Original Article

Mean ecological conditions modulate the effects of group living and communal rearing on offspring production and survival

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Sociality and cooperative rearing may have evolved to increase direct fitness when conditions are challenging to reproduction and/or to reduce environmentally induced variance in fecundity. Examination of these hypotheses comes mostly from studies on singularly breeding birds where reproduction is monopolized by a male–female adult pair. Instead, little is known about plurally breeding species where most group members breed and rear their offspring communally. We used data from an 8-year field study to explore the relationship between the ecology and per capita offspring production and survival (2 components of reproductive success and direct fitness) of the plurally breeding rodent *Octodon degus*. We determined how mean and variance in food abundance, precipitation levels, degu density, soil hardness, predation risk, and thermal conditions modulated the effects of group size and number of breeding females (potential for breeding cooperation) on reproductive success. The effect of number of females per group on the per capita number of offspring produced was more positive during years with lower mean food and degu density. More positive effects of group size (on per capita number of offspring produced and on per capita surviving offspring) and of the number of females (on per capita number of offspring produced) occurred during years with decreasing mean precipitation levels. Thus, the hypothesis that group living and communal rearing are more beneficial (or less costly) under low mean habitat conditions is supported. In contrast, the social effects on reproductive success seem insensitive to variance in ecological conditions.

Key words: **communal rearing, ecological effects, fitness effects, habitat conditions, sociality.**

INTRODUCTION

An important theme in behavioral ecology research is to determine the fitness and life-history effects of sociality (or group living). Group living typically results when conspecifics establish long-term (relative to life span) socially cohesive units. Proximally, sociality involves spatial and temporal proximity of group members that results from the mutual attraction rather than from attraction to a same resource or physical condition (Parrish et al. 1997; Krause and Ruxton 2002). On the appearance of group living, social organisms may evolve different breeding strategies that impact on how direct reproduction and offspring care are shared within social groups (Silk 2007). For example, in singular breeders, a male–female adult pair monopolizes breeding, and other adult group members delay breeding and provide care to the offspring of breeders. Among the vertebrates, singular breeding is observed widely in the birds (Koenig and Dickinson 2004; Cockburn 2006; Jetz and Rubenstein 2011) and some mammals (Ebensperger, Rivera, et al. 2012; Lukas and Clutton-Brock 2012). Plural breeding occurs when most members of a social group breed, resulting in low reproductive skew (Silk 2007). In plural breeders without communal care, females rear offspring independently, a strategy seen in mammals including ground squirrels and primates (Silk 2007). In some plural breeders, adults rear offspring communally, a strategy seen in numerous birds (Stacey and Koenig 1990; Vehrencamp and Quinn 2004) and mammals (Solomon and Getz 1997; Silk 2007; Ebensperger, Rivera, et al. 2012). An examination of how much

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variation in fitness relates to variation in sociality and cooperation during breeding can shed light on whether these aspects of social behavior are adaptive in current-day populations (i.e., Reeve and Sherman 1993).

The striking picture that emerges from available evidence is that effects of group living and cooperation during breeding on fitness measures (e.g., on reproductive success, adult survival) vary widely across similarly social species (Cockburn 1998; Ebensperger, Rivera, et al. 2012). Thus, positive, neutral, or negative effects of parental care provided by nonbreeders to the offspring of breeders have been reported in singularly breeding birds (Cockburn 1998). Likewise, a variety of fitness effects have been reported across studies of social mammals, a variation explained in part by differences in major strategies of cooperation during breeding, but also by major climate conditions (Ebensperger, Rivera, et al. 2012). In mammals, singular breeding seems to result in greater fitness benefits to females than does plural breeding with and without communal care (Ebensperger, Rivera, et al. 2012). However, direct fitness seems to be greater in tropical than in temperate or arid regions of the world, possibly due to an overrepresentation of some mammalian orders such as primates in the tropics (Ebensperger, Rivera, et al. 2012).

How ecological conditions mediate the effects of group living and cooperation during breeding remains a topic of debate and research (Cockburn and Russell 2011; Gonzalez et al. 2013). On the one hand, group living and cooperation during breeding are thought to have evolved to improve (or compensate) reproductive success under conditions that are challenging for reproduction (Magrath 2001; Hayes and Solomon 2004). Challenging environmental conditions during breeding may be caused by relatively low or unpredictable precipitation that translates into scarce food resources, low (or high) ambient temperature that increases energetic costs of maintenance, or by low (poor) breeding experience (Ebensperger 2001; Magrath 2001). Support for the "benefits under harsh conditions" hypothesis comes from studies on singularly breeding birds, where the presence of "helpers at the nest" has positive, detectable effects yet mostly under adverse conditions in terms of rainfall (Covas et al. 2008) or breeding experience (Magrath 2001). In contrast, the "benefits under harsh conditions" hypothesis is not supported by bird and mammalian studies where fitness measures such as reproductive success and survival of breeders increase more under favorable than under unfavorable conditions (Harrington et al. 1983; Solomon and Crist 2008; Koenig et al. 2011). Moreover, the effect size of sociality on multiple fitness measures across studies on social mammals conducted under varying conditions of predation and food abundance is similar (Ebensperger, Rivera, et al. 2012).

