. *Mol Ecol.* 17:4512–4521.
- Mateo JM. 2007. Ecological and hormonal correlates of antipredator behavior in adult Belding's ground squirrels (*Spermophilus beldingi*). *Behav Ecol Sociobiol.* 62:37–49.
- Matoq MD, Lacey EA. 2004. Philopatry, kin clusters, and genetic relatedness in a population of woodrats (*Neotoma macrotis*). *Behav Ecol.* 15:647–653.
- Maynard Smith J. 1964. Group selection and kin selection. *Nature.* 201:1145–1147.
- McShea WJ. 1990. Social tolerance and proximate mechanisms of dispersal among winter groups of meadow voles, *Microtus pennsylvanicus*. *Anim Behav.* 39:346–351.
- Meserve PL, Martin RE, Rodríguez J. 1984. Comparative ecology of the caviomorph rodent *Octodon degus* in two Chilean Mediterranean-type communities. *Rev Chil Hist Nat.* 57:79–89.
- Milligan BG. 2003. Maximum-likelihood estimation of relatedness. *Genetics.* 163:1153–1167.
- Newman MEJ. 2004. Analysis of weighted networks. *Phys Rev E.* 70:056131.
- Nunes S. 2007. Dispersal and philopatry. In: Wolff JO, Sherman PW, editors. *Rodent societies: an ecological and evolutionary perspective.* Chicago: The University of Chicago Press. p. 150–162.
- Paetkau D, Calvert W, Stirling I, Strobeck C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Mol Ecol.* 4:347–354.
- Peakall R, Ruibal M, Lindenmayer DB. 2003. Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution.* 57:1182–1195.
- Perrin N, Goudet J. 2001. Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal.* Oxford: Oxford University Press. p. 123–142.
- Petit E, Balloux F, Goudet J. 2001. Sex-biased dispersal in a migratory bat: a characterization using sex-specific demographic parameters. *Evolution.* 55:635–640.
- Pope TR. 1992. The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). *Evolution.* 46:1112–1128.
- Pope TR. 1998. Effects of demographic change on group kin structure and gene dynamics of populations of red howler monkeys. *J Mammal.* 79:692–712.
- Pusey AE. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol Evol.* 2:295–299.
- Quan YF, MacManes MD, Ebensperger LA, Lacey EA, Hayes LD. 2009. Isolation and characterization of polymorphic microsatellite loci from *Octodon degus*. *Mol Ecol Resour.* 9:999–1001.
- Quirici V, Castro RA, Ortiz-Tollhuysen L, Chesh AS, Burger JR, Miranda E, Cortés A, Hayes LD, Ebensperger LA. 2010. Seasonal variation in the range areas of the rodent *Octodon degus*. *J Mammal.* 9:458–466.
- Quirici V, Castro RA, Oyarzún J, Ebensperger LA. 2008. Female degus (*Octodon degus*) monitor their environment while foraging socially. *Anim Cogn.* 11:441–448.
- Quirici V, Faugeron S, Hayes LD, Ebensperger LA. Forthcoming. The influence of group size on natal dispersal in the communally rearing and semifossorial rodent, *Octodon degus*. *Behav Ecol Sociobiol.* DOI:10.1007/s00265-010-1082-1.
- Randall JA, Rogovin K, Parker PG, Eimes JA. 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behav Ecol.* 16:961–973.
- Raymond M, Rousset F. 1995. An exact test for population differentiation. *Evolution.* 49:1280–1283.
- R Development Core Team. 2006. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Reeve HK, Westneat DF, Noon WA, Sherman PW, Aquadro CF. 1990. DNA 'fingerprinting' reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *Nature.* 358:147–149.
- Rojas M, Rivera O, Montenegro G, Barros C. 1977. Algunas observaciones en la reproducción de la hembra silvestre de *Octodon degus*, Molina y su posible relación con la fenología de la vegetación. *Medio Ambiente (Chile).* 3:78–82.
- Ross KG. 2001. Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Mol Ecol.* 10:265–284.
- Rousset F, Raymond M. 1995. Testing heterozygote excess and deficiency. *Genetics.* 140:1413–1419.
- Schroeder JW, Honeycutt RL, Rooney AP, Hann J, Begall S, Gallardo MH. 2000. Microsatellites from the South American coruro, *Spalacopus cyanus*. *Mol Ecol.* 9:1433–1449.
- Sharp SP, Simeoni M, Hatchwell BJ. 2008. Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. *Proc R Soc B Biol Sci.* 275:2125–2130.
- Solomon NG. 2003. A reexamination of factors influencing philopatry in rodents. *J Mammal.* 84:1182–1197.
- Sonsthagen SA, Talbot SL, Lanctot RB, McCracken KG. 2010. Do common eiders nest in kin groups? Microgeographic genetic structure in a philopatric sea duck. *Mol Ecol.* 19:647–657.
- Soto-Gamboa M. 2004. Formación y estabilidad de estructuras sociales en micromamíferos, su regulación hormonal y la importancia de las interacciones entre machos [PhD Thesis]. Santiago: Pontificia Universidad Católica de Chile.
- Spong G, Creel S. 2004. Effects of kinship on territorial conflicts among groups of lions, *Panthera leo*. *Behav Ecol Sociobiol.* 55:325–331.
- Sugg DW, Chesser RK, Dobson FS, Hoogland JL. 1996. Population genetics meets behavioral ecology. *Trends Ecol Evol.* 11:338–342.
- Túñez JI, Guichón ML, Centrón D, Henderson AP, Callahan C, Cassini MH. 2009. Relatedness and social organization of coypus in the Argentinean pampas. *Mol Ecol.* 18:147–155.
- Viblanç VA, Arnaud CM, Dobson FS, Murie JO. 2010. Kin selection in Columbian ground squirrels (*Urocitellus columbianus*): littermate kin provide individual fitness benefits. *Proc R Soc B Biol Sci.* 277:989–994.
- Villavicencio CP, Márquez IN, Quispe R, Vásquez RA. 2009. Familiarity and phenotypic similarity influence kin discrimination in the social rodent *Octodon degus*. *Anim Behav.* 78:377–384.
- Whitehead H. 2009. SOCPROG programs: analyzing animal social structures. *Behav Ecol Sociobiol.* 63:765–778.
- Williams DA, Rabenold KN. 2005. Male-biased dispersal, female philopatry, and routes to fitness in a social corvid. *J Anim Ecol.* 74:150–159.
- Winters JB, Waser PM. 2003. Gene dispersal and outbreeding in a philopatric mammal. *Mol Ecol.* 12:2251–2259.
- Wolff JO. 1994. More on juvenile dispersal in mammals. *Oikos.* 71:349–352.
- Woods CA, Boraker DK. 1975. Mammalian species: *Octodon degus*. *Am Soc Mammal.* 67:1–5.
- Yáñez JL. 1976. Ecoetología de *Octodon degus* [BS thesis]. Santiago (Chile): Universidad de Chile.