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The influence of group size on natal dispersal in the communally rearing and semifossorial rodent, *Octodon degus*

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Abstract In social or group living species, members of groups are expected to be affected differentially by competition through the effect of group size (i.e., the “social competition hypothesis”). This hypothesis predicts an increase in the probability of dispersal with increasing size of social groups. At a more mechanistic level and based on the known effects of competition on stress hormone levels, a positive relationship between group size and glucocorticoids of juveniles should be observed. We used a demographic approach to test these predictions on a natural population of the communally rearing and semifossorial rodent—*Octodon degus*. Burrow systems provide *degus* with places to rear offspring and to evade stressful thermal conditions and predators. Thus, we predicted dispersal to increase with increasing number of *degus* per main burrow system used, a measure of habitat saturation in *degus*. The probability of dispersal increased with increasing number of *degus* per main burrow system used. Mean fecal metabolites of cortisol in offspring increased, yet not

statistically significantly, with the number of juveniles in groups. These results were consistent with a scenario in which competition drives natal dispersal in juveniles in social *degus*. In particular, competition would be the consequence of high *degu* abundance in relation to the abundance of burrow systems available at the time of offspring emergence.

Keywords Group size · Dispersal · Fecal cortisol metabolites · *Octodon degus*

Introduction

Dispersal is a sequential three-step process, in which individuals leave the natal site or social group (i.e., departure), move across unfamiliar territory (i.e., transfer), and arrive or settle (i.e., settlement) into a new home range or social group (Bélíchon et al. 1996). Given its major ecological and evolutionary implications (Marzluff and Balda 1989; Johnson and Gains 1990; Hanski 2001; Barton 2001; Lenormand 2002; Postma and van Noordwijk 2005; Gros et al. 2006), dispersal has been the focus of much empirical and theoretical research (Clobert et al. 2008). These studies have revealed one major pattern: young and immature individuals are overrepresented among dispersing mammals and birds, a pattern termed natal dispersal (Greenwood 1980). However, difficulties inherent to the study of dispersal have hampered our ability to understand factors underlying its causes (Koenig et al. 1996; Dieckmann et al. 1999; Nathan 2001; Clobert et al. 2008).

Some researchers have argued that competition is the major force behind natal dispersal. Support for this argument includes evidence that juvenile deer mice (*Peromyscus maniculatus*) and song sparrows (*Melospiza leucophrys*) disperse because they are less efficient than

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adults in acquiring resources (Waser 1985; Arcese 1989). In social species, individual members of groups are expected to be affected differentially by competition through the effect of group size (i.e., the “social competition hypothesis”). As group size increases, the costs of remaining in the group are expected to increase because of increasing competition until they outweigh potential benefits (Vander Waal et al. 2009). Three lines of evidence suggest that the social competition hypothesis has considerable explanatory power in social birds and mammals. At a population level, both dispersal and group fission—the split of groups into smaller units—are more frequent whenever group size exceeds a species-specific optimum (Armitage and Schwart 2000; Koyama et al. 2002; Packer et al. 2005; Manno et al. 2007; Vander Waal et al. 2009). At a more proximate level, glucocorticoids (GC), a physiological measure reflecting the effects of social and environmental stressors (including competition), increase whenever group size exceeds some presumably optimal size in lemurs (Pride 2005) or increase with increasing group size in elephants (Foley et al. 2001) and swallows (Raouf et al. 2006). Similarly, aggression from dominants toward subordinate individuals, i.e., a major mechanism of competition by interference, increases with increasing group size (Johnstone and Cant 1999; Cant et al. 2001; Gilchrist 2006). Taken together, this evidence supports that group size is a major determinant of competition within groups in some social species. Therefore, studies of how dispersal varies with group size in social species would provide unique opportunities to determine the extent and nature (e.g., over space, food) to which competition causes natal dispersal.

Natal dispersal of social species varies with varying breeding systems. Among singularly breeding birds and mammals, in which a few members of each group reproduce (sensu Silk 2007), juveniles in some species refrain from dispersing (i.e., remain philopatric) due to a limited availability of nesting sites (Hatchwell and Komdeur 2000; Russell 2001; Russell and Hatchwell 2001), an ecological constraint, or as the consequence of relatively extended time needed to reach adulthood (Field et al. 1998), a life history constraint. Thus, natal dispersal is independent of group size in the singular breeders, a feature that decreases the utility of these species in examining the relationship between group size and natal dispersal. On the other hand, adults of solitary breeding rodents are social during the nonbreeding period but switch to solitary nesting to rear their offspring (Jannett 1982; Lambin and Krebs 1991; Winterrowd et al. 2005); juveniles and sexually immature individuals disperse (Ebensperger and Hayes 2008). As a consequence, dispersal tends to be similarly independent on group size.

The plural breeders with communal care (sensu Silk 2007) are good model organisms to examine the link between group size and natal dispersal. In these species, most adult members breed and rear their offspring communally in a den or nest (i.e., “plural breeders”, sensu Silk 2007). Some individuals in plural breeding rodents disperse while others remain at the natal place (Ebensperger and Hayes 2008), a condition that may result from high density conditions (Wolff 1994). More relevant to this study, dispersal in plural breeding species may depend on the group size.

