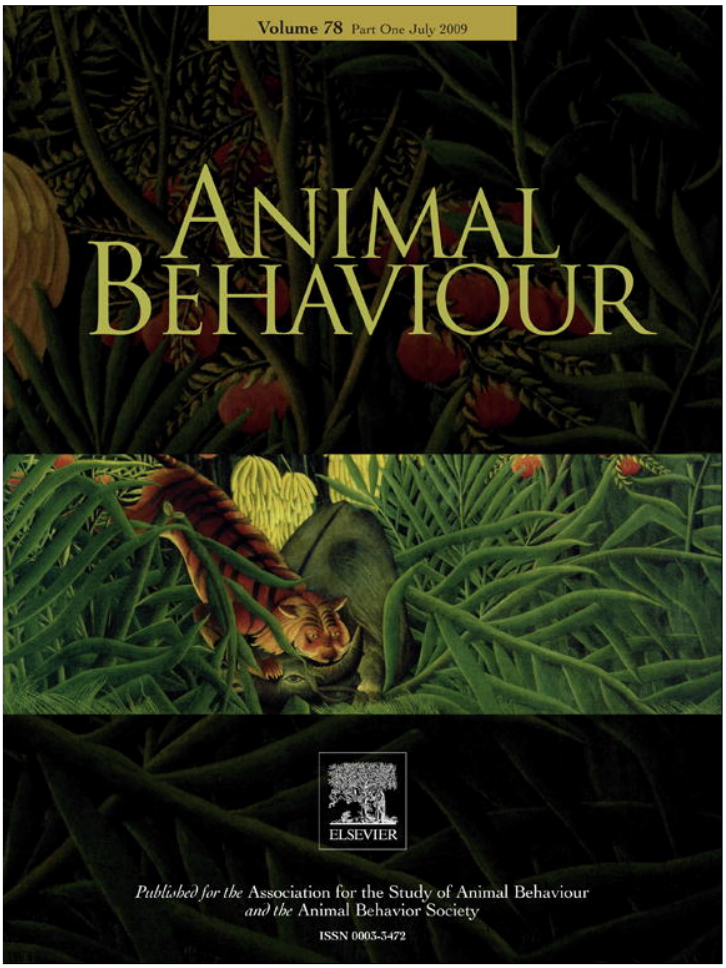

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Fitness consequences of group living in the degu *Octodon degus*, a plural breeder rodent with communal care

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The fitness consequences of plural breeding vary considerably among social vertebrates. We tested three hypotheses for the direct reproductive fitness consequences of group living in the degu *Octodon degus*, a social rodent endemic to central Chile. To test the 'benefits of communal care' hypothesis, we determined the relationship between the number of females per group, per capita direct fitness and offspring survival. To test the 'food abundance and quality' hypothesis, we determined the relationship between the biomass of preferred foods at burrow systems, group size, per capita direct fitness and offspring survival. To test the 'predation risk' hypothesis, we determined the relationship between group size, the density of burrow entrances to which social groups had access, per capita direct fitness, and survival of adults and offspring. Group size of core females (i.e. those with 50% or more nightly overlap) was negatively correlated with per capita direct fitness, but not with the number of females per group or total group size. Group living did not enhance the survival of offspring. Greater biomass of food (at 3 m and 9 m) and burrow density were not linked to larger groups and offspring survival. Our results did not support predictions of the 'benefits of communal care', 'food abundance and quality' or 'predation risk' hypothesis. Pending microsatellite analyses, we hypothesize that survival benefits linked to foraging group size and not reproductive fitness benefits may explain the evolution of sociality in degus.

An important step in understanding the evolutionary significance of sociality, a foundation of behavioural ecology (Owens 2006), is to quantify the reproductive fitness consequences of living in groups of varying size. Most likely, there are species- and habitat-specific group sizes that maximize individual (Silk 2007) and inclusive (Rodman 1981) fitness. When groups are too small, breeders may be at a greater risk of mortality or experience increased intergroup competition (Ebensperger & Wallem 2002; Pride 2005). When groups exceed certain levels, fitness could decrease because of increased intragroup competition for resources (Clutton-Brock et al. 1982; Pride 2005) and infanticide (van Schaik & Janson 2000). However, social groups are complex and the reproductive fitness consequences of group living may be affected by factors other than group size. Individual fitness may be affected by intrinsic factors such as the composition of social groups and the relative extent of competitive and cooperative interactions within groups (Griffin & West 2002; Silk 2007).

In mammalian sociality, the fitness consequences of plural breeding (i.e. when multiple females within groups breed or share direct reproduction; Brown 1987) may depend on both group size and whether breeders communally rear offspring (Silk 2007). In plural breeders without communal care (Silk 2007), the fitness consequences of group living are most closely related to the costs (e.g. competition for resources) and benefits (e.g. reduced predation risk) of group size per se. In several of these species, fitness either decreases (e.g. van Noordwijk & van Schaik 1999; Treves 2001; Lacey 2004) or does not change with increasing group size (Van Vuren & Armitage 1994; Mann et al. 2000; Robbins et al. 2007). However, fitness in some other species increases (Campagna et al. 1992), or is maximized when groups are of intermediate in size, as is the case in some rodents (Armitage & Schwartz 2000), primates (van Noordwijk & van Schaik 1999) and ungulates (Clutton-Brock et al. 1988). In some plural breeders, females communally care for offspring produced by other group members (i.e. plural breeding with communal care; Silk 2007). Theory predicts that plural-breeding females with communal care benefit

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from increased direct fitness, and if group members are kin, from indirect fitness through the enhanced reproductive success of kin (Hamilton 1964; Maynard Smith 1964). While fitness benefits have been observed in some plural breeders with communal care, including carnivores (Cant 2000; Packer et al. 2001) and rodents (König 1994; Manning et al. 1995; Gerlach & Bartmann 2002; McGuire et al. 2002), this strategy is costly (Boyce & Boyce 1988; da Silva et al. 1994; Hoogland 1995; Solomon & Crist 2008) or has no effect on fitness (Wolff 1994; Pilastro et al. 1996; Randall et al. 2005) in other species. Contradictory results from species of the same order and from field-based studies suggest that more studies are needed before we can make generalizations about the fitness consequence of group living in mammalian plural breeders with communal care.

