



Limited and fitness-neutral effects of resource heterogeneity on sociality in a communally rearing rodent

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Contrasting scenarios have been proposed to explain how resource heterogeneity influences group living or sociality. First, sociality may result from individuals in larger groups attaining net fitness benefits by monopolizing access to resources (“resource-defense” hypothesis). Second, sociality may be the fitness-neutral outcome of multiple individuals using a territory with sufficient resources to sustain a group of conspecifics (“resource-dispersion” hypothesis). While previous studies have tended to support the resource-dispersion hypothesis, these analyses have typically examined only 1 or a few predictions, making it difficult to distinguish between the 2 alternatives. We conducted a 4-year field study of *Octodon degus* to quantify the effects of spatial heterogeneity in food and refuge distributions on group size and 2 components of reproductive success (per capita number of offspring, offspring survival) in this plural breeding and communal rearing rodent. We found only a small effect of heterogeneity of food resources on group size; the effect food resource distribution on group territory size varied across years. Group size did not vary with spatial variation in group territory size and quality. Importantly, there was no covariation between group size and quality of an individual’s territory (i.e., a measure of individual access to resources), or between this measure of territory quality and reproductive success, implying no resource-based benefits to social degus. Overall, our results were more consistent with fitness-neutral relationships among spatial heterogeneity of resources, sociality, and territory size. The resource-dispersion hypothesis, however, did not provide a complete explanation for degu socioecology.

Se han propuesto distintas hipótesis para explicar cómo la heterogeneidad de los recursos afecta la vida en grupos, o sociabilidad. Esta puede surgir en situaciones donde individuos en grupos grandes se benefician al monopolizar el acceso a recursos (hipótesis de defensa de recursos). Por otra parte, la vida en grupos también puede ser el resultado neutro (en términos de adecuación) de individuos que comparten un territorio con recursos suficientes (hipótesis de dispersión de recursos). Aunque algunos estudios previos han validado la hipótesis de dispersión de recursos, estos solo han evaluado un número limitado de las predicciones de esta hipótesis, lo que ha dificultado distinguir entre esta y otras hipótesis alternativas. Durante un estudio de 4 años cuantificamos los efectos de la heterogeneidad espacial de alimento y distribución de refugios sobre el tamaño de grupo y dos componentes del éxito reproductivo (número por cápita de crías, supervivencia de las crías) en *Octodon degus*. Se registraron efectos relativamente pequeños de la heterogeneidad espacial del alimento sobre el tamaño de grupo, y variables entre años sobre el tamaño del territorio de cada grupo. El tamaño de grupo no fue afectado por la variación espacial en el tamaño y calidad del territorio de los grupos. No se registró co-variación entre el tamaño de los grupos y la calidad del territorio de cada individuo (una medida individual del acceso a recursos), o entre la calidad del territorio individual y el éxito reproductivo, lo que sugiere ausencia de beneficios derivados del uso social de recursos en degus. En general, los resultados fueron más consistentes con un escenario de efectos neutros de la heterogeneidad espacial de recursos sobre la sociabilidad. Sin embargo, la hipótesis de dispersión de recursos no explicó el conjunto de efectos (o su ausencia) asociados a la socioecología del degu.

Key words: degus, fitness benefits, group home range, group living, resource distribution

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Sociality, defined as group living, occurs when conspecifics establish long-term (relative to life span) and spatially and behaviorally cohesive units. Individuals in these social units determine basic attributes of sociality such as the number of adult members (group size), kin structure (kinship), and influence different forms of cooperative behavior. Thus, sociality typically increases with group size, the extent to which individuals associate spatially and temporally, and the extent to which group members cooperate (directly or indirectly) to obtain food, avoid predators, or rear their offspring (Ebensperger 2001; Krause and Ruxton 2002; Silk 2007).

One ecological factor thought to play a major role in promoting sociality is heterogeneity of critical resources (i.e., food, refuge, mates—Rodman 1988; Ebensperger 2001). Multiple benefit-based hypotheses have been proposed regarding how resources affect sociality (Ebensperger 2001; Lawler 2011; Clutton-Brock and Janson 2012). Particularly, influential is the “resource-defense” hypothesis, which posits that individuals in larger groups benefit from monopolizing access to resources in habitats (populations) where such resources are abundant yet patchily distributed (i.e., Wrangham 1980; Slobodchikoff 1984). In habitats (populations) where resources are scarce or uniformly distributed, resource defense becomes energetically unfeasible and solitary living is favored (Slobodchikoff 1984). Critical predictions of this hypothesis include a positive effect of resource heterogeneity on group size and positive effects of group size on group territory (range) size and quality. Most importantly, this benefit-based hypothesis predicts enhanced access to more or higher quality resources by individuals in larger social groups, which should translate into higher per capita reproductive success for members of larger groups.