The degu, *Octodon degus*, is a plural breeding rodent in which the size of social groups varies within and between populations (Ebensperger et al. 2004; Hayes et al. 2009). Degus are diurnally active (Kenagy et al. 2002; Ebensperger et al. 2004) and semifossorial rodents that dig underground burrow systems, consisting of a variable number of oblique tunnels connecting the surface to a main nest chamber (Yáñez 1976; Lessa et al. 2008). Social groups typically use more than one burrow system, i.e., a group of interconnected burrow openings (Ebensperger et al. 2004; Hayes et al. 2007, 2009). Burrow construction and expansion takes place rather infrequently (i.e., 0.2% of activity time) in degu (Ebensperger and Hurtado 2005b), implying that local abundance of these structures is rather constant across consecutive years. Degus 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 (Ebensperger et al. 2007), the time when aboveground parts of annual grasses and forbs (preferred food of degu, Meserve et al. 1983, 1984) are abundant. At this time, degu abundance increases threefold compared with abundance during the previous autumn (Quirici et al. 2010). This increase in degu abundance, coupled to a rather constant number of burrow systems (Ebensperger and Hurtado 2005a), provides a scenario of competition for space. Therefore, if the “social competition hypothesis” explains the relative importance of dispersal versus philopatry in social degus, a dispersal threshold in relation to the size of social groups might be expected.

Predation risk increases with distance to the nearest burrow entrances in degus (Lagos et al. 2009), implying that predation risk decreases with density of burrow entrances per burrow system. Therefore, we further predicted dispersal to increase with increasing number of degus per main burrow system used and decreasing number of burrow entrances available to each degu, two pertinent measures of habitat saturation in these rodents. Given that GC levels are thought to reflect the social effects of competition (Pride 2005), we further predicted GC levels of juveniles to increase with increasing size of social groups. At a population level, dispersal should increase

with increasing competition (Waser's 1985 competition hypothesis). First, we evaluated the way competition over space would impact on natal dispersal at the population level. If degu disperse to avoid competition, we predicted a positive relationship between competition and dispersal.

Taken together, a major contribution of this study is to examine the influence of competition on dispersal at the population, social group, and individual levels. In addition, this is one of the few studies that uses probability approaches to quantify dispersal in relation to group size.

Methods

Study site and trapping

The study was conducted during the austral spring (October–November), mid summer (January–February), and mid autumn (May–June) months during 2007–2008 and 2008–2009 at the Estación Experimental Rinconada de Maipú (33°23' S, 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 matorral with scattered shrubs (*Proustia pungens*, *Acacia caven*, and *Baccharis* spp.) and annual grasses and forbs (Ebensperger and Hurtado 2005b). Therein, we considered a 4–5-ha study area in an area known as the El Litoral and in which degus were visually abundant. We first randomly selected a rectangular-shaped trapping grid of 100 by 60 m (hereafter referred as the “central grid”). We then established six linear transects with four trap stations at 40, 80, 120, and 160 m and with the distance of 40 m from each other station. All burrow systems inside the central grid ($N=31$ burrow systems) and along all transects ($N=24$ burrow systems)

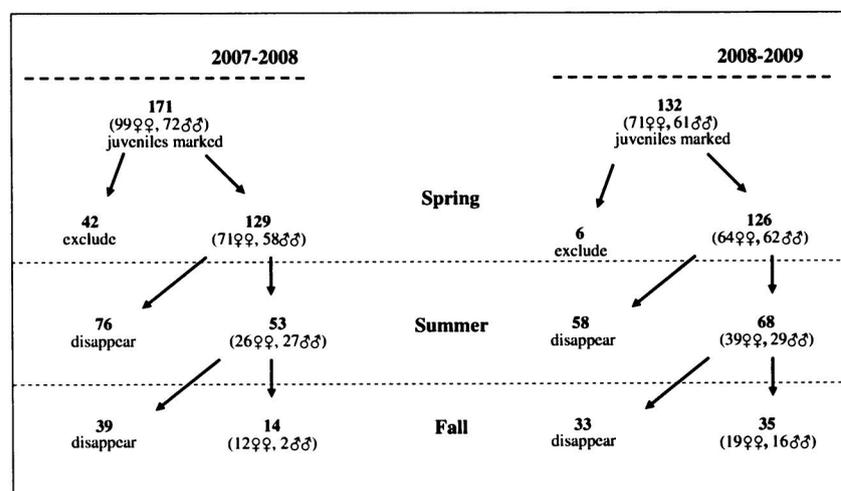
were permanently marked with numbered wooden stakes and coordinates recorded with a global position system. Coordinates were then converted to X–Y (north–east) coordinates with the Locate II software (Pacer Software, Truro, NS, Canada).

We trapped degu using a combination of Tomahawk (model 201, 14×14×40 cm, Tomahawk, WI, USA) and locally produced metal live traps (30×10×9.5 cm, similar to Sherman traps) all baited with rolled oats. We set traps in burrow system entrances for 2 months in spring (32 trapping days in 2007 and 45 trapping days in 2008), 2 weeks in summer (13 trapping days in 2008 and 2009), and 2 weeks in autumns (13 trapping days in 2008 and 2009), prior to the emergence of adults. Thus, traps were set at 0800 hours during spring, 0600 hours during summer, and by 0700 hours during autumn. After 1.5 h, all traps were closed, and individual identity, sex, body weight, and apparent age (adult versus juvenile, determined from body weight) of all individuals were determined. We also determined the reproductive condition of all adult females: nonpregnant, pregnant, and lactating. During trapping, we marked degu at the time of first capture by clipping no more than one toe per foot (see Quirici et al. 2010, for further details) in the period 2007–2008. During 2008–2009, we switched to marking degu with the use of metal tags on both ears (National Band & Tag Company, Newport, KY, USA).