Previous arguments on ecological harshness have emphasized the effects of "average" spatial and temporal differences in environmental conditions on fitness. However, it is possible that intra-annual or interannual variation in ecological conditions place a major challenge to organisms. Thus, fitness benefits of group living and cooperation during breeding may materialize in habitats with unpredictable changes in critical resources (Rubenstein and Lovette 2007). The "benefits under variable conditions" hypothesis has been supported by a long-term study on superb starlings (*Lamprotornis superbus*). Variance but not mean reproductive success of these singularly breeding birds declines with increasing environmental (territory) quality, implying constant levels of mean reproductive success despite variation in ecological conditions (Rubenstein 2011). Across species, the importance of environmental variation

is further supported by the observation that singular breeding in birds is positively associated with living in semiarid savanna habitats and with greater interannual variation in rainfall (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011). In contrast, cooperation during breeding seems positively associated with both inter- and intra-annual climatic stability in hornbills, a taxonomic subset of all singularly breeding birds (Gonzalez et al. 2013). Taken together, these recent studies have been extremely valuable in terms of suggesting new directions to determine how ecological conditions modulate the fitness effects of social environment. However, the relative importance of mean and variance in ecological conditions requires evidence from other social organisms. To advance theory, long-term patterns in fitness–ecology relationships in vertebrates with different strategies of cooperation during breeding are needed. Herein, we used data from an 8-year study on the communally rearing degu (*Octodon degus*) to examine the extent to which mean or variation in ecological conditions across years modulates the effects of group living and cooperation during breeding on offspring production and survival.

Model species and hypothesis

We aimed to examine how mean and variation in ecological conditions predict direct fitness effects of sociality and cooperation during breeding. Degus are diurnal, herbivorous rodents that typically breed annually (Ebensperger and Hurtado 2005a). Degus are social, forming groups consisting of multiple adult male and female group members that share underground nests (Ebensperger et al. 2004; Hayes et al. 2009). Degus also exhibit different forms of cooperation, including the communal rearing of offspring (Ebensperger et al. 2002, 2004). During communal rearing of offspring, females indiscriminately huddle over, retrieve, and nurse nondescendent offspring (Ebensperger et al. 2002, 2010; Jesseau et al. 2009). Similarly, male degus are known to huddle over and groom the pups (Ebensperger et al. 2010). Intriguingly, per capita offspring produced (Hayes et al. 2009) and per capita offspring survival to reproductive age (Ebensperger, Ramírez-Estrada, et al. 2011) decrease with the number of breeding females and total group size, respectively, implying no direct benefits associated with group living or communal rearing. The extent to which the effects on these fitness measures change with mean or variance in ecological conditions remains unknown.

Ecological conditions faced by degus are highly seasonal, implying high within year variation in the amount of precipitation, ambient temperature, food availability, and predation risk (Ebensperger and Hurtado 2005a, 2005b; Quirici et al. 2010). In fact, abundance of preferred food has been shown to predict per capita number of offspring weaned by female members of social groups (Hayes et al. 2009). The potential importance of ecological variation on degu life history and behavior is further supported by long-term ecological studies in north-central Chile. In particular, greater degu density characterizes years with greater abundance of food and precipitation levels, and this relationship is the consequence of positive effects on individual survival and fertility (Previtali et al. 2010).

Thus, we examined the hypothesis that sociality and communal rearing enhances offspring production and survival (i.e., reproductive success) under harsher ecological conditions. We quantified the extent to which mean and variance in ecological factors (relevant to degus) modulate sociality–fitness covariation. In particular, we predicted more positive effects of group size (a general measure of sociality) and the number of breeding females per group (a measure

of cooperation during communal rearing) on reproductive success during years with harsher ecological conditions. Based on sociality theory (Krause and Ruxton 2002; Davies et al. 2012) and on ecological conditions thought to be relevant to degus (Ebensperger and Wallem 2002; Hayes et al. 2009; Ebensperger, Chesh, et al. 2011; Ebensperger, Sobrero, et al. 2012), we considered lower and more variable abundance of preferred food resources, precipitation levels, and degu density to represent harsh conditions. Similarly, we considered higher and more variable abundance of predators and soil hardness to represent harsh conditions. Finally, degus are sensitive to extremes in ambient temperature (Kenagy et al. 2002). Thus, we considered lower minimum, higher maximum, and more variable ambient temperature as harsh conditions to degus.