Alternatively, the “resource-dispersion” hypothesis posits that habitats in which resources are abundant and heterogeneous in space or time may promote group living in the absence of direct benefits to group members (Carr and Macdonald 1986; Johnson et al. 2002). This argument is based on the assumption that the area defended (or used) by a resident individual would encompass enough resources to sustain additional individuals (i.e., group members) without imposing a fitness cost to the animals sharing this area (Johnson et al. 2002). Similar to the resource-defense argument, the resource-dispersion hypothesis predicts greater group size in habitats (or populations) with spatially more heterogeneous resources and predicts that group territory quality should increase with group size. However, the resource-dispersion hypothesis predicts that group territory size will increase with resource heterogeneity rather than group size; critically, this hypothesis does not predict that individual access to resources or reproductive success will vary with group size. In sum, while spatial heterogeneity is an important promoter of sociality in both the resource-defense and resource-dispersion hypotheses, these hypotheses differ with regard to the specific mechanisms by which resources affect group size and generate distinct predictions regarding the effect of group size on individual fitness. Distinguishing between these hypotheses and, more generally, determining how resource heterogeneity influences group living are critical to understanding the adaptive bases for sociality.

While studies of birds and mammals have in general revealed a positive association between patchiness of critical resources and group size (Wrangham 1980; Macdonald 1983; Travis et al. 1995; Schradin and Pillay 2005), relating these findings to a specific conceptual framework (including the resource-dispersion or the resource-defense hypotheses) has been challenging. For example, although several studies of carnivores, rodents, and birds claim to be consistent with the resource-dispersion hypothesis (Johnson et al. 2002), these studies typically examined only some of the predictions needed to distinguish between this and the resource-defense hypothesis (Revilla 2003). In part, this is due to the difficulty of quantifying all relevant behavioral, ecological, and fitness data needed (Johnson et al. 2002). In addition, studies tend not to consider alternative hypotheses regarding the role of resources in sociality (e.g., Valeix et al. 2012; Newsome et al. 2013). Thus, robust contrasts of the resource-defense and resource-dispersion hypotheses should improve our understanding of how critical resources contribute to sociality in mammals.

To address this need, we examined the roles of the resource-dispersion and resource-defense hypotheses in explaining the effect of resources on group size in a species in which multiple factors appear to contribute to sociality. Degus (*Octodon degus*) are octodontid rodents that live in social groups of 1–8 ($\bar{X} = 2.4$) breeding adult females and 0–4 ($\bar{X} = 1$) adult males. Degus are semifossorial and diurnal, meaning that they use underground burrows for protection and to rear offspring, but feed aboveground on green herbaceous vegetation during daytime (Ebensperger et al. 2004; Hayes et al. 2007). Degus exhibit different forms of potential cooperation, including the communal digging of burrows and the communal rearing of offspring (Ebensperger et al. 2002, 2004). The role of resources in shaping degu sociality, however, remains unclear. Previous studies have demonstrated that the availability of food may predict reproductive success (Hayes et al. 2009) and that increasing group size is most beneficial when food resources are limited (Ebensperger et al. 2014), suggesting that degu sociality is potentially consistent with the resource-defense hypothesis. However, social degus are also colonial, implying that social groups may be spatially close to each other, with intergroup agonistic interactions (and presumably territoriality) apparently restricted to the mating season (Ebensperger and Hurtado 2005). As a result, groups may not maintain exclusive access to resources and group members may not benefit from enhanced access to those resources, as predicted by the resource-defense hypothesis. To explore these relationships in greater detail, we followed a degu population across multiple years to examine the extent to which associations among group size, territory size and quality, and reproductive success fit the predictions of the resource-defense versus the resource-dispersion hypotheses.

MATERIALS AND METHODS

Study site.—The study was conducted during July–October of 2005–2008, which corresponds to the months when females are pregnant and lactating. We studied a natural population of

degus at the Estación Experimental Rinconada de Maipú, a field station of Universidad de Chile. This study area is characterized by a Mediterranean climate with cold, wet winters and warm, dry summers. Data from the Pudahuel weather station (Dirección Meteorológica de Chile, Santiago, Chile), located 15 km from the Rinconada field station, indicated that mean annual rainfall was 239 (± 81 SD) mm during the years of the study, with most (73% on average) of precipitation occurring during the austral winter, from June to August. We designated a 4–5 ha area in a locality known as Pajaritos (33°23'S, 70°31'W, elevation 495 m) as our study site; degus were sighted frequently at this location. All applicable international, national, and/or institutional guidelines for the care and use of animals, including those of the American Society of Mammalogists (Sikes et al. 2011), were followed. The study was covered by SAG (Servicio Agrícola y Ganadero, Chile) permits nos. 1-58-2005, 1-52-2007, and 1-109-2008 to LAE.

Degu sociality.—Based on previous studies in degus (Ebensperger et al. 2002, 2004), we considered group size (total male and female adults per social group) to be an appropriate general proxy for sociality. Further, we considered the total number of adult females per group to be a reasonable proxy for the potential for communal rearing of offspring (Ebensperger et al. 2002). Group size in degus consists of the number of adult males and females sharing an underground burrow system as well as an aboveground area (territory) for foraging (Ebensperger et al. 2004). Adult disappearance from the study population is high (Ebensperger et al. 2009), such that only 5–10% of adults recorded 1 year are found again the next year. Thus, for statistical purposes, we considered social groups to be independent units across study years.

