

The modulating role of group stability on fitness effects of group size is different in females and males of a communally rearing rodent

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Summary

1. Group size may influence fitness benefits and costs that emerge from cooperative and competitive interactions in social species. However, evidence from plural breeding mammals indicates that group size is insufficient to explain variation in direct fitness, implying other attributes of social groups were overlooked.

2. We studied the natural population of a social rodent during 5 years to test the hypothesis that social stability – in terms of group composition – modulates the effects of increasing number of breeding females (a proxy of communal rearing) and males on the number of offspring weaned (sired) and on the number of offspring weaned (sired) surviving to breeding age (two proxies of direct fitness). We quantified the effects of social stability (measured as changes in female or male group members between mating and the onset of lactation) on these fitness measures.

3. We used live trapping, telemetry and DNA markers to determine social and fitness measures.

4. Social stability in degus was variable in terms of the number of changes in group composition across groups. Low stability was mostly due to mortality and emigration of group members.

5. Results supported a modulating role of social stability on the relationship between group size and the number of offspring weaned (sired). Stability in female and male group composition were both modulators of fitness to females and males.

6. The modulatory role of stability was sex specific, where high social stability was often fitness beneficial to the females. Instead, low social stability was fitness enhancing to the males.

Key-words: communal rearing, degus, fitness, reproductive success, social instability, sociality

Introduction

Group living is thought to evolve when fitness benefits (e.g. decreased predation risk, enhanced access to resources) outweigh inherent costs (e.g. increased transmission of parasites, competition over resources; Alcock 2001; Ebensperger 2001; Krause & Ruxton 2002; Davies, Krebs & West 2012). Fitness benefits (and costs) are influenced by social group attributes such as the number of adult individuals, or number of caregivers per group (group size). Numerous theoretical and empirical studies

document how predation risk or enhanced access to resources changes with the number of group members (Giraldeau & Caraco 2000; Krause & Ruxton 2002; Caro 2005). The importance of group size is further supported by studies documenting how networks of cooperative and competitive social interactions are connected to fitness, which in turn may be influenced by group size (e.g. Madden *et al.* 2009; Gilby *et al.* 2013; Maldonado-Chaparro, Hubbard & Blumstein 2015). Moreover, group size is suggested to reflect potential for cooperation (Rubenstein 2011).

Evidence from birds and mammals indicates that effects of group size on direct fitness (e.g. reproductive success,

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adult and offspring survival) vary widely across studies and similarly social species (Cockburn 1998; Magrath 2001; Ebensperger, Rivera & Hayes 2012). Positive and significant covariation between group size and individual fitness is observed in mammals exhibiting singular breeding, a cooperative strategy where most group members do not breed and provide care to the offspring of breeders (Silk 2007). In contrast, neutral and negative covariation between group size and fitness is common in mammals exhibiting plural breeding (Ebensperger, Rivera & Hayes 2012), where direct reproduction is shared more equally among adults and group members rear offspring communally (Silk 2007). These findings show how fitness effects of group size are not only contingent on the main strategy of cooperation, but also may depend on social attributes other than group size.

A salient feature of social groups is that their composition may vary permanently due to mortality, individuals leaving a group (i.e. emigration), or to individuals joining a group (i.e. immigration; Christal, Whitehead & Lettevall 1998; Ebensperger & Hayes 2008; Bateman *et al.* 2013; Port & Johnstone 2013). Few studies have examined the fitness effects of variation in group composition to group members, a lack of interest that seems unjustified. Benefits to social individuals may be contingent upon the existence of close social bonds (Silk, Alberts & Altmann 2003; Cameron, Setsaas & Linklater 2009; Schülke *et al.* 2010), social relationships that are established and maintained by affiliative social interactions (Sachser, Dürschlag & Hirzel 1998). Decreasing social stability in the form of permanent changes in group composition may disrupt adult partnerships reflecting social bonds, with potentially negative consequences. A recent field study on singularly breeding male and female Alpine marmots (*Marmota marmota*) revealed how the number of lifetime breeding events decreases in groups with decreasing stability (Lardy *et al.* 2015). Additionally, biomedical studies demonstrate how decreasing social stability may result in increased agonistic social interactions, elevated metabolic rates, elevated stress hormone levels, immune suppression and higher parasite loads (Sapolsky 1983; Mormède *et al.* 1990; Cristol 1995; Hawley 2006; Fairbanks & Hawley 2012; Nuñez *et al.* 2014). Most critically, decreasing social stability may disrupt communal rearing (Champagne & Curley 2009; Cirulli *et al.* 2010) and other forms of cooperation (Soares *et al.* 2010).