Extrinsic factors such as the distribution and abundance of food resources (e.g. Slobodchikoff 1984) and predation risk (Ebensperger 2001b) may lead to variation in social systems (see Emlen & Oring 1977; Brashares & Arcese 2002), and in turn, affect the fitness consequences of social animals. For example, the distribution and overlap of female ungulates and rodents is affected by the distribution of food resources (Slobodchikoff 1984; Brashares & Arcese 2002). Consequently, male behaviour changes with the distribution of females, leading to mating system variation (Emlen & Oring 1977; Brashares & Arcese 2002; Schradin & Pillay 2005). In numerous species, group living reduces predation risk through a number of potential mechanisms (e.g. dilution effect; Ebensperger 2001b), a benefit that may be particularly important if safe havens such as tree cavities, overhead cover or burrows are limited. All of these factors may be linked to the density of animals (Emlen 1982), which in turn could influence dispersal, social group size and fitness (Komdeur et al. 1995; Lucia et al. 2008). Quantifying the fitness consequences of animal sociality requires consideration of these ecological factors.

The degu *Octodon degus*, a caviomorph rodent endemic to central Chile, lives in kin groups consisting of males and reproductive females (Ebensperger et al. 2004). Laboratory data suggest that degus meet Silk's (2007) definition of a plural breeder with communal care. Females indiscriminately retrieve (Ebensperger et al. 2006a) and nurse (Ebensperger et al. 2002; Becker et al. 2007) their own and nondescendant offspring and engage in other forms of communal care, including huddling and grooming of nondescendent offspring (Ebensperger et al. 2007). In contrast, males provide significantly less care to offspring (L. A. Ebensperger, unpublished data). Degus living in large groups benefit from reduced predation risk and per capita costs of preparing burrows (Ebensperger & Bozinovic 2000; Ebensperger & Wallem 2002). In the wild, litters consist of approximately five to six offspring (Meserve et al. 1984); in the laboratory, the mean litter size is 6.5 (Ebensperger et al. 2007). Plural breeding with communal care does not increase the survival and mass gain of pups in the laboratory (Ebensperger et al. 2007). However, the reproductive consequences of group living may differ in the wild, where maternal investment in offspring can be affected by variation in available resources, and the composition of groups may be variable (McGuire et al. 2002; Solomon & Crist 2008). Thus, we tested hypotheses for the influence of ecological variation on social group size and composition, and subsequently the fitness of social degus. The 'benefits of communal care' hypothesis predicts that independent of ecological variation, females associated with large groups should experience reproductive fitness benefits from communal rearing (König 1994). In degus, this hypothesis would be supported if both the per capita direct fitness (i.e. number of offspring produced per female) and the proportion of offspring surviving to an age that is predisposed to disperse (estimated by body mass: Ebensperger et al. 2007) increase with the number of adult females, but not adult males, per group. The 'food abundance and quality' hypothesis predicts that the size and composition of social groups are determined by the abundance of food resources (Brashares & Arcese 2002). In degus, this hypothesis would be supported if the biomass of food at burrow systems is positively correlated with the number of adults per group (Ebensperger 2001b), and consequently, per capita fitness of females. Finally, the 'predation risk' hypothesis predicts that group living reduces the risk of predation (Ebensperger 2001b), possibly through enhanced detection of predators, dilution of predation risk and access to safe havens from predators. Degus in larger groups respond more quickly to approaching terrestrial predators because of the many eyes effect (Ebensperger & Wallem 2002). We tested the prediction that group size is positively linked with per capita direct fitness, offspring and adult female survival, and the number of burrow entrances and whole burrow systems (safe havens) accessible to a group.

METHODS

Study Site

This study was conducted during the austral winter and spring months of June–November 2005, 2006 and 2007 at the Estación Experimental Rinconada de Maipú (33°23′S, 70°31′W, altitude 495 m), a field station of the Universidad de Chile. The site is characterized by a Mediterranean climate with cold, wet winters and warm, dry summers. The habitat, known as Chilean matorral, is dominated by scattered shrubs and abundant grasses and forbs. In June 2005, two study grids were established approximately 150 m from each other in areas where degus were visually abundant. The grids were characterized by a similar distribution of grasses, forbs and shrubs and covered 0.18 ha (30 × 60 m; Grid 1) and 0.25 ha (50 × 50 m; Grid 2), respectively. Our study involved three stages: (1) grid trapping for animal density and to assign radiocollars to animals (June), (2) night-telemetry and burrow trapping for the determination of social group size and composition (June–October) and (3) measurements of ecological variation at burrow systems used by known social groups (September–October). Our study was conducted on Grids 1 and 2 in 2005 and 2006 and Grid 1 in 2007.

Grid Trapping

Grid trapping for the purposes of assigning radiocollars and estimating density was conducted at the two study grids during mid-June (late austral autumn). We extrapolated adult degu densities from grid trapping to estimate the number of animals per hectare. Adult degus were captured using Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, FL, U.S.A.) and locally produced metal live traps (similar to Sherman live traps) baited with rolled oats. Traps were set at fixed stations at 5 m intervals resulting in 91 (7 × 13 array) traps on Grid 1 and 121 (11 × 11 array) traps on Grid 2. Traps were opened for 5 days during the morning (0800–0900 hours) prior to emergence of degus from burrows and closed after 3 h. We determined the sex, body mass (to 0.1 g), reproductive condition (whether females were perforated, pregnant or lactating) and identification of all degus. Adult females were fitted with 8 g (BR radiocollars, AVM Instrument Co., Colfax, CA, U.S.A.) or 7–9 g radiotransmitters (RI-2D, Holohil Systems Limited, Carp, ON, Canada, and SOM-2190A, Wildlife Materials Incorporated, Murphysboro, IL, U.S.A.) with unique pulse frequencies. We then radiotracked females to burrow systems (see below).