MATERIALS AND METHODS

Study population

The study was conducted between 2005 and 2012 on a natural population of degus located at the Estación Experimental Rinconada de Maipú, a field station of Universidad de Chile. This study area is characterized by a highly seasonal, Mediterranean climate with cold, wet winters and warm, dry summers (di Castri and Hajek 1976).

Degu sociality and communal rearing

Based on previous studies (Rubenstein 2011), and our own observation that most female members of groups rear their litters communally in degus (Ebensperger et al. 2002, 2004), we considered the number of females per social group as a measure of the breeding cooperation. In addition, we considered group size (total male and female adults per social group) as a general but adequate proxy of sociality.

The size and composition of social groups used for this study were determined in September–October, a time encompassing main parturition, lactation, and offspring weaning. Degus are diurnally active and remain in underground burrows overnight. Thus, the main criterion used to assign degus to social groups was the sharing of burrow systems (Ebensperger et al. 2004). The sharing of burrow systems was established by means of 1) nighttime telemetry and 2) burrow trapping in August–October. During burrow 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 (Fulk 1976; Hayes et al. 2007). Eight traps (Tomahawk model 201, Tomahawk Live Trap Company, Tomahawk, WI) were used per day at each burrow system. The total area examined at Rinconada was 1–2 ha, depending on the abundance and spacing of degu groups. Traps were set prior to the emergence of adults during morning hours (06:00 h). After 1.5 h, traps were closed until the next trapping event. We determined the identity, location, sex, body mass (to 0.1 g) of all degus, and reproductive condition of all females (perforated, pregnant, or lactating). We marked every degu at the time of first capture with tags on each ear (Monel 1005-1, National Band and Tag Co., Newport, KY). Based on experience from previous years, we used 2 ear tags (with identical ID) to reduce the probability that an animal could not be reliably identified. Most adults (i.e., $67 \pm 8\%$ of 358 degu study subjects) weighing greater than 170 g were fitted with 6–7 g (BR radio-collars, AVM Instrument Co., Colfax, CA) with unique pulse frequencies. During nighttime telemetry, females were radiotracked to their burrows. Previous studies at Rinconada confirmed that nighttime 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 radio collars tuned to 150.000–151.999 MHz frequency; AVM Instrument Co., Auburn, CA) and a handheld, 3-element Yagi antenna (AVM Instrument Co.).

The determination of group composition required the compilation of a symmetric similarity matrix of pairwise association of the burrow locations of all adult degus during trapping and telemetry (Whitehead 2008). We determined the association (overlap) between any 2 individuals by dividing the number of evenings that these individuals were captured at or tracked with telemetry to the same burrow system by the number of evenings that both individuals were trapped or tracked with telemetry on the same day (Ebensperger et al. 2004). To determine social group composition, we conducted hierarchical cluster analysis of the association matrix in SOCPROG software (Whitehead 2008). We confirmed the fit of data with the cophenetic correlation coefficient, a correlation between the actual association indices and the levels of clustering in the diagram. In this procedure, values above 0.8 indicate that hierarchical cluster analysis has provided an effective representation of the data (Whitehead 2008). We chose maximum modularity criteria (Newman 2004) to cut off the dendrogram and define social groups. All adults with radio collars that survived the period of parturition and lactation (September–October) were included in this analysis. To be included in the analysis, adults without radio collars had to be captured with another individual in the same burrow system 4 or more times (see Hayes et al. 2009; Ebensperger, Ramírez-Estrada, et al. 2011 for details).

Measures of reproductive success

We recorded 2 life-history parameters as components of reproductive success (Solomon and Crist 2008) and, thus, of direct fitness. We determined the number of offspring produced by each social group during spring by quantifying the number of offspring captured for the first time at active burrow systems used by social groups during burrow trapping in September–October. Per capita offspring produced was determined by dividing the number of offspring captured at burrow systems by the number of adult female group members known to live in groups that used these same burrow systems. We also calculated an index of offspring survival based on the recapture of offspring. We focused on offspring that were recaptured during May–June (austral autumn) of the year after these offspring were born. Offspring reach sexual maturity and mate at this time (Ebensperger and Hurtado 2005a), implying that survival to the following autumn has a major impact on lifetime fitness in degus. We used burrow trapping in autumn (May–June) and spring (September–October) of the subsequent year to estimate the number of offspring that were alive. Per capita surviving offspring was determined by dividing the number of offspring previously assigned to a social group during spring and that were recaptured in autumn (at any burrow system) by the number of female group members of the social group in spring. Given that dispersal in degus is not sex biased and animals settle relatively close to their burrows of origin (i.e., within 30–40 m; Quirici et al. 2011), our estimates of survival were unlikely to be underestimated by offspring alive that were not recaptured.