The size and composition of social groups were determined August–September of each year; this period encompasses most parturition and lactation. Degus are active aboveground during the day but remain in underground burrows at night. Thus, the main criterion used to assign degus to social groups was nocturnal sharing of burrow systems (Ebensperger et al. 2004), which was assessed via early morning trapping at burrow entrances at our study site and nighttime telemetry. During trapping, we defined a burrow system as a group of burrow openings surrounding a central location where individuals were repeatedly found during nighttime telemetry and usually spanning 1–3 m in diameter (Hayes et al. 2007). A mean of 10 traps (range = 8–12; Tomahawk model 201; Tomahawk Live Trap Company, Hazelhurst, Wisconsin), baited with rolled oats,

were used per burrow system per day; traps were spread over an area of 1–2 ha, depending on the abundance and spacing of degu groups. Traps were set prior to the emergence of adults each morning (0600h) and were closed after 1.5h. For all individuals trapped, we determined the identity, capture location, sex, and body mass (to 0.1 g); for all females, we also determined reproductive condition (perforate, pregnant, or lactating). Upon 1st capture, we marked each degu with 2 ear tags, 1 per pinna (Monel 1005-1; National Band and Tag Co., Newport, Kentucky).

To conduct nocturnal telemetry, adults weighing greater than 170 g were fitted with 6–7 g radiocollars (AVM Instrument Co., Colfax, California, or Holohil Systems Ltd, Carp, Ontario, Canada) with unique pulse frequencies. Previous studies at Rinconada had confirmed that nighttime locations represent nest sites where degus remain underground (Ebensperger et al. 2004). Locations for females were determined once per night approximately 1 h after sunset using an LA 12-Q receiver (for radiocollars tuned to 150.000–151.999 MHz frequency; AVM Instrument Co., Auburn, California) and a handheld, 3-element Yagi antenna (AVM Instrument Co., Auburn, California). Table 1 includes the total number of burrow systems trapped, the mean number of trapping days per burrow system, the total number of adults captured and assigned to each social group, the number of radiocollared individuals, and the mean number of nighttime fixes per radiocollared individual.

Determining group composition required the construction of a symmetric similarity matrix of pairwise associations of the burrow locations identified for all adult degus via trapping and telemetry. We determined the association (overlap) between any 2 individuals by dividing the number of times that these individuals were captured at or radiotracked to the same burrow system, by the number of mornings or evenings, respectively, that both individuals were trapped or radiotracked on the same day (Ebensperger et al. 2004; Hayes et al. 2009). To determine social group composition, we conducted hierarchical cluster analysis of the association matrix in SOCPROG (Whitehead 2009). We confirmed the fit of our data with the cophenetic correlation coefficient, a correlation between the actual association indices and the levels of clustering revealed by SOCPROG. In this procedure, values above 0.8 indicate that hierarchical cluster analysis has provided an effective representation of the data (Whitehead 2008). We used the maximum modularity index as the cutoff threshold in the dendrograms to define social groups. To be included in the analysis, adults without radiocollars had

Table 1.—Trapping, radiocollaring, and nighttime telemetry effort on degus (*Octodon degus*) during each study year.

	Year			
	2005	2006	2007	2008
Number of burrow systems trapped	32	58	32	43
Number of trapping days per burrow system ($\bar{X} \pm SE$)	16.8 \pm 0.5	17.3 \pm 0.5	31.4 \pm 1.2	45.3 \pm 1.6
Total number of adults trapped and assigned to a social group	82	65	60	44
Total number of radiocollared individuals	30	40	34	21
Nighttime locations per radiocollared individual ($\bar{X} \pm SE$)	24.8 \pm 1.8	34.0 \pm 3.2	18.3 \pm 4.2	16.0 \pm 0.9
Total number of social groups identified	14	22	9	13

to be captured with another individual in the same burrow system 4 or more times (Hayes et al. 2009; Ebensperger et al. 2011a).

Territory size.—As in previous studies, we quantified home range areas and used these values as estimates of territory size (e.g., Schradin and Pillay 2005; Newsome et al. 2013). Because degus are diurnally active (Ebensperger et al. 2004), we used daytime telemetry to quantify home ranges. All radio-collared degus were given 2–5 days to habituate to the transmitters before daytime telemetry began; telemetry data were collected during August of 2005, 2006, and 2008 and during early September of 2007. Daytime home ranges were determined by locating the position of animals through triangulation (Kenward 2001) at hourly intervals, between 0930 to 1230 and 1430 to 1730h (8 locations per day). Every hour, 2 teams (2 observers per team) simultaneously recorded bearings of every radiocollared subject ($\pm 0.5^\circ$) using the same, previously defined sequence of individuals. Radiotracking was conducted with an LA 12-Q receiver (for radiocollars tuned to 150.000–151.999 MHz frequency) and a 7-element null peak antenna system (AVM Instrument Co.) tuned to the 150.000–151.999 MHz frequency range. Antenna stations were located at fixed positions near the edge of our study grid. Pairs of bearings were then converted to X-Y (north-east) coordinates with Locate II software (Pacer Software, Truro, Nova Scotia, Canada) for subsequent analyses. We used these data to calculate the size of individual and group range areas.