Social Group Identification

Degus are diurnally active and remain in underground burrows during the evening. Thus, the criterion to assign degus to social groups was the sharing of burrow systems (in which they sleep and interact) during night-time (Ebensperger et al. 2004). The determination of active burrow systems was made by night-telemetry and burrow trapping in June–October, the period when females were pregnant and lactating.

Night Telemetry

Previous studies confirmed that night time locations represent nest sites where degus remain underground (Ebensperger et al. 2004). Locations were determined once per night approximately 1 h after sunset using an LA 12-Q receiver (for transmitters tuned to 150.000–151.999 MHz frequency; AVM Instrument Co., Colfax, CA, U.S.A.) or FM-100 receiver (for transmitters tuned to 164.000–164.999 MHz frequency; Advanced Telemetry Systems, Isanti, MN, U.S.A.) and a hand-held, three-element Yagi antenna (AVM instrument Co., or Advanced Telemetry Systems). Additional radiocollars were assigned to males and females during burrow trapping (see below) conducted after we located active burrow systems. Ultimately, there were 30, 16 and 34 radiocollared individuals with sufficient data to be assigned a group membership in 2005, 2006 and 2007, respectively. Animals were located 24.8 ± 1.8 times (range 8–37 locations per individual) in 2005, 34.0 ± 3.2 times (range 12–46 locations per individual) in 2006 and 18.3 ± 4.2 times (range 5–20 locations per individual) in 2007. This effort is sufficient for determining group membership (Ebensperger et al. 2004).

Burrow Trapping

A burrow system was defined as a group of burrow openings surrounding locations where individuals were repeatedly found during night time telemetry and usually spanning several meters in diameter (Fulk 1976; Hayes et al. 2007). Two rounds of burrow trapping at degu burrows were conducted each year. The first round of burrow trapping corresponded with the period when females were pregnant (July–August). Tomahawk (Tomahawk Live Trap Company, Tomahawk, WI, U.S.A.), Sherman live traps and locally produced metal live traps (similar to Sherman live traps) were placed at burrow openings at each burrow system for 9–12 days on each grid each year. Traps were set prior to the emergence of adults during morning hours (0800–0900 hours). After 1–2 h, the identity and location of all captures were determined and traps were closed until the next trapping event. All newly captured animals were permanently marked for future identification, sexed and weighed to the nearest 0.1 g. We did not capture any juveniles during July and August.

The second round of burrow trapping corresponded with the period when females were lactating or in postlactation (September–November). Eight to 14 traps were set at active burrow systems for 4–7 days during three to eight periods of trapping per grid per year. Traps were opened during the early morning and closed 1–2 h after sunrise. Some burrow systems were added to trapping effort after animals were tracked to these systems during telemetry observations made during the period between the two burrow trapping sessions (August–early September). Burrow systems were trapped for 13–20 days during September and October on each grid in 2005 and 2006 and 36 days during September–early November on Grid 1 in 2007. Trapping ended when less than 5% of captured offspring were new individuals.

Quantifying Group Membership

The determination of group size required the compilation of a matrix of pairwise comparisons of the burrow locations of all adult degus during trapping and telemetry. To determine the range overlap of two individuals, we divided the number of evenings that two adults were captured at or radiotracked to the same burrow system overnight by the number of evenings that both individuals were trapped or radiotracked on the same day (Ebensperger et al. 2004). Within groups, we categorized animals based on their degree of range overlap with other individuals (McShea & Madison 1984; McGuire et al. 2002; Lucia et al. 2008). Core members of a group were defined as individuals whose ranges overlapped on 50% or more of nights, an estimate based on previous observations at our study site (Ebensperger et al. 2004). Associate members were defined as individuals whose ranges overlapped with a core member on 10–49.9% of nights. Animals with less than 10% range overlap with core members were not considered part of group.

Fitness Estimates

We determined the number of offspring produced per female in social groups by quantifying the number of offspring captured for the first time at active burrow systems used by social groups during the second round of burrow trapping (September–November). Per capita direct fitness of females was determined by dividing the number of offspring captured at burrow systems by the number of female group members (or core females) known to live in groups using the burrow systems. This index has been used in the past as an estimate of direct fitness for plural breeding hystricognath rodents (Lacey 2004). We included all offspring in this analysis, including those individuals with higher probabilities of moving between social groups (i.e. offspring weighing >100 g). We determined that the per capita direct fitness trend reported below did not change with and without the inclusion of offspring heavier than 100 g.

The mortality of degu offspring by 2 months of age is high ($>$65%) in the wild (Meserve et al. 1984). Thus, we also calculated an index of offspring survival based on the recapture of a sample of offspring. In this analysis, we wanted to determine the survival of offspring that were less than 2 months of age (i.e. <70 g; based on Ebensperger et al. 2007) and greater than 2 months of age (juvenile age, 70 g). Thus, we determined the proportion of offspring caught during the first 2 months of life (up to 70 g) that were recaptured as juveniles (i.e. when individuals become more active aboveground; Ebensperger & Hurtado 2005; Ebensperger et al. 2007). Offspring were included in this analysis if they weighed less than 70 g at first capture and they weighed less than 70 g during a future recapture during the austral winter–spring. All individuals were recaptured at least 1–2 weeks after their last capture before the 70 g threshold. We included individuals that were not recaptured during the austral winter–spring but that were captured during subsequent spring, summer (part of another study) or autumn trapping. We excluded three social groups located on Grid 1 (one in 2005 and two in 2006) without offspring weighing less than 70 g at first capture. We also excluded one group from Grid 2 in 2006 because we did not monitor social groups on this grid in 2007.

Ebensperger & Wallem (2002) suggested that group living may have survival benefits to adults. Thus, we also determined the survival of adult females by quantifying the proportion of adult females that were members of social groups in consecutive years during 2005–2006 and 2006–2007. In both analyses of survival (adult and juvenile), we assumed that 'disappearance' of individuals indicated mortality. Like other studies of rodents (e.g. Randall et al. 2005), we cannot exclude the possibility that individuals that

were not recaptured had moved out of the population. However, given our intense trapping effort, it is likely that a large proportion of individuals that disappeared were lost to mortality.