Determination of dispersal

We first aimed to describe the timing and intensity of degu dispersal in relation to philopatry. Fates of juveniles (depicted in Fig. 1) were assessed by individual mark-recapture (Turchin 1998). With the aim of collecting a sample of natal individuals (i.e., 35–75 g), we trapped degus during spring of 2007 and 2008 on the central grid,

Fig. 1 Fates of juveniles of *O. degus* marked during emergence from natal burrows during 2 years of study



near the time of offspring emergence. Thus, we excluded from this analysis individuals that weighed more than 75 g at first capture. Individuals of this size or larger exhibit much greater mobility (Fulk 1976; Ebensperger and Hurtado 2005b; Hayes et al. 2009). It is well known that measures of dispersal distances are underestimated whenever juveniles leave their natal burrow before they can be captured and individually recognized (Waser et al. 2006). Overall, we trapped 98% of burrow systems that were located inside the central grid ($N=31$ burrow systems). Subsequently, during the summers of 2008 and 2009 and autumns of 2008 and 2009, we expanded our trapping area to include the central grid along with six 120-m linear transects (Turchin 1998).

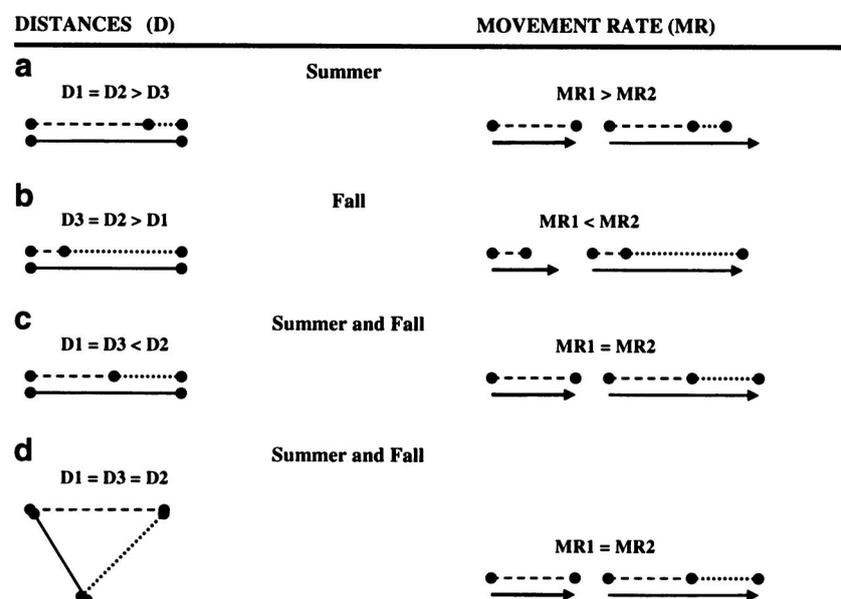
We followed Hanski and Selonen (2008) and classified an individual as disperser whenever it has moved to a distance equal to or larger than two times the radius of the circle enclosing the size of an adult's home range; for degu, this distance was 75 m (Quirici et al. 2010). Dispersal distance was calculated as the straight-line distance from the natal burrow where an animal was first captured as a pup to the burrow where the same individual was first recaptured in summer (i.e., spring–summer distance, $D1$) and in autumn (spring–autumn distance, $D2$). We complemented the previous estimates based on absolute distance with the approach of Turchin (1998), based on movement rates. We defined movement rate 1 (MR1) as the distance moved by an individual between spring and summer ($D1$) divided by the number of days between first capture in spring and first capture in summer. We defined movement rate 2 (MR2) as the cumulative distance from spring to summer ($D1$), plus the distance moved from summer to autumn ($D3$), and divided this difference by the number of days between first capture in spring and first capture in

autumn. Given that MR2 uses a cumulative distance ($D1 + D3$), this may not be an appropriate measure whenever an individual moves in summer but then returns to its natal site during autumn. To solve this problem, we considered the distance an animal moved between spring and autumn ($D2$). Therefore, (a) if dispersal takes place mostly from spring through summer, we predicted $D1 = D2 > D3$. Alternatively, (b) whenever dispersal takes place between spring through autumn, we predicted $D3 = D2 > D1$; (c) if dispersal takes place from spring through summer and autumn, we predicted either $D1 = D3 < D2$ or $D1 = D2 = D3$. Finally, (d) whenever an individual disperses from spring through summer, but then returns to its natal site in autumn, we expected $D1 = D3 > D2$ (Fig. 2).