We aimed this study to determine the fitness effects of social stability in a free-living, social mammal. We examined these effects in the degu (*Octodon degus*), a plurally breeding rodent in which multiple adult group members share one or more underground burrows (Ebensperger *et al.* 2004; Hayes *et al.* 2009). Degu social groups vary in size and adult sex composition (1–9 females, 0–3 males), spanning from multifemale–multimale groups to solitary nesting males and females. Degus also exhibit cooperation in the form of communal rearing of offspring, which may include the nursing of non-descendent offspring

(Ebensperger, Veloso & Wallem 2002; Ebensperger *et al.* 2004; Jesseau, Holmes & Lee 2009). Intriguingly, short-term (2–3 years) studies indicated no positive effects of group size to the females in terms of per capita weaned and surviving offspring (Hayes *et al.* 2009; Ebensperger *et al.* 2011), a relationship that has not been investigated in male degus.

Permanent changes in group composition are known to occur in degus during the period between the austral winter (i.e. mating time) and austral spring (i.e. lactation time). On average ($\pm$ SD), $29 \pm 6\%$ of adult members of social groups disappear from winter through spring, and $15 \pm 5\%$ of adult group members immigrate into different social groups (Ebensperger *et al.* 2009). The observation that degus treat conspecifics differentially as a function of familiarity (Jesseau, Holmes & Lee 2009; Villavicencio *et al.* 2009) supports the possibility that variation in group composition disrupts partnerships reflecting social bonds, and negatively impacts communal rearing. Therefore, we hypothesized that effects of group size on reproductive success (i.e. direct fitness, Brown 1987) are modified (i.e. modulated) by stability in group composition in these communally rearing rodents (i.e. modulation hypothesis). Specifically, group size–direct fitness relationships would be modulated by changes in group composition resulting in different social interactions (e.g. communal care), which in turn are linked to fitness. Thus, we predicted that (P1) the effects of the number of breeding females per group (i.e. potential for communal rearing; Ebensperger, Veloso & Wallem 2002; Ebensperger, Hurtado & León 2007) on female reproductive success would be more positive in groups experiencing higher stability in female group composition (Silk, Alberts & Altmann 2006).

Females may benefit from the stable presence of males if males are mates, provide offspring with parental care and protection from predators, or acquire and defend critical resources (Clarke & Glander 1984; Kaseda, Khalil & Ogawa 1995; Møller 2000; Treves 2001). In contrast, decreasing stability in male group composition may interfere with an ability of resident males to monopolize the females (Heckel & Von Helversen 2003) and enhance costly male harassment to the females (Maklakov, Bilde & Lubin 2005; Gasparini, Devigili & Pilastro 2012; Li, Fail & Shelton 2015). Thus, we also predicted that the effects of number of males on female reproductive success would be more positive in groups with increasing stability in male group composition (P2).