We calculated home range sizes using the Ranges 6 program (Kenward et al. 2003). Individual home ranges were quantified as follows. First, we calculated 95% minimum convex polygons (MCP95%) based on all locations recorded for each degu. Alternative home range algorithms (e.g., 95% fixed kernels) provide similar estimates in degus (Hayes et al. 2007; Quirici et al. 2010). We used the MCP95% option and selected the kernel option to compute location of home range cores (1 per degu). We chose MPC95% to make our results more comparable with most previous studies. Secondly, for each radiocollared degu, we calculated the straight line distance between every spatial location and the animal’s central location. We labeled locations as outliers whenever a point was farther than 300 m from estimated core locations. This distance was chosen based on the maximum extent of the area containing the study population. As a result, we excluded 4 data points identified as outliers from 4 individuals in austral winter 2007. A total of

22 outliers from 13 individuals were discarded in 2008 (i.e., 1.7 per individual, $SD = 0.95$). Individual degu home ranges were then recalculated using MPC95% after removing these outlier locations. We used Ranges 6 to quantify the number of locations at which home range size stabilized (i.e., sampling saturation). Sampling saturation was noted after 25 locations in 2005, 30 in 2006, 30 in 2007, and 18 in 2008. We also calculated home range sizes for social groups using the software Ranges 6 (Kenward et al. 2003). Group home range size (based on MCP95%) was calculated without outlier locations, and after combining locations from all group members for which data were available.

The number of radiocollared degus that contributed daytime telemetry locations, the mean number of daytime locations per radiocollared degu, and the mean number of daytime locations per social group are given in Table 2.

Mean and variance of territory quality.—Based on data regarding the preferred foods of degus at our study site (Quirici et al. 2010), we sampled biomass of green annual herbs and forbs to quantify mean and variation in group and individual territory quality. Samples of green herbs were taken at 3 and 9 m from the center of each burrow system to quantify the abundance of primary food resources at the spatial scale of social groups (Hayes et al. 2009; Ebensperger et al. 2012b). We randomly chose 1 location at 3 m and 1 at 9 m in the north, east, south, or west directions (total = 2 samples per burrow system used by social groups). At each of these 2 sampling points, we established a 250×250mm quadrant and removed the aboveground parts of all green grasses and forbs within that area. During this process, we distinguished between monocotyledonous and dicotyledonous plant species. Samples were immediately stored inside 2-kg paper bags. In the laboratory, we oven-dried each plant sample at 60°C for 72h to determine its dry mass (biomass in g—Ebensperger and Hurtado 2005). Data from 3- and 9-m sampling points were averaged per burrow system and standardized to gram per square meter of vegetation for subsequent analysis. In addition to quantity and quality of food conditions, we quantified density of burrow openings at a burrow system. Given that degus use burrows to evade predators, density of burrow openings (hereafter “refuge density”) represents a measure of territory quality in terms of access to safe havens. Density of burrow openings (number per square meter) was determined by quantifying the number of burrow openings in the circular area encompassing a 9 m radius from the center of each burrow system.

Table 2.—Daytime telemetry effort used to calculate individual and social group home range size of degus (*Octodon degus*) during each study year.

	Year			
	2005	2006	2007	2008
Total number of radiocollared individuals with home range data	26	40	33	19
Number of valid daytime locations per radiocollared degu ($\bar{X} \pm SE$)	34±1	32±1	31±1	13±1
Number of daytime locations per radiocollared degu discarded as outliers ($\bar{X} \pm SE$)	0	0.1±0.1	1.4±0.3	2.0±0.3
Number of radiocollared degus with data on home range and assigned to a social group	21	20	30	14
Number of social groups with data on group home range	11	14	9	8
Daytime locations per social group ($\bar{X} \pm SE$)	67±11	48±5	105±18	25±3

We used Ranges 6 to overlay individual home ranges on the spatial locations of the burrow systems sampled. Thus, individual territory quality was calculated as the mean food biomass and density of burrow openings within an animal's home range, a measure of individual access to critical resources. We subjected group range areas to the same procedure to calculate group territory quality. For group estimates, we also computed the coefficient of variation (CV) of food biomass and density of burrow openings among individual areas located within the group range to provide a measure of resource heterogeneity.

Reproductive success.—We recorded reproductive success (a measure of direct fitness) from the number of offspring produced by each social group during the spring breeding period. To this end, we quantified the number of offspring first captured within the area occupied by each social group during September–October of each year. Per capita offspring produced (PCOP) was determined by dividing the number of offspring captured per group by the number of adult female group members living in the same burrow system. Since mortality of degu offspring is high (Ebensperger et al. 2013), we also calculated an index of offspring survival based on the recapture of offspring during May–July (austral autumn) of the year after those offspring were born. Offspring reach sexual maturity and mate at this time (Ebensperger and Hurtado 2005), implying that survival to the following autumn has a major impact on lifetime fitness. Per capita surviving offspring (PCSO) was determined by dividing the number of offspring surviving until the autumn by the number of adult female group members. Per capita offspring counts have been used as estimates of direct fitness for other plural breeding rodents (Lacey 2004), including degus (Hayes et al. 2009; Ebensperger et al. 2011a); although such estimates do not capture individual variation in direct fitness within a social group, they should provide an important estimate of the relative fitness of different social groups.