Per capita offspring counts have been used as estimates of direct fitness for plurally breeding rodents (Lacey 2004), including degus (Hayes et al. 2009; Ebensperger, Ramírez-Estrada, et al. 2011). However, we note that these estimates do not capture individual variation in direct fitness in the same social group. Although

egalitarian reproduction is observed in some carnivores (Packer et al. 2001), within-group variation in the direct fitness occurs in other plural breeders (Pilastro et al. 1996; Dugdale et al. 2008).

Ecological conditions

Ecological conditions thought to be relevant to degus included availability of preferred food resources, soil hardness, predation risk, ambient temperature, precipitation levels, and degu density (Ebensperger and Wallem 2002; Hayes et al. 2009; Ebensperger, Chesh, et al. 2011; Ebensperger, Sobrero, et al. 2012).

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 at the spatial scale of social groups (Hayes et al. 2009; Ebensperger, Sobrero, et al. 2012). In particular, we randomly chose one location at 3 m and one at 9 m in the north, east, south, or west directions. At each of these 2 sampling points, we placed a 250×250 mm quadrant and removed the aboveground parts of all green herbs found. Samples were immediately stored inside 2-kg paper bags. In the laboratory, we oven-dried each plant sample at 60 °C for 72 h to determine its dry mass (biomass in g) (Ebensperger and Hurtado 2005a). Data from 3- and 9-m sampling points were averaged per burrow system and standardized to gram per square meter for subsequent analysis (sample sizes described as above). We used the same sample pattern to record soil penetrability as an index of soil hardness (Ebensperger, Sobrero, et al. 2012). Given that soil hardness is related to the energetic cost of burrow digging in degus and that these rodents can cooperate during this process (Ebensperger and Bozinovic 2000a, 2000b), we also recorded soil hardness. Soil hardness was measured as soil penetrability with the use of a hand-held soil compaction meter (Lang Penetrometer Inc., Gulf Shores, AL), and units transformed to kPa.

At the level of social groups, predation risk was estimated based on the density of burrow openings (i.e., available refuges to evade predators). Density of burrow openings (number m-2) at each burrow system was determined by quantifying the number of burrow openings in the circular area encompassing a 9 m radius from the center of burrow systems. At the level of the entire population, we conducted scan sampling from 2 fixed vantage points located 50–100 m from where degus were active to record sightings of predators known to prey on degus. Every 30 min, the same observer recorded every predator observed over the entire area during a 20-min circular sweep. Observations were conducted during morning (07:30–12:00 h) and afternoon hours (17:00–19:30 h), that is, when degus were observed aboveground. A total of 40 scan samplings per year were conducted at Rinconada from 2006 through 2012.

To examine the effects of ambient temperature and precipitations at the level of the study population, we used mean monthly values of minimum and maximum ambient temperature (°C) and monthly records of accumulated precipitation (mm) recorded 5–10 km north of the Rinconada study site (i.e., the Pudahuel weather station, 33°23′S, 70°47′W, 475 m of altitude). Monthly records of ambient temperature and precipitation included data from June through October, a time period that matches breeding in degus (Ebensperger and Hurtado 2005a).

To quantify degu density, we established 2 grids approximately 150 m apart. The grids were characterized by a similar distribution of grasses, forbs, and shrubs (Hayes et al. 2007) and covered 0.18 ha (30×60 m; grid 1) and 0.25 ha (50×50 m; grid 2), respectively. Every year we conducted grid trapping to determine density of the population in June. Degus were captured using locally produced metal live traps (similar to Sherman live traps [H. B. Sherman Traps, Inc., Tallahassee, FL] in design) baited with rolled oats. Traps were set at fixed stations at 5-m intervals, resulting in 91 traps (7×13 array) on grid 1 and 121 traps (11×11 array) on grid 2. Traps were opened for 5 days during the morning (08:00 h) prior to emergence of degus from burrows and closed after 3 h. Data from these 2 grids were used to calculate mean and the coefficient of variation (CV) degu density for each study year.

Statistical analysis

We used hierarchical regression and random coefficient modeling techniques (i.e., linear mixed effects models) to test if relevant combinations of ecological conditions modulated sociality–fitness relationships. These models are appropriate to examine data sets with a nested or hierarchal structure. Specifically, we examined the following models based on biotic and abiotic hypotheses: 1) mean and CV of food abundance and degu density, 2) mean and CV of predation risk, 3) mean and CV of soil hardness and precipitation levels, and 4) mean and CV of ambient temperature. For all of these models, sociality measures included group size and number of adult females per group and fitness metrics included per capita offspring production and per capita offspring surviving to reproduction. Thus, a total of 16 different models are reported. In addition, we explored some alternative models that combined variables from our proposed ecological–environmental interactions but are not reported due to a lack of statistical support (e.g., precipitation–food abundance). Given that predictions involved ecological (or environmental) by social factor interactions, our results emphasize these findings over potentially significant main factor effects.