Fitness effects of group living can be sex specific (e.g. Garg *et al.* 2015; Lardy *et al.* 2015). Reproductive success of males typically depends on mating opportunities, which generally increase in groups with a relatively large and stable number of adult females (e.g., Breuer *et al.* 2010; L'Italien *et al.* 2012). In contrast, paternity of males typically decreases in multimale groups (Belle & Estrada 2008; Fedigan & Jack 2011; Lardy *et al.* 2012) through different mechanisms, including inability of males to

prevent mating attempts by male competitors, which may act singly or in coalitions (Ryder *et al.* 2011; Lardy *et al.* 2012; Wiszniewski *et al.* 2012). Male degus are not known or suspected to cooperate during breeding (*sensu* Díaz-Munoz *et al.* 2014), implying that the effects of social stability in keeping male social bonds are unimportant. Instead, social groups facing decreasing stability may provide males with further mating opportunities. Thus, we predicted that effects of number of males (P3) and females (P4) on male reproductive success would be stronger and positive in groups experiencing decreasing stability in terms of female group composition.

Materials and methods

STUDY POPULATION

The study was conducted during 2009 through 2013 on a natural population of degus located at the Estación Experimental Rinconada de Maipú (33°23'S, 70°31'W), a field station of Universidad de Chile. This study area is characterized by a Mediterranean climate with cold, wet winters and warm, dry summers (di Castri & Hajek 1976). The site consisted of open areas with scattered shrubs (*Acacia caven*, *Baccharis* spp., *Lithraea caustica* and *Quillaja saponaria*) that on average covered 14.5% of ground (Ebensperger & Hurtado 2005). The total area examined at Rinconada was nearly 2–3 ha.

DETERMINATION OF SOCIAL GROUPS

Each year, social groups were determined in June–July (early winter or mating time) and in September through October (a time encompassing parturition, lactation and offspring weaning). Degus are diurnally active and remain in underground burrows overnight (Ebensperger *et al.* 2004). Thus, the main criterion used to assign degus to social groups was the sharing of burrow systems overnight. The sharing of burrow systems was established by means of (i) burrow trapping during early morning activity, and (ii) night-time telemetry. Specific details on burrow trapping, degu tagging and radiocollaring can be obtained from Ebensperger *et al.* (2011, 2014).

During night-time telemetry, females were radiotracked to their burrows. Previous studies at Rinconada 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 before sunrise using a LA 12-Q receiver (for radiocollars tuned to 150 000–151 999 MHz frequency; AVM Instrument Co., Auburn, CA, USA) and a hand held, 3-element Yagi antenna (AVM instrument Co.). The number of burrow systems monitored, the number of days that each burrow system was trapped, the number of radiocollared degus and the number of night-time telemetry locations per radiocollared degu per season and year of study are given in Table S1 (Supporting Information). This effort has been shown to be sufficient in determining group composition (Hayes *et al.* 2009; Ebensperger *et al.* 2011).

The determination of group size and composition during each study season and year was based on the compilation of a

symmetric similarity matrix of pairwise association of burrow locations of all adult degus during trapping and telemetry (Whitehead 2008). The association (overlap) between any two individuals was determined by dividing the number of early mornings that these individuals were captured at or tracked with telemetry (respectively) to the same burrow system, by the number of early mornings that both individuals were trapped or tracked with telemetry on the same day, respectively (Ebensperger *et al.* 2004; Hayes *et al.* 2009). The size and composition of social groups were then determined from cluster analysis outputs (Hayes *et al.* 2009; Ebensperger *et al.* 2014) generated with the socPROG software (Whitehead 2009).

SOCIAL STABILITY

We quantified social stability from the total number of changes in adult membership within groups between two consecutive seasons each year: (i) austral winter (June–July): the period of mating and pregnancy and (ii) austral spring (September–October): the period when adult females are lactating, rearing offspring communally, and occasionally undergo through post-partum oestrus. Thus, maximum stability (or minimum instability) characterized a social group where all individual members recorded during winter consistently associate through spring. In contrast, minimum stability characterized social groups in which most members recorded during winter did not associate through spring, even if total group size does not change.