Statistical analysis.—We used generalized mixed linear effects models to examine effects of predictor–response variable combinations relevant to testing predictions 1 through 4 (Table 6) of the 2 resource-based hypotheses examined (Pinheiro and Bates 2000; Zuur et al. 2009). These models considered social groups as sampling units. A total of 12 models were evaluated to examine prediction 1, and 4 models were evaluated to examine prediction 2. A total of 3 models were considered in the context of prediction 3, and 12 other models addressed prediction 4. Study year was added to all models as a random factor, which allowed consideration of random intercepts and slopes. Response variables in models associated with predictions 1 through 4 were assumed to fit a Poisson distribution.

Since individuals within groups were the relevant sampling units to examine predictions 5 and 6 of the hypotheses examined (Table 6), these were verified with the use of linear mixed effects models. A total of 12 and 16 additional models were used to examine predictions 5 and 6, respectively. Study year and social group of origin were added to each of these models as random components.

For all models examined, model parameters were estimated using maximum likelihood approaches. Hypothesis testing was conducted using likelihood ratio tests to compare random intercept or random coefficients (random intercept and slope) models against intercept only (plus the random component—Garson 2013) null models. All analyses were done in the R statistical environment using the lme4 library (Pinheiro and Bates 2000).

RESULTS

Variation in degu sociality, reproductive success, territory size, and quality.—In total, 57 social groups were identified during the 4 years of this study. In spring, groups averaged 3.8 ($SD = 2.0$) adults (range = 1–9 adults). Social groups were composed mostly of females. The number of females averaged 2.7 ($SD = 2.0$) adults per group (range = 0–8). The number of males averaged 1.1 ($SD = 1.1$) adults per group (range = 0–4). Mean PCOP was 5.3 ($SD = 2.6$) per group (range = 1–10). Mean PCSO was 1.1 ($SD = 0.8$) per group (range = 0–3).

Estimates of individual home range areas did not change substantially after 25 locations in 2005, 30 in 2006, 30 in 2007, and 18 in 2008. The number of valid daytime locations per radio-collared degu averaged 13 in 2008 (Table 2), suggesting that individual home range areas in 2008 were underestimates of the true range areas. Group territory size averaged 0.8 ($SD = 0.9$) ha (range = 0.1–3 ha). Distance between the home range cores for different social groups averaged 46.9 ($SD = 29.4$) m (range = 3–161 m). Total biomass of herbs within group territories averaged 114.3 g per m^2 (mean $CV = 0.4$). When monocotyledonous and dicotyledonous herbs were separated, monocotyledonous herbs tended to be less abundant but spatially more variable. Thus, monocotyledonous herbs averaged 39.4 g per m^2 (mean $CV = 0.8$), while dicotyledonous herbs averaged 74.9 g per m^2 (mean $CV = 0.6$). Refuge density averaged 0.12 burrow entrances per m^2 (mean $CV = 0.3$).

Effect of resource heterogeneity on sociality.—Only 2 of the 12 models used to examine the association between resource heterogeneity and group size revealed significant effects, suggesting that resource heterogeneity was not a strong predictor of sociality. Of the 2 models that revealed significant effects, one indicated that the number of males per social group increased with CV for total herb biomass (Table 3A); the other indicated that group size decreased with increasing CV of dicotyledonous herb biomass (Table 3B). No other models revealed significant effects of resource heterogeneity on sociality (Tables S1–S12 of Supporting Information S1).

Effect of resource heterogeneity on group territory size.—Only 1 of the 4 models examined revealed a significant association between group territory size and CV of monocotyledonous herb biomass (Table 4). In this variable slope model, the relationship between CV of monocotyledonous herb biomass and group territory size was positive during 2005 and 2006, not significant in 2007, and negative in 2008 (Fig. 1). All other models revealed nonsignificant effects of resource heterogeneity on sociality (Tables S13 and S16 of Supporting Information S1).

Table 3.—(A) Generalized linear mixed effects models (GLMM) for group size in response to CV of total herb biomass and (B) to CV of dicotyledonous herb biomass. Tables show fixed effects only. Information on model fit, including Akaike (AIC) and Bayesian (BIC) information criteria estimates, and the likelihood ratio test used to compare the random intercept and the random coefficient models against the null model (intercept only) is provided in [Supporting Information S1](#) (Tables S3 and S7 under prediction 1 subheading). Bold typing is used to highlight statistically significant estimates.