For each analysis, a hierarchical model was defined where social variables were declared at level 1 layer and ecological factors were declared at level 2 in the model hierarchy. Study years were used as grouping factors to control for correlations among contrasting ecological conditions. Slope and intercept of predictors at level 1 were allowed to vary between years, and effects of level 2 ecological variables on the sociality–fitness slopes were tested by means of interactive terms involving the level 1 predictors (i.e., number of females per group and group size), all customary routines in mixed modeling analysis (Zuur et al. 2009). A mathematical description of the model building approach used is provided in the Supplementary Material.

Model fit was tested against 2 null models, an intercept only formulation, and a random intercept model with study year as a grouping variable. The Akaike information criterion and likelihood ratio test were used to test statistical significance of each full model against their respective null models. We further verified model fit with the use of heterogeneous variance structure followed by examination of residuals. All analyses were implemented in R Statistical Software (version 2.13.2, R Development Core Team 2012).

RESULTS
Modulating roles of food abundance and degu density

Yearly mean and CV of ecological conditions, namely food abundance and degu density, did not influence the relationship between group size and per capita number of offspring produced or the relationship between group size and per capita number of offspring surviving to breeding age (Supplementary Table S1, models 1 and 2). However, yearly mean, but not CV, of food abundance and degu density influenced the relationship between the number of females

and per capita number of offspring produced (Supplementary Table S1, model 3). In particular, this effect implied that positive effects of the number of females on per capita number of offspring characterize years with relatively low mean levels of food abundance and low degu density (Figure 1a). In contrast, relatively negative effects of the number of females characterize years with relatively high mean levels of food abundance and high degu density (Figure 1b,c). Yearly mean and CV of food abundance and degu density did not influence the relationship between the number of females and per capita number of offspring surviving to breeding age (Supplementary Table S1, model 4).

Modulating role of predation risk

Yearly mean and CV of ecological variables linked to predation risk, namely rate of predator sightings and density of burrow openings (i.e., safe heavens) did not influence the relationship between group size and per capita number of offspring produced or the relationship between group size and per capita number of offspring surviving to breeding age (Supplementary Table S2, models 1 and 2). Likewise, yearly mean and CV of predator sightings and density of burrow openings did not influence the relationship between number of females and per capita number of offspring produced or the relationship between number of females and per capita number of offspring surviving to breeding age (Supplementary Table S2, models 3 and 4).

Modulating roles of soil hardness and precipitation levels

Yearly mean of precipitation, but not soil hardness, negatively influenced the relationship between group size and per capita number of offspring produced and the relationship between group size and per capita number of offspring surviving to breeding age (Supplementary Table S3, models 1 and 2). Thus, negative effects of group size on per capita number of offspring and on per capita offspring surviving to breeding age characterized years with increasing mean precipitation levels (Figure 2a,b). More positive effects of group size characterized years with decreasing mean precipitation levels. Likewise, mean precipitation levels influenced the relationship between the number of females and per capita number of offspring produced (Supplementary Table S3, model 3). That is,

relatively negative effects of the number of females on per capita number of offspring characterized years with increasing mean precipitation (Figure 2c). More positive effects of the number of females characterized years with decreasing mean precipitation. Variation based on CV of soil hardness and precipitation levels did not modulate any of the relationships between group size or the number of females and per capita offspring produced or per capita offspring surviving to breeding age (Supplementary Table S3, models 1–4).

Modulating role of ambient temperature

Yearly mean and CV of maximum and minimum ambient temperatures did not influence the relationship between group size and per capita number of offspring produced or the relationship between group size and per capita number of offspring surviving to breeding age (Supplementary Table S4, models 1 and 2). Likewise, yearly mean and CV of maximum and minimum ambient temperatures did not influence the relationship between number of females and per capita number of offspring produced or the relationship between number of females and per capita number of offspring surviving to breeding age (Supplementary Table S4, models 3 and 4).