Social group determinations and burrow systems used

We needed to identify members of the same social groups and, therefore, quantify group size. Given that degus remain in their underground burrows overnight, we assigned adults 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 August–October, i.e., from late pregnancy through lactation. We then determined group composition using the SOCPROG software (Whitehead 2009) based on a matrix of associations. This symmetric matrix is an estimate of the proportion of time that two any individuals spend together or interact. In our case, we determined the association between any two individuals by dividing the number of occasions that these two animals were captured to the same burrow system by the number of trapping days that both individuals were caught simultaneously (Ebensperger et al. 2004). We performed hierar-

Fig. 2 Four possible scenarios for juvenile dispersal: *A* dispersal occurred from spring to summer; *B* dispersal occurred from spring to autumn; *C*, *D* dispersal occurred from spring to summer and into autumn. $D1$ (segmented line), $D2$ (continuous line), and $D3$ (spotted line)



chical cluster analysis of the association matrix. We confirmed the correlation between the association indices and the levels of clustering in the diagram with the cophenetic correlation coefficient (Whitehead 2009) with values above 0.8 implying an effective representation. We used the maximum modularity criteria (Newman 2004) to cutoff the dendrogram and define social groups.

Upon defining social groups, we determined burrow systems used by each group. The number of burrow entrances at each burrow system was quantified in a circular area encompassing a 3-m radius from the center of each burrow system.

Fecal cortisol metabolites

We examined whether patterns of variation in physiological stress levels were consistent with a competitive effect mediated by group size as one major determinant of dispersal in degus. We used noninvasive fecal glucocorticoid analysis to extract fecal cortisol metabolites (hereafter FCM) as a means of assessing secretion of stress hormones levels in degus. Fecal cortisol assays reliably reflect endogenous changes in adrenal activity in degus (Soto-Gamboa et al. 2009). At first capture and previous to any other handling procedure of the trapped animals (e.g., marking), we collected 3–4 fresh fecal pellets for subsequent hormonal assay of 39 juveniles in spring 2008. Fecal samples were collected within 1–2 h of capture, an adequate time to avoid a handling effect on fecal cortisol in degus (Soto-Gamboa et al. 2009). Eleven out of 39 juveniles were recaptured in summer 2009, and of these, 6 were recaptured during autumn 2009. Collected feces (spring, summer, and autumn) were immediately stored into Eppendorf tubes with 0.8 mL of 95% ethanol and refrigerated at 5°C until assayed.

We extracted FCM with 80% ethanol, as recommended in a previous study (Mateo and Cavigelli 2005). We first dried the samples in an oven (95°C; 4–5 h). Dried feces were crushed and carefully homogenized. A portion (0.1 g; in case of two samples only 0.05 g) of each sample was mixed with 1 mL of 80% ethanol, vortexed for 5 s, and centrifuged at 3,000×g for 20 min. The supernatants were removed and stored at –20°C until determination of FCM. Cortisol metabolites in feces were quantified in the Radio Immune Essay Laboratory at P. Universidad Católica de Chile. Fecal samples were assessed with the use of steroid-free human serum (standard zero) to provide similar protein environments (Mateo and Cavigelli 2005). The intra- and inter-assay coefficients of variation of the immunoassay were 6.9% and 14.5%, respectively (Soto-Gamboa et al. 2009). Data were reported and analyzed as nanogram of fecal metabolites of cortisol per gram of dry fecal sample assessed.

Degu abundance and competition measures

Given its potential influence on dispersal, we monitored changes in degu abundance between years. To avoid the potential bias generated by heterogeneity in individual capture probabilities that arise from trap happy versus trap shy animal effects (Efford 1992), we calculated degu abundance using a closed capture with heterogeneity model (Pledger 2000). The analysis was performed using the MARK software, release 5.1 (White and Burnham 1999; Cooch and White 2008). Given that this model rests on the assumption of a closed population (no emigration, immigration, death, or birth), we restricted this analysis to the first 11 days of each trapping season. As a measure of competition at the population level, we further divided degu abundance (total, adults and offspring) by the total number of burrow openings in the central grid.

Analytical procedure

To meet assumptions of data homocedasticity and normality, dispersal distance was squared-root-transformed. We used repeated measures analyses of variance (ANOVA) with season (spring–summer–autumn) as a repeated measure and year (period 2007–2008 versus period 2008–2009) as factors to examine dispersal distance (D1–D2–D3) and movement rate (MR1–MR2) of females. We also used repeated measures ANOVA to examine the effect of season on males' dispersal distance and movement rate during the 2008–2009 periods. We used the permutation test to examine variation in movement rate (MR1 and MR2) and dispersal distance (D1, D2, and D3) across sexes.

We calculated the percentage of individuals recaptured at 10-m intervals and generated a dispersal distance distribution (i.e., DDD), upon which we fitted the data to a probability distribution using a nonlinear model (Koenig et al. 1996). Given the low number of recaptures observed for the spring–autumn period, we were able to calculate DDDs for the spring–summer period exclusively (i.e., for D1).