Source of variation	Estimate	SE	Z-value	P-value
(A) Fixed effects for random intercept model				
Intercept	−1.1092	0.6468	−1.72	0.0864
CV total herb biomass	2.7921	1.2129	2.30	0.0213
(B) Fixed effects for random intercept model				
Intercept	1.7581	0.1641	10.71	< 0.0010
CV dicotyledonous herb biomass	−0.6517	0.2749	−2.37	0.0178

Table 4.—Linear mixed effects models (LMM) for group territory size (based on MPC95%) in response to CV of monocotyledonous herbs. The table shows fixed effects and separate year slope estimates. Information on model fit, including Akaike (AIC) and Bayesian (BIC) information criteria estimates, and the likelihood ratio test used to compare the random intercept and the random coefficient models against the null model (intercept only) is provided in [Supporting Information S1](#) (Table S14 under prediction 2 subheading). Bold typing is used to highlight statistically significant estimates.

Fixed effects for random coefficients model					
Source of variation		Estimate	SE	Z-value	P-value
Intercept		1.594	1.1322	1.41	0.1590
CV monocotyledonous herbs		−0.881	0.9560	−0.92	0.3566
		Year			
		2005	2006	2007	2008
CV monocotyledonous herbs	Slope	1.331	1.390	−0.500	−2.220
	Lower IC95%	0.650	0.706	−1.103	−3.206
	Upper IC95%	2.012	2.074	0.102	−1.235

These analyses indicate only limited effects of resource heterogeneity on group territory size, with the specific nature of this relationship varying across years.

Effect of sociality on group territory size and quality.—None of the 3 models examined revealed significant effects of sociality on group territory size (Tables S17–S19 of [Supporting Information S1](#)). Similarly, none of the 12 models examined revealed significant effects of sociality on group territory quality (Tables S20–S31 of [Supporting Information S1](#)).

Effect of sociality on individual territory quality (individual access to resources).—None of the 12 models examined revealed significant effects of sociality on individual territory quality and thus, by implication, individual access to resources (Tables S32–S43 of [Supporting Information S1](#)).

Effect of individual access to resources (individual territory quality) on reproductive success of females.—A total of 4 out of 8 models that examined the relationship between individual territory quality and PCOP revealed significant negative effects of individual territory quality (total herb biomass and dicotyledonous biomass) on PCOP (Table 5). All 8 models indicated that PCOP decreased with either group size or the number of breeding females per group (Table 5). None of these models, however, revealed statistically significant effects of individual territory quality on PCSO (Table 5). Three of these models revealed a significant negative effect of the number of breeding females on PCSO (Table 5); the remaining 5 models did not reveal any significant relationships with PCSO (Tables

S52–S59 of [Supporting Information S1](#)). Thus, individual territory quality had a generally small, negative effect on female reproductive success.

DISCUSSION

Degu sociality.—Our analyses revealed several new insights into the potential effects of variation in resources (food, refuge density) on sociality in a communally nesting rodent. Overall, our findings did not provide consistent support for either of the 2 hypotheses considered. First, spatial heterogeneity of food resources had only a limited influence on group size and group territory size, which correspond to predictions 1 and 2 of our hypotheses (Table 6). Although some of the specific outcomes of these analyses (e.g., number of males per social group and CV of total herb biomass) were consistent with one or both the hypotheses tested, others (e.g., lack of consistent relationship between group territory size and resources) did not. Second, none of the 3 measures of degu sociality (including group size) examined were sensitive to variation in group territory size (prediction 3, Table 6) or quality (prediction 4, Table 6). While a lack of relationship between group size (and the other sociality measures) and group territory size is consistent with the resource-dispersal hypothesis, a similar lack of relationship between group size and group territory quality is not consistent with either the resource-dispersal and resource-defense models (Table 6). Third, we found relationships between group size and quality of

individual territory (prediction 5, [Table 6](#)), which contradicts the resource-defense hypothesis but is potentially consistent with the resource-dispersion hypothesis. Finally, we found either

no or negative relationships between individual territory quality and estimates of reproductive success, implying no fitness benefits to sociality associated with resource heterogeneity; this

Table 5.—Linear mixed effects models (LMM) for per capita offspring produced (PCOP) and per capita surviving offspring (PCSO) to sexual maturity in response to sociality (group size), communal rearing (number of females), and mean food conditions within territory (i.e., territory quality based on total, monocotyledoneous, and dicotyledoneous herb biomass). The table shows statistically significant fixed effects only. Information on model fit, including Akaike (AIC) and Bayesian (BIC) information criteria estimates, and the likelihood ratio test used to compare the random intercept and the random coefficient models against the null model (intercept only) is provided in [Supporting Information S1](#) ([Tables S44–S51](#), [S53](#), [S57](#), and [S59](#) under prediction 6 subheading). Bold typing is used to highlight statistically significant effects. Only models with at least one significant effect are shown; all other models examined are included in [Supporting Information S1](#). Bold typing is used to highlight statistically significant effects.