We first contrasted degu membership of social groups in spring with that of social groups in winter. Table S2 includes the sex composition of all winter and spring social groups monitored per year, and the number of spring groups with social membership connections to winter groups each year. Based on this examination and for each social group during spring, we determined (i) the number of group members that continued to associate with other members of a previous winter group (i.e. exhibiting social fidelity). We also recorded (ii) the number of group members that immigrated alone or with members from a previous winter group (i.e. immigrants), (iii) the number of group members that left their former winter groups to remain solitary (i.e. emigrants) and (iv) the number of group members that disappeared. Degus that joined a spring social group from a previously unknown winter group, but with sufficient trapping information in the study area during winter (i.e. residents in the study area) were also considered as immigrants. Likewise, degus that left a winter social group and that remained in the study area as residents in an unknown spring social group were considered emigrants. All degus that had sufficient trapping information (i.e. with a number of captures equal or higher than 1 SD below the population mean for that particular year and season) were included in the analyses. Table S3 shows means, standard deviations and minimum number of captures per year and season used to fulfil this criterion. Degus that disappeared and were not recaptured for at least three subsequent trapping seasons were presumed to have died. Two observations suggest this assumption is valid to the study population. First, 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.* 2011b). Secondly, only 5 out of 1310 individually marked degus (i.e. 0.4%) have been recaptured after disappearance during 3 consecutive trapping seasons between 2009 and 2015.

DIRECT FITNESS MEASURES: NUMBER OF OFFSPRING WEANED (SIRE)

We combined offspring capture and recapture records with maternity and paternity estimates based on molecular approaches to estimate the number of female and male offspring weaned (i.e. known to be alive when first caught), an appropriate estimate of reproductive success in degus. Degus have long gestation periods (c. 3 months) and thus typically breed once annually during the austral spring, though occasionally, females will reproduce twice in the same year (Ebensperger & Hurtado 2005; Ebensperger *et al.* 2013). Given that most adults do not survive to a second year of breeding (Meserve, Gutiérrez & Jaksic 1993; Ebensperger *et al.* 2009, 2013), first breeding event in these animals has a major impact on lifetime reproductive success (i.e. direct fitness). At a population level, our estimates indicate that 88% of offspring are weaned during the spring, the main breeding event in the study population.

We used DNA microsatellite loci to quantify the number of offspring weaned by each female and sired by each male group member during the austral spring. We genotyped a total of 1006 adult and offspring degus from 2009 through 2013 (Table S4). DNA was extracted from a small piece (1 × 5 mm) of one ear cartilage tissue per individual, using the ReliPrep DNA animal tissue miniprep system kit (Promega) and the tail mouse protocol. We conducted maternity and paternity analyses with a total of 12 highly polymorphic loci, including 11 from *O. degus* (Quan *et al.* 2009) and one from *S. cyanus* (Schroeder *et al.* 2000; Table S5). These loci were amplified via polymerase chain reaction (PCR) containing only one marker labelled with a fluorescent dye (FAM, VIC, NED or PET). Locus-specific annealing temperatures are provided in Table S5. All loci were amplified successfully and were polymorphic (Table S5). Genotypes for all individuals across years were complete with no missing data. We tested the Hardy–Weinberg observed and expected heterozygosity for each study year with the use of CERVUS 3.0 software (Marshall *et al.* 1998). Deviations from Hardy–Weinberg expectations were detected in 4 out of 5 years (Table S6). This finding was not surprising for our degu population was finite, open, not panmictic, and with a relatively high level of genetic relatedness. However, these deviations involved different loci per year and were not the consequence of null alleles. All markers were checked for null alleles with the MICROCHECKER software (van Oosterhout *et al.* 2004).