To examine the effect of group size on the probability to disperse, we used logistic regression. The probability of dispersal was estimated using general linear model with a binomial distribution of residuals and a logistic link function (Nelder and Wedderburn 1972). The response variable took two values: 1, whenever an individual moved twice the radius of an adult's home range (i.e., 75 m), and 0, whenever an individual moved less than this distance. We began the analysis including all predictor variables and subsequently removed the variable with highest *P* value (backward stepwise). The best model was selected from all tested using the corrected Akaike's Information Criterion (AICc) (Akaike 1974). Models were assumed to be equivalent if AICc values < 2 and the model with the fewest

parameters resulted in the best model. We used the following measures as predictors: (a) total number of adults per group, (b) total number of offspring per group, (c) total group size (adults and offspring), (d) total number of adults per group per burrow system, (e) total number of offspring per group per burrow system, and (f) total group size per group per burrow system used. In addition, we examined other variables known to affect dispersal in mammals (Holekamp 1984, 1986; Lambin 1994; Jacquot and Vessey 1995), including (g) the sex ratio (female/male) of offsprings in the group, (h) offspring sex, and (i) body growth rate of offspring (calculated as grams per day—between first capture in spring and first capture in summer).

We used Spearman's rank correlation to examine how mean FCM was influenced by the number of offspring, number of adults, and total group size. All statistical tests were two-tailed and conducted using the R 2.4.1 software (R Development Core Team 2006).

Results

Pattern of natal dispersal

The proportion of juveniles that dispersed did not differ between males and females within season (Table 1). When comparing between observation periods, the proportion of males and females that dispersed from spring to summer was higher in 2007–2008 compared with 2008–2009 ($\chi^2=4.16$, $df=1$, $P=0.04$, $\chi^2=17.28$, $df=1$; $P<0.001$). The proportion of females that dispersed from spring to autumn did not differ between 2007–2008 and 2008–2009 ($\chi^2=$

2.87, $df=1$, $P=0.09$). No males were recaptured during autumn 2008.

Dispersal distance distributions (DDD) of females and males both fit to a negative exponential function during spring 2007–summer 2008 and spring 2008–summer 2009 (Fig. 3). Dispersal distance of females was not influenced by observation period ($F_{1, 27}=3.26$, $P=0.08$), season ($F_{2, 54}=0.94$, $P=0.39$) or by a year \times season interaction ($F_{2, 54}=2.11$, $P=0.13$) (Table 1). For males, dispersal distances were statistically similar in 2008–2009 ($F_{2, 24}=2.14$, $P=0.14$). There were no sex differences linked to D1 ($P=0.89$), D2 ($P=0.99$), or D3 ($P=0.99$) during 2008–2009 (Table 1).

For females, there were no statistically significant main effects of season ($F_{1, 26}=0.57$, $P=0.46$) or year by season interactions ($F_{1, 26}=0.003$, $P=0.98$) on movement rates (Table 1). For males, movement rates were statistically similar in 2008–2009 ($F_{1, 13}=4.24$, $P=0.06$). There were no sex differences in MR1 ($P=0.92$) or MR2 ($P=0.472$) (Table 1). To summarize, there was no sex bias linked to the onset of dispersal, distance moved, or movement rate. These findings are consistent with (C) and (D) dispersal scenarios (Fig. 2).

Degu abundance, FCM, and competition over space

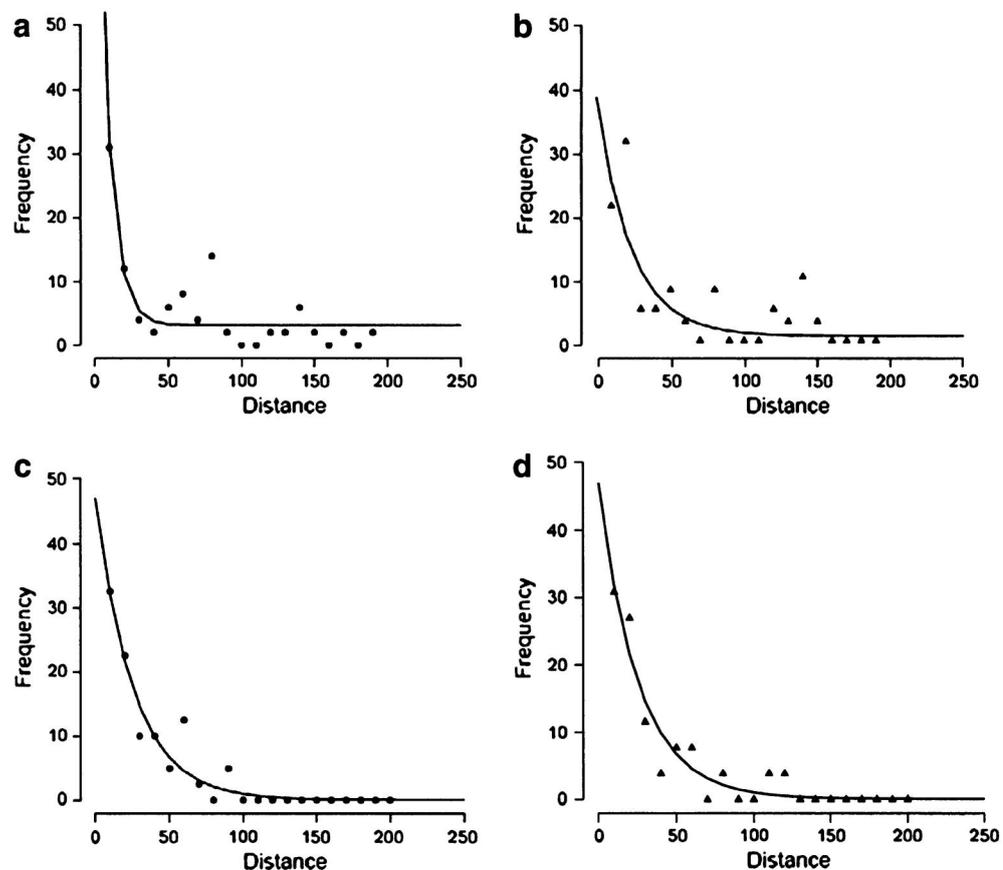
Degu abundance was higher in spring and summer than in autumn (Table 2). Mean FCM of offspring was higher in spring (149.95 ± 41.22 ng/g) and summer (150.73 ± 41.71 ng/g) compared with autumn (114.78 ± 14.37 ng/g) (Friedman ANOVA by ranks, $\chi^2=6.33$, $df=2$, $N=6$, $P<0.04$; $Z=0.31$, $P=0.75$ for spring versus summer; $Z=2.2$,