Response variable	Predictor	Slope	SE	<i>t</i> -value	<i>P</i> -value
PCOP	Group size	−0.5261	0.1237	−4.253	< 0.001
	Total herb biomass	−0.0168	0.0076	−2.221	0.031
PCOP	Number of females	−0.545	0.1539	−3.540	< 0.001
	Total herb biomass	−0.020	0.0077	−2.588	0.013
PCOP	Group size	−0.5432	0.1281	−4.238	< 0.01
	Monocotyledoneous herbs	0.0076	0.0104	0.724	0.472
PCOP	Number of females	−0.5365	0.1611	−3.3300	0.002
	Monocotyledoneous herbs	0.0089	0.0111	0.805	0.425
PCOP	Group size	−0.460	0.1308	−3.521	0.001
	Dicotyledoneous herbs	−0.023	0.0076	−3.055	0.004
PCOP	Number of females	−0.448	0.1607	−2.790	0.007
	Dicotyledoneous herbs	−0.027	0.0075	−3.583	0.001
PCOP	Group size	−0.5840	0.1241	−4.708	< 0.01
	Refuge density	5.2498	4.1332	1.270	0.209
PCOP	Number of females	−0.5926	0.1563	−3.792	< 0.01
	Refuge density	5.4723	4.3176	1.267	0.209
PCSO	Number of females	−0.195	0.0715	−2.732	0.006
	Total available food	0.0032	0.0033	0.960	0.337
PCSO	Number of females	−0.174	0.0819	−2.136	0.033
	Dicotyledoneous herbs	0.0006	0.0031	0.2212	0.825
PCSO	Number of females	−0.170	0.0730	−2.336	0.019
	Refuge density	0.511	2.2196	0.230	0.817

Table 6.—Associations predicted under the resource-defense and the resource-dispersion hypotheses. The number of models used to examine each prediction is related to the different predictors examined (see [Supporting Information S1](#)). The number of models that revealed none, negative, or positive effects in each case is shown in parentheses. Bold typing is used to highlight associations detected (or its absence) that were relevant to each hypothesis prediction.

Association examined	Effect predicted by the resource-defense hypothesis	Effect predicted by the resource-dispersion hypothesis	Number of models examined	Number and nature of variable associations revealed	Hypothesis supported
(1) Association between group size and resource heterogeneity	Positive	Positive	12	None (10) Negative (1) Positive (1)	Resource-defense and Resource-dispersion
(2) Association between group territory size and resource heterogeneity	None	Positive	4	None (4) Negative (1) Positive (1)	Resource-defense and Resource-dispersion
(3) Association between group size and group territory (range) size	Positive	None	3	None (3) Negative (0) Positive (0)	Resource-dispersion
(4) Association between group size and group territory quality	Positive	Positive	12	None (12) Negative (0) Positive (0)	None
(5) Association between group size and individual access to resources	Positive	None	12	None (12) Negative (0) Positive (0)	Resource-dispersion
(6) Association between per capita access to resources and reproductive success	Positive	None	16	None (12) Negative (4) Positive (0)	Resource-dispersion

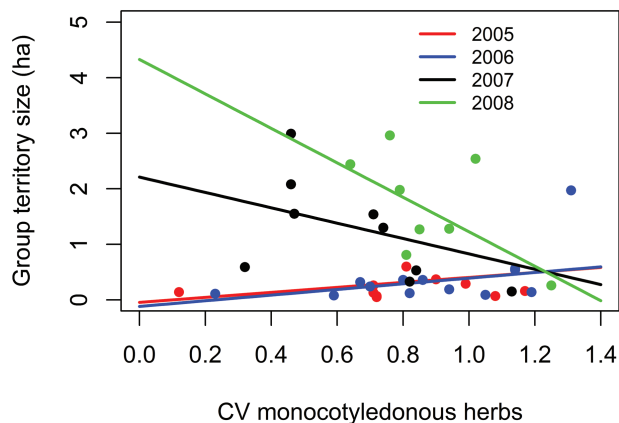


Fig. 1.—Effect of spatial heterogeneity of monocotyledonous herb biomass on group territory size across 4 years in the communally rearing rodent, *Octodon degus*. Regression lines were calculated with the use of linear mixed effects models, all of which included random intercepts and slopes, and where year was a random component.

fitness-neutral outcome is more consistent with the resource-dispersion hypothesis (prediction 6, Table 6). Thus, overall, our analyses do not provide consistent support for either the resource-defense or the resource-dispersion hypotheses.

Sociality is a complex phenomenon and understanding the factors that contribute to its origin and maintenance remain central topics in behavioral research (Lacey and Ebensperger 2007; Ebensperger and Hayes, in press). Results of this study highlight how effects of spatial heterogeneity of resources can be complex and can have variable impacts on social structure. Although we found some support for the resource-dispersion hypothesis, degu socioecology was not well explained by this hypothesis. Thus, while heterogeneity in food resources may contribute, it does not seem to be the sole ecological driver of within-population variation in degu sociality. A 2nd potentially important contributing factor is predation risk, a major ecological driver of animal sociality (Krause and Ruxton 2002; Davies et al. 2012) that may function via multiple different mechanisms (Ebensperger 2001). For degus in particular, individuals in larger foraging groups enhance collective vigilance and ability to detect approaching predators (Ebensperger and Wallem 2002; Ebensperger et al. 2006), supporting the “many eyes” hypothesis (Pulliam 1973). The general importance of predation risk to degu sociality is further supported by differences in risk across populations. Total group size is larger in populations and years with more abundant predators, lower density of burrow openings, and in groups whose burrows are far from overhead cover (Ebensperger et al. 2012a). Since social benefits associated with predation risk do not preclude benefits associated with resources, multiple ecological factors may contribute to variation in degu sociality and efforts are needed to establish the relative importance of each. Most likely, the relative costs and benefits of different ecological parameters vary dynamically and differ between populations characterized by different environmental conditions.