Ecological Predictors

Ecological sampling was conducted during the late winter–early spring (September and October), when most offspring emerge from burrows and forage aboveground. To track changes in the abundance of primary food (Meserve et al. 1983, 1984), we collected samples of monocot and dicot green herbs at 3 and 9 m from the centre of each burrow system in the north, east, south or west directions. At each sampling point, we placed a 25×25 cm quadrant and removed the aboveground parts of all green herbs found (Ebensperger & Hurtado 2005). Samples were immediately stored inside 2 kg capacity paper bags. In the laboratory, we oven-dried each plant sample at 60 °C for 72 h to determine its dry mass (biomass in grams). Density of burrow entrances was determined by quantifying the number of burrow openings in the circular area encompassing a 9 m diameter from the centre of burrow systems.

Statistical Analyses

Statistical tests were conducted using Statistica 6.0 (Statsoft, Inc. Tulsa, OK, U.S.A.) or SPSS 16.0 (Chicago, IL, U.S.A.). ANCOVAs with group size estimates (all females, core females, or total group size) as covariates and year as the fixed factor were used to test the prediction that per capita direct fitness increased with increasing group size ('benefits of communal care' hypothesis). ANCOVAs with total group size as a covariate and year as a fixed factor were used to test the predictions of the 'food abundance and quality' and 'predation risk' hypotheses. ANCOVAs with burrow density and food biomass at 3 m and 9 m, respectively, were used to determine the relationship between ecological variation and fitness. Post hoc Student–Neuman–Keuls tests were used to determine interaction effects. We used a Levene's test to determine whether the distribution of data was homogenous. If necessary, we transformed log $(x + 1)$ data that did not meet this assumption or used nonparametric Kruskal–Wallis tests. In the Kruskal–Wallis tests, we ranked variables into categories (burrow systems per group: 1, 2, 3 or 4 or more; associates per group: 0, 1, or 2 or more). We used a Mann–Whitney U test to compare adult female survival during 2005–2006 and 2006–2007 and a Spearman rank correlation test to determine the relationship between adult female survival and group size. All data are reported as means $\pm$ SE. All statistical tests were two tailed. For all statistical analyses, $P = 0.05$ was used.

Ethical Note

We marked degus at the time of first capture by clipping no more than one toe per foot. We chose this method after careful consideration of marking needs and the benefits and costs of alternative methods of marking. We used toe clipping because of the need to permanently mark a large number individuals required to monitor a statistically adequate number of social groups. Typically, we moved tissue to the first or second 'knuckle', attempting to minimize pain by making rapid cuts with sharp blades. In the event that an individual was bleeding (qualitative estimate was $<$20%), we applied light pressure to stop bleeding before an individual was released. We also applied a topical antibiotic to reduce infections; infections to the foot were rare. In 2005, toe marking started with the fewest number of removals, limiting the number of individuals requiring three or four toe clips. Although rare, degus can live for 2–3 years. Thus, we had to use more three- or four-toe patterns in subsequent years to ensure that we did not give individuals identical markings. High recapture rates in this study supported previous studies that toe clipping has minimal effects on survival (reviewed in McGuire et al. 2002, *Ethical Note*). In 2005, for example, 92% of adult females ($N = 26$ individuals) captured in June were recaptured a mean $\pm$ SD of 13.0 ± 6.9 times during the subsequent trapping periods in July–August and September–November. Sixty-four per cent of adult males ($N = 28$ individuals) were recaptured a mean $\pm$ SD of 8.7 ± 5.7 times. Male recaptures are typically lower because males frequently wander into our study population and do not show philopatry to natal groups (Ebensperger et al. 2009). A potential concern is that we used this method on juveniles. The potential effect of toe clips on juvenile development is probably low because degu offspring are precocial; such offspring were well along in development at the time that tissue was removed. In our study population, approximately 80% of offspring disappeared between years of the study, making it difficult to quantify marking effects.

We considered alternative methods before deciding to use toe clipping in this study. For example, like toe clipping, the use of ear punches rather than toe clips would have allowed us to simultaneously collect tissue and mark animals. However, ear punches are easily torn, leading to ear damage and difficulties in determining individual identifications. In addition, male degus typically tear each other's ears during mating time. We also considered the use of eartags but decided against them for several reasons. First, we were concerned that eartags would make degus more conspicuous to predators, increasing mortality. Aerial raptors and foxes are generally abundant predators at our study site (Ebensperger & Hurtado 2005), and observations of degu killings are not infrequent, suggesting that these predators affect degu mortality. Second, occasional observations on a captive degu colony and systematic observations on free-ranging animals (Ebensperger & Hurtado 2005) indicate that degus engage in frequent allogrooming, which could lead to the loss of eartags and damage to ears. We observed that numerous radiocollars had signs of chewing, even in areas where collared individuals would not have been able to reach with their mouths. These observations further confirmed that degus allogroom in the wild. During 2005 and 2006, our laboratory observations confirmed that about 40% ($N = 122$) of degus housed with pairs or trios lost eartags (L. A. Ebensperger, unpublished observations). A later study (2007) indicated that placement of tags at the base of the ear greatly reduces loss under laboratory conditions (3 of 60 animals). Given these results, we are now evaluating the effectiveness of eartags placed on animals near our study site.

During the first year of the study (2005), we also tested the effectiveness of passive integrated transponder (PIT) tags. We injected tags by intraperitoneal injection in the scapular region of a few individuals. The application of PIT tags caused considerable pain to the animals and tore a large area of the skin. We determined that this pain and stress, along with the potential for infection and loss of PIT tags was too costly for use in degus. The use of anaesthesia to reduce pain during the process was not possible because of the large number of animals in the study and the risk of mortality during application of the anaesthetic. Likewise, the financial cost of PIT tagging can be prohibitive for a long-term study such as ours. Finally, nonpermanent markings (e.g. hair dye) are not appropriate for a long-term study because marks are easily lost.