Table 1 Frequency of philopatric and dispersing individuals during summer and autumn

Observation period	Offspring sex	Philopatric	Dispersing	% Dispersing	Distances: D1, D2, D3 (m \pm SD)	Movement rate (m/day)
Spring 2007–summer 2008	Female	13	12	48.0	43.32 \pm 48.79	0.56 \pm 0.62
	Male	19	8	29.6	34.56 \pm 54	–
		$\chi^2=1.85$, $df=1$, $P=0.17$				
Spring 2007–autumn 2008	Female	10	2	16.6	38.94 \pm 48.03	0.35 \pm 0.35
	Male	–	–	–	–	–
Summer 2008–autumn 2008	Female	10	2	–	45.82 \pm 50.37	–
	Male	–	–	–	–	–
Spring 2008–summer 2009	Female	39	2	4.9	18.91 \pm 18.84	0.20 \pm 0.19
	Male	24	2	7.7	33.49 \pm 34.45	0.33 \pm 0.35
		$\chi^2=0.22$, $df=1$, $P=0.64$				
Spring 2008–autumn 2009	Female	16	0	0.0	28.64 \pm 21.74	0.18 \pm 0.12
	Male	13	1	7.1	23.08 \pm 30.28	0.25 \pm 0.22
		$\chi^2=1.18$, $df=1$, $P=0.28$				
Summer 2009–autumn 2009	Female	16	–	0	14.49 \pm 16.5	–
	Male	13	1	1	16.76 \pm 15.81	–

Dispersing individuals were those that moved more than 75 m from natal burrows
Dispersal distances (D1, D2, and D3) and movement rates (MR1 and MR2)

Fig. 3 Distribution of dispersal distance in males and females during the spring–summer period. Data fitted to a negative exponential distribution in all cases: $y = a + b \cdot \exp(c \cdot x)$. **a** Females 2008: $a=3.14$, $b=-97.26$, $c=-0.12$ ($\chi^2=1.29$, $df=1$, $P=0.25$); **b** males 2008: $a=1.7$, $b=-37$, $c=-0.04$ ($\chi^2=0.97$, $df=1$, $P=0.32$); **c** females 2009: $a=0.12$, $b=-46.8137$, $c=-0.039$ ($\chi^2=2.97$, $df=1$, $P=0.08$); and **d** males 2009: $a=0.45$, $b=-49.72$, $c=-0.04$ ($\chi^2=3.37$, $df=1$, $P=0.07$)



$P=0.03$ for spring versus autumn; and $Z=1.99$, $P=0.05$ for summer versus autumn). Competition for space (degu abundance/total number of openings ($N=413$)) was higher in spring 2007 than in spring 2008 (Fig. 4).

The effect of group size and habitat saturation on dispersal

Observations of philopatric and dispersing juveniles between spring 2007 and summer 2008 were fitted to a logistic regression; not enough dispersing individuals were recorded from spring 2008 through summer 2009 (Table 1). Using the backward stepwise algorithm, the probability that a juvenile dispersed increased as the ratio of the number of offspring to the number of burrow systems per group increased (four offspring per burrow system) (Fig. 5). This

ratio was greater for dispersing (6.94 ± 1.55) than for philopatric juveniles (4.23 ± 1.86) (Mann–Whitney U test— $U=107$, $P<0.001$, $N=20$, $N=32$).

The effect of group size on FCM

FCM was not significantly different between female (176.75 ± 70.65 ng/g) and male offspring (213.03 ± 138.66 ng/g) (Mann–Whitney U test— $U=164.5$, $P=0.65$, $N=15$ males, $N=24$ females), so data on both sexes were pooled. There was no statistically significant relationship between mean FCM of offspring and total group size (Spearman's rank correlation, $r_s=0.05$, $P=0.95$) (Fig. 6a). Intriguingly, mean FCM of offspring tended to decrease with increasing number of adults ($r_s=-0.90$, $P=0.083$)

Table 2 Degu abundance and group size composition

	Degu abundance (\pm SE)			Group size (spring 2007: $N=9$; spring 2008: $N=7$)		
	Adults	Offspring	Total	Adults	Offspring	Total
Spring 2007	69 (19)	179 (4)	248	6.9 (1.0)	17.8 (7.8)	24.6 (8.5)
Summer 2008	75 (43)	102 (4)	177			
Autumn 2008	18 (1)	36 (1)	54			
Spring 2008	47 (2)	105 (7)	152	6.4 (2.1)	21.2 (2.4)	27.6 (1.8)
Summer 2009	74 (4)	88 (40)	162			
Autumn 2009	29 (1)	35 (2)	64			