Resource heterogeneity and mammalian sociality.—The limited ability of the resource-heterogeneity hypothesis to predict relationships between sociality and spatial heterogeneity of

resources in degus appears to be typical of studies of social mammals. Among primates, the sizes of territories defended by groups of male chimpanzees (*Pan troglodytes*) increased with the number of days receptive females were encountered (i.e., mate availability to males—Williams et al. 2004). This observation is consistent with the resource-dispersion hypothesis. Interbirth interval (a measure of reproductive success), however, is shorter in groups with larger territories (Williams et al. 2004), a reproductive benefit that is more consistent with the resource-defense hypothesis. Among carnivores, the observation that foraging group size in dingos (*Canis dingo*) increases in patches with greater food abundance (i.e., territory quality) supports both the resource-dispersion and resource-defense hypotheses (Newsome et al. 2013). However, the finding that territory size decreases with group size in this species (Newsome et al. 2013) is inconsistent with both hypotheses. Finally, long-term (~30 years) data on social groups of European badgers (*Meles meles*) support a positive relationship between territory size and group size, suggesting that the resource-dispersion hypothesis alone cannot explain social behavior and territoriality in this species (Robertson et al. 2015).

Similar inconsistencies have been reported for social rodents other than degus. For example, capybara (*Hydrochoerus hydrochaeris*) groups actively defend sources of water against other groups throughout the wet season, when lagoons are more abundant and evenly distributed (Herrera and Macdonald 1987, 1989). Group territoriality declines and group size increases, however, when pools become scarce and patchily distributed (Herrera and Macdonald 1987); this change in behavior with changing resource availability is consistent with both hypotheses. The size of capybara group territories increases with group size in Venezuela (Herrera and Macdonald 1987, 1989) but not in Colombia (Jorgenson 1986) or Argentina (Corriale et al. 2013). Thus, the effect of resource availability on social behavior appears to vary among populations of this species. Similarly, inconsistent support for predictions of both hypotheses has been revealed by experimental field studies such as those of Gunnison’s prairie dogs (*Cynomys gunnisoni*) in which experimental increases in the heterogeneity of food resources were associated with a decrease in group territory size (Verdolin 2009).

Overall, available evidence suggests that resource heterogeneity influences mammalian sociality but that neither the resource-dispersion nor the resource-defense hypotheses adequately explain the effects of resource abundance and heterogeneity on the social structure of any given species. This mismatch between predicted and observed outcomes may be due in part to the fact that the effects of resource patchiness are scale dependent (Johnson et al. 2002; Clutton-Brock and Janson 2012). For example, spatial heterogeneity in abundance of wet meadows appears to be an important factor limiting dispersal and favoring group living in the colonial tuco-tuco (*Ctenomys sociabilis*) when examined within a single population, but less so at the scale of populations throughout the geographic distribution of this species (Tammone et al. 2012). Accordingly, appropriate tests of hypotheses may require measures of resource heterogeneity at multiple temporal or spatial scales. Meta-analytic

analytical approaches may be useful to assess how the effects of resource heterogeneity on sociality and territory size change with the spatial scale used across available studies.

The inability of the resource-dispersion and resource-defense hypotheses to explain fully the effects of resource abundance and heterogeneity may also occur because these theoretical models do not adequately capture the complexity of the phenomenon studied. In particular, the effects of resource heterogeneity on sociality may be contingent upon other ecological factors. For example, territory size in coyotes (*Canis latrans*) is determined by competitor pressure in areas with high resource abundance and by prey abundance and dispersion in low resource abundance areas (Wilson and Shivik 2011). During our study, covariation between group territory size and heterogeneity of monocotyledonous herbs was positive during 2005 and 2006, did not occur during 2007, and then changed to negative in 2008. Degu density was higher during 2005 through 2007, but dropped in 2008 (Ebensperger et al. 2011b), implying that density may modulate resource heterogeneity–sociality interactions in degus. A previous study aimed at understanding variation in the fitness consequences of degu sociality demonstrated how measures of mean food and density influenced the effects of sociality on fitness across years (Ebensperger et al. 2014). Density-dependent effects on sociality are relatively common in other social species (e.g., Randall et al. 2005; Vander Wal et al. 2013); thus, exploration of resource-based models of sociality that include density-dependent or other condition-dependent effects should be a fruitful line of inquiry (e.g., Fronhofer et al. 2011; Bateman et al. 2012).

Overall, our analyses illustrated how the effects of resource heterogeneity on degu and mammalian sociality are complex and not easily predicted by some of the most frequently examined hypotheses. A potentially fruitful approach to unravel this complexity is to generate comparative data for multiple species of variables examined in this study. This would allow interspecific analyses of general relationships between ecology and social behavior.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Details of all 59 models used to examine each of the 6 hypothesis predictions tested.

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