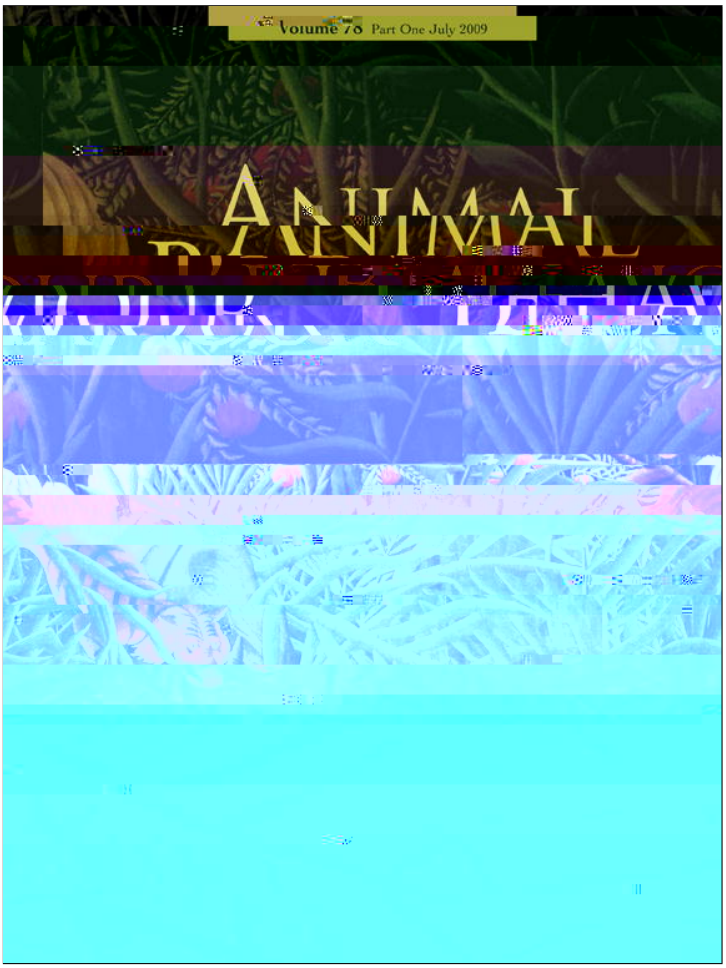

Fitness consequences of group living in the degu *Octodon deg s*, a plural breeder rodent with communal care

Loren D. Hayes [a,*], Adrian S. Chesh [a,]

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

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 >

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 Anal ses

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 ($+1$) 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

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

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

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.

Concl sions

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.

We are indebted to the Universidad de Chile, particularly to José Daniel García and Aurelio Soto, former and current Field Station Administrators, for providing the facilities during field work. We thank María José Hurtado, Cecilia León, Verónica Quirici, Danielle Lahr, Jason Childers and Matt Pardue for their assistance. The criticisms of Eileen Lacey and Nancy Solomon greatly improved this manuscript. L.D.H. was funded by National Science Foundation EPSCoR (no. 0553910), the Louisiana Board of Regents (LEQSF 2007-09-RD-A-39), the University of Louisiana at Monroe (ULM) HHMI Program, the ULM Office of Academic Affairs and the Percy Sladen Memorial Fund (England). A.S.C. and J.R.B. were funded by the American Society of Mammalogists and Sigma Xi, respectively. L.A.E. was funded by FONDECYT grants 1020861 and 1060499 and by the Center for the Advancedite.CLaJ[Ameg-497.4-299i7y(e)11(.TJ0-(Cy7(Amer[edite)-5tS1T(e)-314(some)-3ctS129(1386.o)-332Th(is)-225(dv)(y)-

[illegible], C[illegible] J., [illegible] & [illegible] 1992.