DISCUSSION

This study revealed some important findings regarding the potentially modulating role of ecology on the effects of degu sociality and communal rearing on direct fitness. The effect of the number of females per group on the per capita number of offspring produced tended to be positive during years with relatively low mean abundance of food and degu density. Similarly, more positive effects of group size (on per capita number of offspring produced and per capita offspring survival to breeding age) and of the number of females (on per capita number of offspring produced) were associated with years with decreasing mean precipitation levels. Taken together, the effects of mean abundance of food and mean precipitation support the hypothesis that group living and cooperation in terms of communal rearing is more beneficial when habitat quality in terms of yearly mean food availability and precipitation decreases. We suggest that the effect of degu density
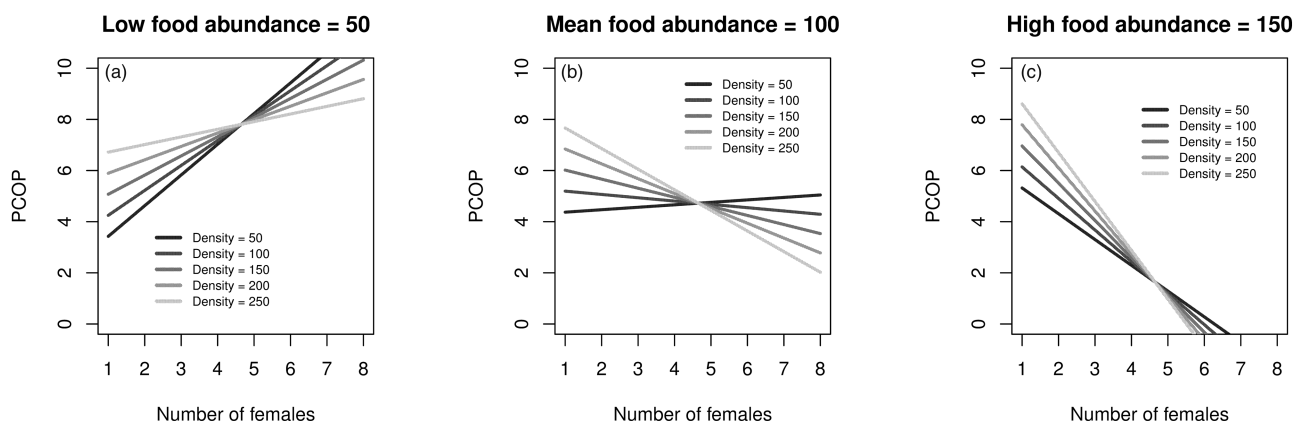
Figure 1
Effect of number of females on the per capita number of offspring produced (PCOP). The figure illustrates how this effect changes from positive to negative with increasing levels of mean food abundance (i.e., compare panels a, b, and c) in gram per square meter and with increasing levels of degu density (i.e., compare regression lines within each panel) in degus per hectare. Lines represent predictions from the fitted mixed model 3 of Supplementary Table S1. Levels of food abundance and degu density were chosen to represent conditions below, near, and above mean recorded values.
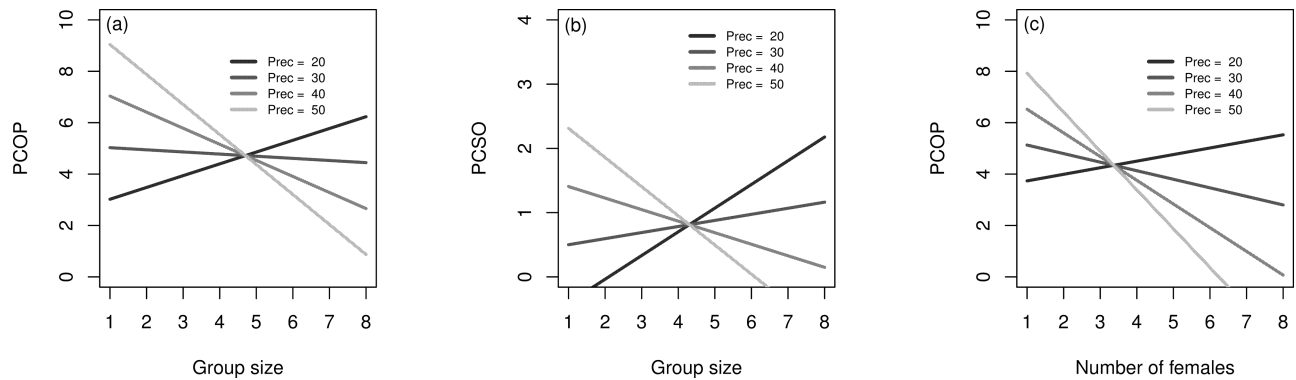
Figure 2
Effect of group size on the per capita number of offspring produced (PCOP; panel a) and on the per capita surviving offspring (PCSO; panel b). Panels a and b illustrate how these effects change from positive to negative with increasing levels of mean precipitations (in mm per month). Panel c represents the effect of group size on the per capita number of offspring produced (PCOP) and how effect changes from positive to negative with increasing levels of mean precipitations. Lines from panel represent predictions from the fitted mixed model 1 of Supplementary Table S3. Lines from panel b represent predictions from the fitted mixed model 2 of Supplementary Table S3. Lines from panel c represent predictions from the fitted mixed model 3 of Supplementary Table S3. Levels of precipitation were chosen to represent conditions below, near, and above mean recorded values.

is similarly consistent with this conclusion. In particular, low degu density conditions likely reflect low rainfall and low food availability or mean harsh ecological conditions. In contrast, we found that average and variance conditions linked to predation risk and ambient temperature did not influence direct fitness effects of social environment. Most likely, predation risk does not directly affect the fitness of degus through variation in breeding group structure but rather through variation in foraging group size (Ebensperger and Wallem 2002). Aboveground ambient temperatures may not have a significant impact on reproductive success if degus can maintain a relatively warm microclimate in underground burrows.