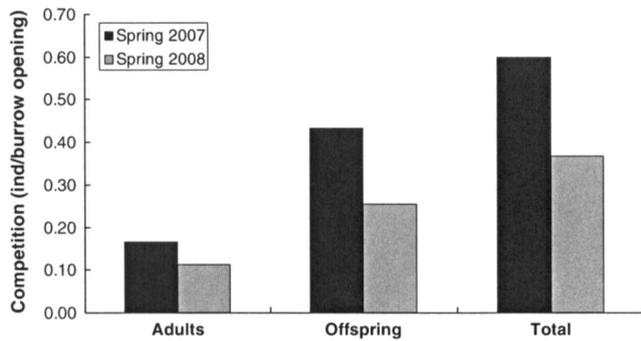


Fig. 4 Estimates of competition in the population during spring 2007 and spring 2008

(Fig. 6b) and increase with increasing number of offspring in groups ($r_s=0.7$, $P=0.23$) (Fig. 6c).

Discussion

Pattern of natal dispersal

The proportion of offspring that dispersed was similar during both years of the study. Dispersal distance distribution was similar in male and female offspring. Although we did not correct for sampling bias (Koenig et al. 1996; Sharp et al. 2008), dispersal movement rates of males and females were similar. Together, these data suggest a pattern of unbiased natal dispersal in degus.

Our results of unbiased dispersal do not fit to the general trend according to which dispersal is male biased in mammals like (e.g., *Microtus arvalis*—Gauffre et al. 2009). However, similarly unbiased dispersal patterns have been observed in some lagomorphs, e.g., American pika (*Ochotona princeps*—Smith and Ivins 1983) and rodents, e.g., pine voles (*Microtus pinetorum*—Solomon et al. 1998) and mole rats (*Cryptomys hottentotus*—Spinks et al. 2000).

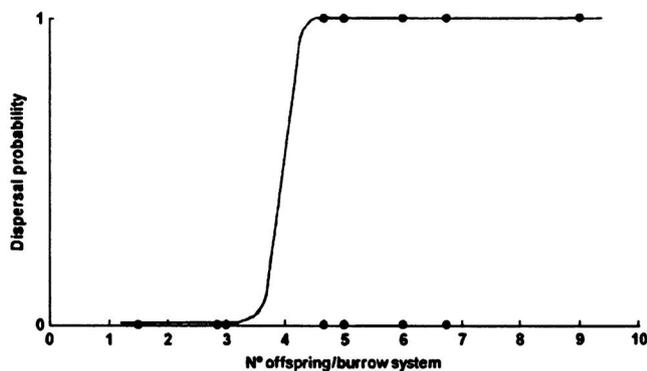


Fig. 5 Logistic regression between the ratio number of offspring per burrow system and the probability of natal dispersal: $\exp(-6.96+1.21x)/(1+\exp(-6.96+1.21x))$ ($P<0.001$)

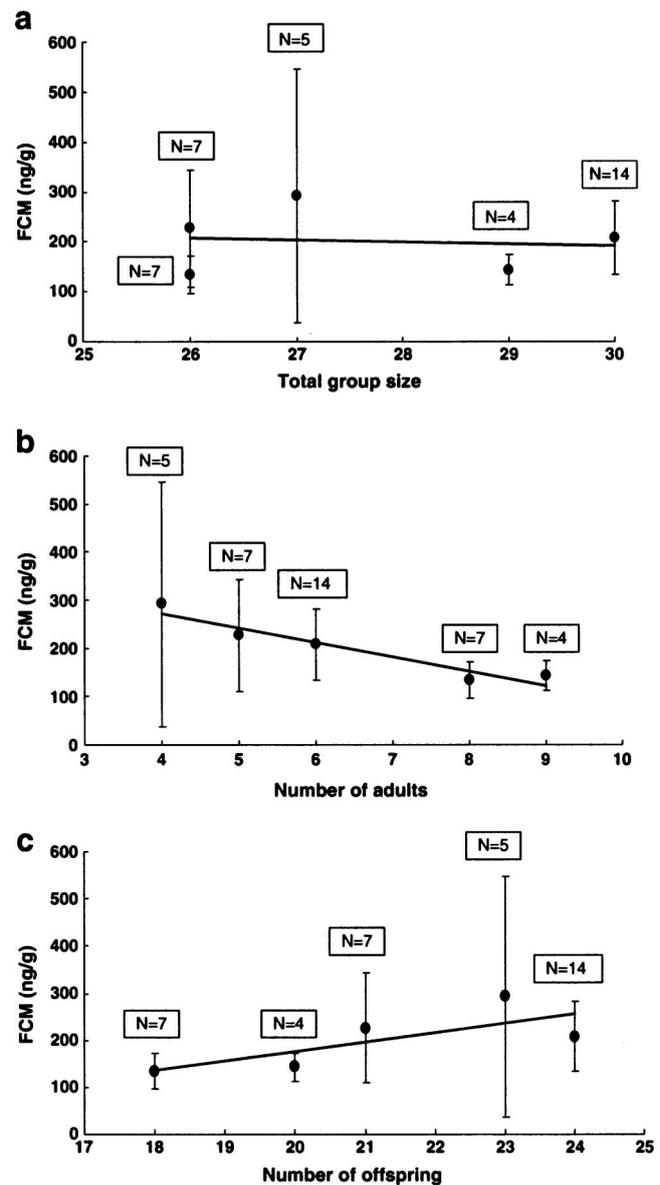


Fig. 6 Spearman's rank correlation between mean FCM (nanogram/gram) of offspring per group and **a** total group size, **b** number of adults per social group, and **c** total number of offspring per social group. Error bars are used to describe within-group variation, but do not represent statistical replicates during statistical analysis