Toe clips were not wasted. We stored toe clips in ethanol for the future development of microsatellite primers. To date, we have developed 14 primers from these tissue samples (Quan et al. 2009). In future research projects, we may use a combination of eartagging (two ears) and microsatellite methods to accurately identify

Table 1
Descriptive statistics for degu social groups monitored at Rinconada de Maipú, central Chile during the austral winter–spring of 2005–2007

Variable	2005	2006	2007
Population density/ha			
Grid 1	161	306	333
Grid 2	104	92	92
Number of social groups	13	11	9
Adult females per group*	4.1 (1–8)	3.8 (1–8)	5.0 (3–7)
Adult males per group*	2.2 (0–5)	2.1 (0–4)	1.7 (1–3)
Core females per group*	3.9 (1–8)	2.6 (1–6)	4.0 (3–5)
Associates per group*	0.4 (0–1)	1.6 (0–4)	1.3 (0–2)
Offspring per group*	17.8 (6–30)	16.1 (2–32)	17.1 (7–31)

* Values in parentheses are ranges.

individuals with minimal suffering. Future tissue samples will be collected by taking a small cut of the dorsal ridge of one ear.

Degus held in traps during processing were either placed in the shade and given additional oats, or placed in areas with access to grasses (when held in Tomahawk traps). Periodically, we returned degus to the field during processing to limit time away from the population. The University of Louisiana at Monroe Institutional Animal Care and Use Committee approved of our animal care protocol.

RESULTS

Descriptive Statistics

Mean adult degu densities per year varied between 133–213 degus/ha (Table 1). We monitored the size and composition of 33 social groups (Table 1). The mean number of adults per social group was 6.3 ± 0.5 individuals (range 2–12; Fig. 1). The mean total number of adults (ANOVA: $F_{2,30} = 0.19$, $P = 0.83$), adult (i.e. core and associate) females (ANOVA: $F_{2,30} = 0.88$, $P = 0.43$) and core females (ANOVA: $F_{2,30} = 2.01$, $P = 0.15$) did not differ between years of the study (Table 1). However, the number of associates per group was greater in 2006 and 2007 than in 2005 (Kruskal–Wallis test: $H_{2,33} = 9.36$, $P = 0.01$; Table 1). The mean number of offspring per social group did not differ between years (ANOVA: $F_{2,30} = 0.13$, $P = 0.88$; Table 1).

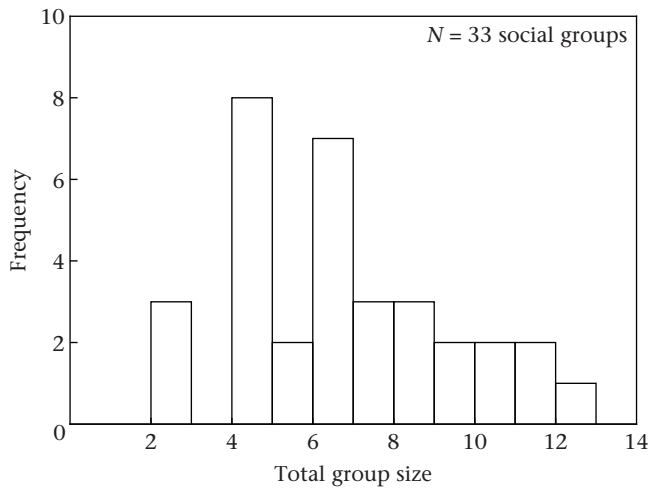

Figure 1. Frequency of social groups of degus of different sizes across years at Rinconada de Maipú, Chile. Total group size of adults includes associate individuals and males.

Per Capita Direct Fitness

All females belonging to social groups showed physical signs of pregnancy and lactation. Thus, all adult females probably contributed to the production of offspring in each social unit. Per capita direct fitness of core females was marginally affected by the number of core females per social group (ANCOVA: model $r^2 = 0.35$; beta $= -0.38$; $F_{1,27} = 3.30$, $P = 0.08$), but not by the total number of adults per social group (ANCOVA: $F_{1,27} = 0.87$, $P = 0.36$). In both analyses, there was no year effect (Core females: $F_{2,27} = 0.51$, $P = 0.61$; Total number of adults: $F_{2,27} = 0.28$, $P = 0.76$) or a year*group size interaction (Core females: $F_{2,27} = 0.26$, $P = 0.77$; Total number of adults: $F_{2,27} = 0.75$, $P = 0.48$). There was no year effect, so we regressed the per capita direct fitness of core females against the number of core females per group and total group size. In this analysis, the per capita direct fitness of core females decreased with increasing number of core females ($r^2 = 0.29$, $P = 0.001$; Fig. 2a) but marginally so for the total number of adults per group ($r^2 = 0.11$, $P = 0.08$). The per capita direct fitness of core females did not differ between groups with zero, one, or two or more associates (Kruskal–Wallis test: $H_{2,33} = 4.36$, $P = 0.11$).

Since groups included reproductive females that were not considered core females (Table 1), we also analysed per capita direct fitness of all females per social group. The per capita direct