Harsh and favorable ecological conditions

The nature and extent to which mean ecological conditions modulate fitness effects of sociality and cooperation during breeding remains under scrutiny. Evidence from singularly breeding birds generally (yet not always: Komdeur 1994; Koenig et al. 2011) supports an influence of mean harsh conditions on fitness effects of group living (Magrath 2001). In these species, "helpers at the nest" counteract the negative effects of group (or colony) size on reproductive success under low-quality conditions in terms of low prey density, available space for food storing, high predation risk, low rainfall, or low breeding experience (e.g., Austad and Rabenold 1985; Lennartz et al. 1987; Curry and Grant 1990; Reyer 1990; Magrath 2001; Covas et al. 2008). Our study on plurally breeding degus was supportive of this trend in that years with less abundant food and precipitations as well as low degu density were associated with more positive effects of group size and number of breeding females on per capita offspring produced (and of group size on per capita offspring surviving to breeding age).

These findings depart from previous studies of singularly breeding mammals in which positive effects of sociality and cooperation during breeding on reproductive success has been recorded under relatively "favorable" conditions. For example, litter size and pack size in wolves (*Canis lupus*) are negatively correlated with low prey availability (Harrington et al. 1983). Similarly, a positive relationship between per capita reproductive success and group size characterizes food-supplemented prairie vole (*Microtus ochrogaster*) populations living in

semi-natural conditions (Solomon and Crist 2008). Thus, the overall importance of low- versus high-quality ecological conditions remains diverse across mammals. Indeed, we recently noted a nonsignificant trend of group living resulting in more positive effects on direct fitness estimates under low-food (poor), than under high-food (favorable), conditions in mammals (Ebensperger, Rivera, et al. 2012). To some extent, lack of differences in these effects may reflect the small number of studies on social mammals assessing these effects.

Our study revealed that degus benefit from living in groups and communally rearing their offspring under conditions of low mean precipitation, low mean food availability, and low mean degu density. At the ultimate level, it is possible that group living and cooperation linked to communal rearing in degus reduces environmentally induced variance in fecundity and offspring survival during years in which mean conditions are harsh. Intriguingly, this possibility would depart from that reported in the singularly breeding bird, *L. superbus*, where harsh conditions involve temporally more variable effects of precipitation and food availability (Rubenstein 2011). A potentially interesting evolutionary question that emerges from this comparison is "did singular and plural breeding in vertebrates evolve in response to predictably poor or unpredictable environments?" To answer this question, we need to compare the distribution and prevalence of breeding strategies with mean and variance in worldwide patterns of rainfall and food (sensu Jetz and Rubenstein 2011) within birds or mammals, an objective of an ongoing study.

At this time, the proximate mechanisms driving the relationship between group size and reproductive success in degus are poorly understood. Although laboratory studies have shown that group living degus rear offspring communally (Ebensperger et al. 2002, 2007) to date, we have not been able to quantify details of parental behavior in naturally occurring populations. It is possible that communal rearing reduces the costs of leaving offspring unattended while foraging and provide enough milk to offspring (Hayes and Solomon 2006) during years in which food resources are limited. However, a previous observation that communal rearing does not enhance the growth rates of offspring in the lab even when food is limited (Ebensperger et al. 2007) does not support this hypothesis. An alternative hypothesis is that group living and communal rearing buffer the stress response of group members and offspring

to the variety of stressors that characterize "harsh" environmental conditions during breeding (Hennessy et al. 2009; Bauer C, Romero LM, Hayes LD, Ebensperger LA, unpublished data). In this sense, communal rearing may reduce variability in the quality of maternal care during bad years.

In contrast to harsh conditions, we noted that the effects of sociality remain costly under more favorable mean ecological conditions. Potentially, burrow use may be constrained under high degu density conditions that would result when food resources are abundant. Adult members of the same social groups share a variable number of burrow systems (Hayes et al. 2009). Mean and stable conditions are thought to lead to habitat saturation and subsequent offspring philopatry, which in turn result in group living, delayed breeding, and cooperation during offspring rearing in singular breeders (Arnold and Owens 1999). However, a mechanism based on habitat saturation to link mean ecological conditions to group living and communal rearing remains unclear in degus. Although burrows are critical nest sites for rearing offspring communally (Ebensperger et al. 2004), no association was evident between burrow use and degu density during a more limited, 4-year study (Ebensperger, Chesh, et al. 2011).