As it has been observed in other small mammals, including American pikas (Smith and Ivins 1983), banner-tailed kangaroo rats (*Dipodomys spectabilis*—Winters and Waser 2003) and Columbian ground squirrels (*Urocitellus columbianus*—Viblanco et al. 2010), dispersing degu offspring settled within the radius of an adult's home range, implying that spatially, degus settle near their natal burrows. This pattern of settlement could result in the formation of temporally stable kin groups, a prerequisite for kin selection to operate (Hamilton 1964; Maynard Smith 1964; Chesser 1991). Indeed, kin-selected behavior has

been implied by some lab studies (Jesseau et al. 2009; Villavicencio et al. 2009), but not others (Ebensperger et al. 2007; Quirici et al. 2008). However, recent demographic analyses have revealed high turnover rates of offspring and adults (Ebensperger et al. 2009) and mean sanguinity coefficients within social groups not different from background levels (Quirici et al. unpublished results, this study). Therefore, opportunities for the evolution of kin-selected social behavior appear to be limited in this population.

Resource competition hypothesis

At the level of population, dispersal was higher in 2007 than in 2008, a pattern that tracked estimates of competition, implying competition may have caused dispersal. This suggestion is further supported by the observed relationship between population size and FCM. Offspring were more stressed in spring and summer (i.e., when competition was higher) than in autumn (i.e., when competition was lower).

Our results indicated that the probability of dispersal increases with increasing number of offspring per burrow system, a measure of habitat saturation in degus. Offspring raised in groups with relatively large numbers of offspring tended to exhibit higher levels of fecal cortisol metabolites though not statistically, suggesting that large groups might be stressful to degu offspring. Together, these observations tend to be consistent with the social competition hypothesis for natal dispersal.

That dispersal increases with increasing number of degus per burrow system opposes previous studies documenting an inverse relationship between measures of habitat saturation and dispersal (Wolff et al. 1988; Sandell et al. 1991; Getz et al. 1993; McGuire et al. 1993; Cochran and Solomon 2000; Lin and Batzli 2001; Lucia et al. 2008, but see Gaines et al. 1979). Instead, our results parallel those of Negro et al. (1997) and VanderWaal et al. (2009). The probability of dispersal in the lesser kestrel (*Falco naumanni*) increases with the degree of saturation in natal colonies (Negro et al. 1997). Similar to degus, the probability of dispersal in lions (*Panthera leo*) increases with increasing group size (VanderWaal et al. 2009). In contrast to degus, however, group size interacted with food abundance to influence dispersal in lions. Thus, dispersal decreases in social groups that inhabit areas with abundant prey, but increases in groups using areas with less abundant prey (VanderWaal et al. 2009). In degus, food abundance is not a predictor of degu group size or dispersal (Hayes et al. 2009; Quirici 2010). In contrast, burrow systems appear to be more relevant for degus to hide from predators and rear their offspring (Ebensperger et al. 2004, 2007; Lagos et al. 2009). The increase in degu abundance in late spring and in summer coupled to a rather constant number of burrow system (Ebensperger and Hurtado 2005a) provides a

scenario of high competition over burrow systems. FCM levels were higher in spring and summer and then decreased in autumn, a pattern that mirrored degu abundance, and was consistent with that juveniles were more stressed during spring and summer. Studies aimed to understand how the ability of groups to hold burrow systems is influenced by ecological or social conditions are strongly needed.

Alternative explanations

Our results contradict some alternative causal hypotheses for mammalian natal dispersal. For example, offspring may disperse from large groups if such conditions are attractive to predators (Mateo 2007). In this scenario, a positive relationship between the total number of adults and FCM is expected. Our observations of a negative correlation between the number of adults and offspring fecal cortisol metabolites suggest that this hypothesis does not explain natal dispersal in degus. One hypothesis that we have yet to explore is that social parasitism drives natal dispersal in degus (Sorci et al. 1994; Boulinier et al. 2001; Tschirren et al. 2007). If bigger social groups contained more parasites (Brown and Brown 1992; Raouf et al. 2006), we might expect dispersal to increase with increasing group size. However, our result of no effect of social group alone in the probability of natal dispersal makes this hypothesis unlikely.

A scenario for natal dispersal in degus

Our results suggest a scenario in which dispersal in degus is driven by social competition. In particular, the threefold increase in degu abundance after parturition would limit the ability of burrow systems to hold this higher pool of individuals present. As a result, juvenile male and female disperse to avoid competition for space with other juveniles within their social group. Eventually, juveniles would compete with individuals from neighboring groups as they disperse. As a result, DDDs would fit a negative exponential distribution. Currently, we are conducting genetic analyses to complement our dispersal estimates based on demographic approaches.

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