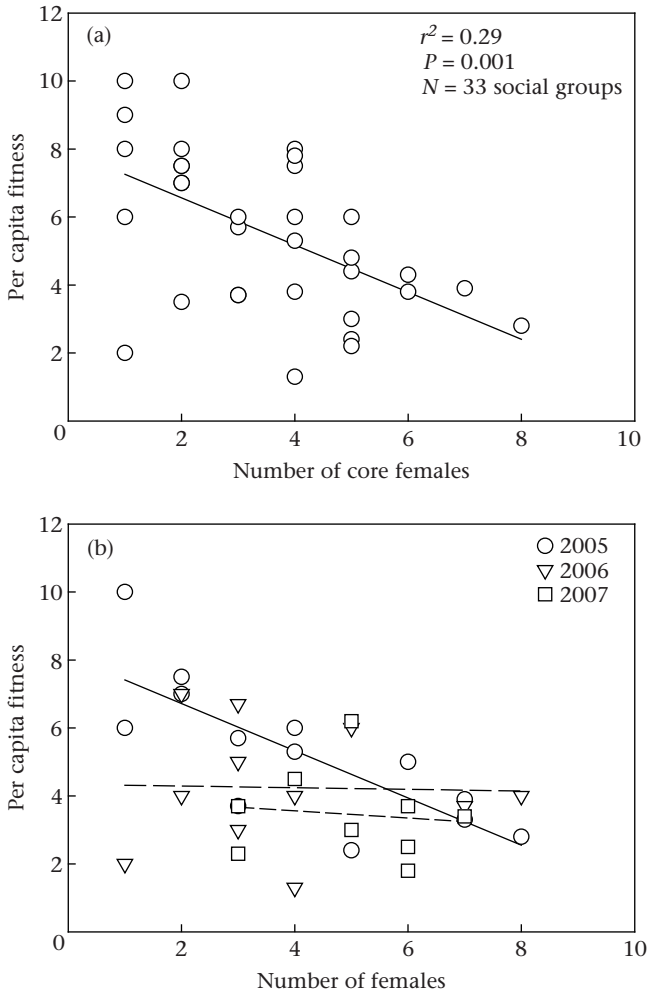

Figure 2. The relationship between (a) per capita direct fitness of core female degus and the number of core females per group across years and (b) per capita direct fitness of all degu females and the number of females per group for 2005, 2006 and 2007.

fitness of all females was not affected by the number of females per social group (ANCOVA: model $r^2 = 0.42$, beta $= -0.29$; $F_{1,27} = 2.69$, $P = 0.11$) or the total number of adults per social group (ANCOVA: $F_{1,27} = 1.97$, $P = 0.17$). A year effect was detected in the analysis of total number of females (ANCOVA: $F_{2,27} = 4.46$, $P = 0.02$). In this analysis, the per capita direct fitness of females in 2005 (5.3 ± 0.6) was statistically greater than the per capita direct fitness of females in 2007 (3.5 ± 0.4) (Student–Neuman–Keuls: $P = 0.04$). Per capita direct fitness of females in 2006 (4.2 ± 0.5) was not significantly different from per capita direct fitness of females in 2005 ($P = 0.15$) or 2007 (Student–Neuman–Keuls: $P = 0.27$). There was a marginally significant year*group size interaction for the relationship between per capita direct fitness of females and the number of females per group (ANCOVA: $F_{2,27} = 2.72$, $P = 0.08$; Fig. 2b). There was no statistically significant year*group size interaction for the relationship between per capita direct fitness of females and total group size (ANCOVA: $F_{2,27} = 1.12$, $P = 0.34$). The per capita direct fitness of females did not differ between groups with zero, one or two or more associates (Kruskal–Wallis test: $H_{2,33} = 0.40$, $P = 0.82$).

Survival

The proportion of offspring that survived beyond 2 months of age (i.e. 70 g) was not affected by the number of core females per group (ANCOVA: $F_{1,23} = 0.03$, $P = 0.86$), all females per group (ANCOVA: $F_{1,23} = 0.01$, $P = 0.91$) and total group size (ANCOVA: $F_{1,23} = 1.21$, $P = 0.28$). We detected no statistically significant interactions in these analyses (Core females: $F_{2,23} = 0.89$, $P = 0.43$; All females: $F_{2,23} = 1.37$, $P = 0.27$; Total group size: $F_{2,23} = 1.69$, $P = 0.21$). In each of these analyses, we detected a significant year effect (Core females: $F_{2,23} = 3.84$, $P = 0.04$; All females: $F_{2,23} = 4.75$, $P = 0.02$; Total group size: $F_{2,23} = 5.58$, $P = 0.01$). Since group size had no effect on offspring survival, we then compared offspring survival by year in an ANOVA. The proportion of offspring surviving was 0.65 ± 0.05 in 2005, 0.88 ± 0.04 in 2006 and 0.89 ± 0.04 in 2007. The proportion of offspring surviving to juvenile age was lower in 2005 than in 2006 (Student–Neuman–Keuls test: $P = 0.001$) and 2007 (Student–Neuman–Keuls test: $P = 0.002$). Offspring survival did not differ between 2006 and 2007 (Student–Neuman–Keuls test: $P = 0.87$).

The proportion of adult females that survived during 2005–2006 (0.09 ± 0.08) was lower than the proportion of adult females that survived during 2006–2007 (0.28 ± 0.08) (Mann–Whitney U test: $U = 83$, $N_1 = 13$, $N_2 = 8$, $P = 0.03$). Adult female survivorship to a consecutive year was not affected by total group size in 2005 (Spearman rank correlation: $r_S = -0.08$, $N = 13$, $P = 0.81$) and 2006 ($r_S = 0.04$, $N = 8$, $P = 0.93$).