Mean and variance in ecological conditions

In contrast to mean conditions, the effect of variance in ecological conditions has been examined only recently. In superb starlings, variance in (but not mean) fecundity decreases with increasing spatial (among territories) and temporal (among years) environmental variations (Rubenstein 2011). These observations are consistent with the hypothesis that cooperative rearing of offspring represents a risk-averse strategy to maximize direct fitness by reducing environmentally induced variance in fecundity (Rubenstein 2011). Further support to this hypothesis comes from the observation that habitats used by singular breeding birds are associated with relatively high across year variation in rainfall (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011). However, the extent to which variance in ecological conditions is generally a major modulator of fitness effects of group living and cooperation during breeding remains unclear. On the one hand, our current study on plurally breeding degus indicated that social effects on direct fitness estimates were insensitive to ecologically relevant variation to these rodents. Years with less abundant food, precipitations, and degu density were associated with more positive effects of group size and number of breeding females on per capita offspring produced (and of group size on per capita offspring surviving to breeding age). In addition, cooperation during breeding across hornbills, a taxonomic subset of singularly breeding birds, seems insensitive to climatic fluctuations (Gonzalez et al. 2013). Comparative studies across social mammals would be useful to provide stronger generalizations about the extent to which mean and variance in ecological conditions predict the evolution of singular and plural breeding strategies.

Far from being mutually alternative explanations, we concur with Gonzalez et al. (2013) in that the relative strength of mean and variance in ecological conditions as modulators of social effects on fitness is likely to vary (i.e., interact) with differences in life history and other intrinsic attributes of species or clades. For instance, relatively large body size coupled to low reproductive output and long life span or the feeding on more temporally predictable prey may have contributed to singularly breeding hornbills being less sensitive to variance in ecological conditions (Gonzalez et al. 2013). The scarce (if any) role of variance in ecological conditions on

the effects of social environment on reproductive success in plural breeding degus may be explained in part by life-history characteristics. Typically, 80% or more males and females breeding during one particular year do not survive to the next breeding season in nature (Ebensperger et al. 2009, 2013). Because degus typically breed annually, and only occasionally twice within a same year (Ebensperger et al. 2013), most animals in the population breed only once in their lifetime. Under these life-history (or demographic) conditions, group living and communal rearing are less likely to reduce environmentally mediated variance in fecundity of degus.

In contrast, the hypothesis that sociality and cooperation during breeding represents a strategy to face variable and generally unpredictable ecological conditions may apply to other social mammals. Group living and singularly breeding have been hypothesized to represent a strategy used by African Bathyergids (mole-rats) to face unpredictable rainfall and the effects of these climatic conditions on food distribution (subterranean tubers) and the associated costs and risks of unsuccessful foraging (Jarvis et al. 1994). This hypothesis is supported by the observation that more social populations and species of mole-rats are associated with spatially and temporally unpredictable resources (Bennett and Faulkes 2000), yet this evidence remains restricted to African mole-rats. Most critically, the extent to which variance in ecology modulates the effects of group living and communal rearing on fitness remains undetermined in mole-rats or in other social rodents.

Long-term population studies in northern Chile indicate that degu survival and fecundity decrease during La Niña year events, characterized by low rainfall and food conditions (Previtali et al. 2010). In contrast, degu survival and fecundity increase during years with high rainfall and low food conditions or El Niño events. Results from our study indicate that group living and communal rearing provide degus with potential fitness benefits, but mostly during years with low precipitation, low food availability, and a resulting low degu density. An intriguing implication of these findings is that group living may contribute to counteract the direct negative effects of ecological conditions during La Niña years. In contrast, the effects of sociality and communal rearing would be unimportant during El Niño events. Given the ancient history of El Niño-La Niña events in South America (e.g., Moy et al. 2002), the hypothesis that these climatic events have contributed to maintain sociality and communal rearing in degus remains intriguing.

Concluding remarks

With some notable exceptions (Johnson et al. 2001; Packer et al. 2001; Clutton-Brock et al. 2008; Schradin et al. 2010), most field studies on social mammals aimed to address the sociality–ecology or the sociality–fitness covariation have been conducted within a time frame span over a few (1–4) years (e.g., Travis et al. 1995; Brashares and Arcese 2002; Schradin and Pillay 2005; Verdolin and Slobodchikoff 2009; White and Cameron 2009). The scarce evidence on long-term patterns in sociality–fitness relationships adds value to our 8-year field study and highlights the importance of long-term field studies to reveal how mean and variance in ecological conditions modulate fitness consequences of sociality and cooperation. Previously, the effect size of sociality on fitness measures across studies of social mammals was reported not to vary significantly across mean "favorable" and "harsh" ecological conditions (Ebensperger, Rivera, et al. 2012), a finding that might be influenced by the relatively short-term nature of available data.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco. oxfordjournals.org/

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