Ecological Relationships

The mean biomass of food at 3 m was 7.92 ± 0.72 g, 4.39 ± 0.83 g and 6.80 ± 0.55 g in 2005, 2006 and 2007, respectively. The mean biomass of food at 9 m was 9.72 ± 0.48 g, 4.29 ± 0.79 g and 6.79 ± 0.78 g in 2005, 2006 and 2007, respectively. Total group size did not affect the biomass of food at 3 m (ANCOVA: $F_{1,27} = 1.41$, $P = 0.25$) and 9 m (ANCOVA: $F_{1,27} = 1.11$, $P = 0.30$). There was no statistically significant year*social group size interaction for the biomass of food at 3 m or 9 m (3 m: $F_{2,27} = 0.57$, $P = 0.58$; 9 m: $F_{2,27} = 0.56$, $P = 0.58$). Since group size had no effect on the biomass of food, we then compared the biomass of food by year in an ANOVA. This analysis suggested that the biomass of food at 3 m (ANOVA: $F_{2,30} = 6.37$, $P = 0.01$) and 9 m (ANOVA: $F_{2,30} = 17.76$, $P = <0.001$) differed across years. The biomass at 3 m in 2006 was lower than that in 2005 (Student–Neuman–Keuls test: $P = 0.01$) and 2007 (Student–Neuman–Keuls test: $P = 0.03$). The biomass of food at 3 m in 2005 did not differ from that in 2007 (Student–Neuman–Keuls test: $P = 0.30$). All comparisons of biomass at 9 m were different (Student–Neuman–Keuls test: all Ps ≤ 0.01). The biomass of food at 3 m (ANCOVA: model $r^2 = 0.33$; beta $= 0.49$, $F_{1,28} = 7.07$, $P = 0.01$), but not at 9 m (ANCOVA: $F_{1,28} = 0.59$, $P = 0.45$), was a significant predictor of per capita direct fitness of females. The biomass of food at 3 m (ANCOVA: model $r^2 = 0.27$, beta $= 0.41$, $F_{1,28} = 4.56$, $P = 0.04$), but not 9 m (ANCOVA: $F_{1,28} = 1.48$, $P = 0.23$), was a significant predictor of the per capita direct fitness of core females. The biomass of food at 3 m (ANCOVA: $F_{1,23} = 0.25$, $P = 0.62$) and 9 m (ANCOVA: $F_{1,23} = 1.94$, $P = 0.18$) did not affect the proportion of offspring surviving. There were no year effects (biomass at 3 m: $F_{2,23} = 0.80$, $P = 0.46$; biomass at 9 m: $F_{2,23} = 1.31$, $P = 0.29$) or statistically significant interactions (biomass at 3 m: $F_{2,23} = 3.04$, $P = 0.07$; biomass at 9 m: $F_{2,23} = 1.41$, $P = 0.26$) in the analyses of biomass and offspring survival.

The mean number of burrow entrances/m^2 was similar for each year of the study (2005: 0.14 ± 0.01; 2006: 0.15 ± 0.02; 2007: 0.14 ± 0.01; ANCOVA: $F_{2,27} = 0.14$, $P = 0.87$) and was not affected by total group size (ANCOVA: $F_{1,27} = 0.07$, $P = 0.79$). There was no statistically significant year*group size interaction (ANCOVA: $F_{2,27} = 0.23$, $P = 0.80$). The mean density of burrow entrances did not affect the per capita direct fitness of females (ANCOVA: $F_{1,28} = 0.26$, $P = 0.62$), core females ($F_{1,28} = 0.34$, $P = 0.57$), or the proportion of offspring surviving (ANCOVA: $F_{1,23} = 1.17$, $P = 0.29$). The number of burrow systems used per group could influence fitness if burrow systems provide places to rear young. The number of burrow systems increased with increasing group size (ANCOVA: $F_{2,27} = 7.45$, $P = 0.01$; post hoc regression: $r^2 = 0.20$, beta $= 0.45$, $F_{1,32} = 7.78$, $P = 0.01$). There was no statistically significant year*group size interaction ($F_{2,27} = 0.97$, $P = 0.39$). The mean number of burrow systems used by social groups was greater in 2007 (3.7 ± 0.6) than in 2005 (2.2 ± 0.2) and 2006 (2.1 ± 0.3) (ANOVA: $F_{2,32} = 5.01$, $P = 0.01$). However, the number of burrow systems used by social groups did not affect the per capita direct fitness of females (Kruskal–Wallis test: $H_{3,33} = 1.68$, $P = 0.64$) or core females ($H_{3,33} = 0.78$, $P = 0.85$). Likewise, the number of burrow systems used by social groups did not affect offspring survival ($H_{3,29} = 5.70$, $P = 0.13$).

DISCUSSION

Across years, the per capita direct fitness of core females decreased with increasing number of core females but not with the total number of females and adults (i.e. including males) per group. The negative relationship disappeared when we compared the per capita direct fitness of all females versus the number of females and adults per group. Moreover, adult female and offspring survival were not influenced by group size. Individuals living in larger groups had access to more burrow systems but not to more food resources and burrows per system than individuals living in smaller groups. Biomass of food (3 m and 9 m), adult survival and offspring survival differed between years. The availability of food at burrow systems (independent of group size) was the only significant predictor of the per capita direct fitness of all females and core females (at 3 m only).

Benefits of Communal Care Hypothesis

In some mammals, communal rearing of offspring enhances investment in offspring (König 1994; Cant 2000; Packer et al. 2001; Hayes & Solomon 2004, 2006) and improves the defence of offspring from predators or infanticide (Manning et al. 1995).

Communal rearing may also improve immune function (Roulin & Heeb 1999; Becker et al. 2007), reduce parasite infection from allogrooming (Hart & Hart 1992) and enhance thermoregulation (Madison 1984). The 'benefits of communal care' hypothesis predicts that these benefits should result in enhanced reproductive fitness, a prediction that was not supported by our observations. In terms of direct fitness estimates, our results support previous laboratory studies on degus (Ebensperger et al. 2007) and field studies on rodents suggesting that group living has neutral (Wolff 1994; Pilastro et al. 1996; Randall et al. 2005) or negative (Boyce & Boyce 1988; da Silva et al. 1994; Hoogland 1995; Lacey 2004; Solomon & Crist 2008) fitness consequences.

Food Abundance and Quality Hypothesis

Numerous studies have supported the prediction that more localized resources influence sociality (Ebensperger 2001b). However, there is little evidence that these benefits translate into reproductive fitness advantages. Not surprisingly, the biomass of food was linked to fitness in this study. Our observation that food resources were not correlated with larger groups suggests that we can reject the 'food abundance and quality' hypothesis for degus at our study site. However, we cannot completely exclude this hypothesis as an explanation for the cause of degu group living without first determining interpopulation variation in group sizes. Several compelling studies support the hypothesis that variation in the distribution of resources along a species range can lead to plasticity in social systems (e.g. Brashares & Arcese 2002; Schradin & Pillay 2005). Fitness consequences of sociality may be relative to local conditions (i.e. increased group size and/or fitness could be a response to the distribution and/or quality of resources in some habitats but not others). Degus may be an ideal species to test these predictions because populations can be found in habitats characterized by varying degrees of aridity, allowing for intraspecific comparisons of group size in relation to variability in the distribution and quality of food resources.

Predation Risk Hypothesis

Per capita risk of predation decreases with increasing group size in some mammals (e.g. Ebensperger 2001b), suggesting that predation risk or pressure could select for large social groups (Brashares & Arcese 2002; Waterman 2002). Reduced risk could result from dilution and enhanced detection of predators (many eyes effect; Ebensperger 2001b), which is one benefit of group living to adult degus (Ebensperger & Wallem 2002; Ebensperger et al. 2006b). Individuals in larger groups may also have access to more burrows than individuals in smaller groups, increasing the probability of finding a safe haven when an aerial or large terrestrial predator attacks. Consequently, greater adult and juvenile survival was expected with increasing social group size. Although larger social groups had access to more burrow systems (but not more burrows per system), our observations that access to burrows and survival (adult and juvenile) were not positively correlated with group size did not support predictions of the 'predation risk' hypothesis.

Provided that a higher proportion of social interactions between group members takes place underground compared with aboveground, our measures of social group size examined here may have little effect on survival when animals are active aboveground. Thus, survival benefits in degus might be more linked to the size of foraging groups aboveground than to the number of individuals sharing underground burrows (Ebensperger & Wallem 2002). The mean size of degu foraging groups is typically smaller than the size of social groups reported in this study (mean = 2 individuals, range 1–10; Ebensperger & Hurtado 2005; Ebensperger et al. 2006b). Manipulations of foraging and social group sizes are necessary to test the causality of this hypothesis.

Neutral and Costs-based Hypotheses

Our results may support the 'ecological constraints' hypothesis for sociality, which predicts that animals form groups when offspring remain at the natal group when conditions do not favour independent reproduction (Emlen 1982; Koenig et al. 1992; Komdeur et al. 1995; Lucia et al. 2008). A prediction stemming from this hypothesis is that direct fitness consequences are neutral (e.g. Wolff 1994). However, we need to test some additional, critical predictions and consider other mechanisms (Ebensperger & Hayes 2008) before we can accept this hypothesis as the primary explanation for degu sociality. For example, intraspecific comparisons may be needed to determine whether dispersal and group size are influenced by variation in food or nesting resources. In this study, groups were similar in size each year of the study despite a 1.6-fold increase in the density of adults from 2005 to 2006 and 2007. Although preliminary, offspring survival, but not production, varied between years. Thus, we require several more years of data to make a strong test of the relationship between density, group size and fitness.

Our results suggest that the consideration of costs-based hypotheses is warranted. Females could experience reduced fitness if competition for resources (e.g. food, space) and infanticide are costs of increasing group size. Additionally, large groups may deplete local food resources, reducing the amount available to lactating females and emerging offspring. However, in this study, larger groups were not linked to the availability of food resources and did not have fewer burrow entrances or burrow systems than did smaller groups. Increased infanticide is an unlikely cost to degu sociality because females do not kill offspring in the laboratory (Ebensperger 2001a). It is possible that competition among females for resources, mates, or reductions in communal care (Hayes & Solomon 2004) could increase stress, affecting the ability of females to invest in offspring. Moreover, chronic exposure to stress hormones could reduce immune function, increasing the risk of parasitism (Alexander 1974). Increased parasitism could reduce offspring survival if parasites are transferred from adults to offspring (Poulin 1991; Roulin & Heeb 1999).

Interannual Variation

Theory predicts that interannual variation in rainfall affects the availability of food and other resources, possibly explaining variation in fitness. Although we do not have rainfall data for the duration of our study, our observation that per capita direct fitness was positively related to the biomass of food at 3 m suggests that factors other than group size per se must be built into future models for degu sociality (see Brashares & Arcese 2002). An abundance of food close to burrow entrances affects fitness by influencing the amount of maternal investment in offspring (Hayes & Solomon 2004) and offspring nutrition (and thus, growth and survival) after emergence. However, in this study, food availability alone did not explain interannual variation in fitness. Interannual variation in offspring survival did not correspond with interannual patterns in the availability of food at 3 and 9 m. It is possible that interannual variation in predation risk could, in part, explain interannual variation in fitness. Support of this hypothesis requires a positive relationship between the abundance of predators with offspring and adult survival. At this time, we cannot test this hypothesis because we did not attempt to quantify predator abundance at our site. Finally, it is possible that other factors such

as breeder density and abundance of parasites could influence fitness (independent of social group size). For example, the breeding densities observed during this study were high compared to previous years at our study site (L. A. Ebensperger, unpublished data) and in relation to a population located in an arid shrubland (Yunger et al. 2002), possibly influencing social group dynamics and offspring survival. Further long-term studies are needed to tease apart these potential variables in relation to group size and fitness, an objective of our ongoing research of degu sociality.

Conclusions

Contrary to some (Ebensperger & Wallem 2002), but in agreement with other (Ebensperger et al. 2007) previous studies, sociality did not lead to reproductive fitness benefits in degus. However, we make this conclusion while acknowledging that two caveats need to be addressed. Determining the causes of variation in fitness in plural breeders with communal care is difficult, especially in semifossorial and fossorial species. For example, the growth of offspring could be affected by postnatal care prior to (Hayes & Solomon 2004, 2006) and after burrow emergence (Armitage 1981; Clutton-Brock et al. 2001), which could influence offspring survival (Lindström 1999). Likewise, group size effects (e.g. dilution) could influence offspring survival after emergence. Second, the reproductive consequences of sociality are not limited to direct fitness benefits when groups consist of closely related kin (Hamilton 1964; Maynard Smith 1964). Closely related individuals living together in social groups may benefit from increased inclusive fitness, which includes the indirect benefits of assisting with the care of nondescendent offspring produced by kin (Hamilton 1964; Maynard Smith 1964; but see Griffin & West 2002). Selection could favour smaller group sizes to maximize direct fitness while favouring larger group sizes to maximize inclusive fitness (Rodman 1981). As is the case in many other social vertebrates, degus may live in groups that consist of related individuals (Ebensperger et al. 2004). The use of microsatellite primers (Quan et al. 2009) is necessary to elucidate some of the remaining questions about the evolutionary significance of degu sociality.

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