We used the CERVUS 3.0 software (Marshall *et al.* 1998) to conduct maternity analyses, where all offspring were checked against all potential mothers in the population. We repeated the same approach during paternity analyses. Confidence calculation on CERVUS 3.0 was made using the LOD score option. All 12 loci selected had a combined exclusion probability of 99.9% for all study years when neither parent was previously known (Table S7). The settings of the simulation file were based on allele frequency data from the entire population, 10 000 cycles, and a genotyping error rate of 1%. The proportion of the population sampled was set to 0.9 for females and males. We set the program to determine the most likely mother (and father). All parent assignments were made using a strict (95%) level of statistical confidence (i.e. criterion 1, Marshall *et al.* 1998). Thus, we accepted the most likely mother (and father) as real mother (and father) only when the following two additional criteria were met: (criterion 2) the LOD score for the pair mother–offspring tested was positive, and (criterion 3) there were no mismatches. In some

few cases where two individuals achieved all these previous criteria, we assigned offspring to the adult with highest LOD score. We had several cases in which only criteria 1 and 2 were met, yet the offspring–mother (or father) pair exhibited 1 mismatch. We reviewed these genotype pairs to determine which loci were involved. Whenever single mismatches affected two repeat motif loci and involved contiguous alleles (i.e. separated by two base pairs), we accepted these offspring–mother (or father) pairs as correct (Duchesne, Castric & Bernatchez 2005). Instead, single mismatches between offspring–mother (or father) found in a four repeat motif loci or that involved non-contiguous alleles in two repeat motif loci were discarded. Based on the fact that our degu population exhibit a relatively high level of genetic relatedness (Ebensperger *et al.* 2004; Quirici *et al.* 2011a), all maternity and paternity assignments with two or more mismatches were discarded. Based on these criteria, Table S7 shows the number of female and male offspring that were assigned mother, father, mother and father, and without parents assigned.

DIRECT FITNESS MEASURES: NUMBER OF SURVIVING OFFSPRING

We recorded weaned offspring that were recaptured during their subsequent winter to estimate the number of offspring per female or male that survived to breeding age. The number of offspring weaned is probably influenced primarily by communal rearing (i.e. number of females per group). In contrast, offspring survival to reproductive age is likely to be influenced by other social and ecological conditions, including social vigilance during foraging and predation risk (Ebensperger & Wallem 2002). The number of offspring that survived to reproductive age was estimated from trapping records of newborn offspring from the spring that were recaptured during the subsequent winter. From this information, we then determined the number of offspring weaned by females and sired by males that survived to reproductive age. The trapping effort per year is given in Table S1.

STATISTICAL ANALYSIS

We specified separate model sets to test each of the four predictions based on our *a priori*, modulation hypothesis (Fig. 3). Each model set consisted of a full model that included third-order factor interactions (involving sex of adults, stability in female or male group composition and number of adult females), and three other simpler models. We used model selection based on an information theoretical approach (Burnham & Anderson 2002; Anderson 2008) to contrast how the high-order interaction model was well-supported compared with simpler, low-order models. Thus, 4 sets of models were examined on the number of offspring weaned (Table 1), and 4 additional sets of models were assessed on the number of weaned offspring that survived to breeding age (Table 2). Main predictors included in the models were sex of degus (male vs. female), two measures of group stability (stability in female group composition, stability in male group composition) and two measures linked to group size (number of females in winter and spring groups, number of males in winter and spring groups). All models assessed included random intercept terms to account for non-independency in the data set due to study year, social group ID in winter and social group ID in spring (Garson 2013). Data were analysed using generalized linear mixed models (Bolker *et al.* 2009; Zuur *et al.* 2009).

Table 1. Comparison of models built to predict the number of offspring weaned by female and male degus. Fixed effects included sex, stability in male (SMGC) and female (SFGC) group composition, number of males (NM) and females (NF) per social group in winter and spring, and biologically relevant two-factor and three-factor interactions. All models examined also included year of study, winter and spring group ID as random effects. Bold typing is used to highlight the best and well-supported models (delta AIC < 2 and Akaike weight close to 1) exclusively. Overdispersion associated with submodels 1.4 and 3.4 were 1.70 (95% CI = 1.21–1.99) and 1.50 (95% CI = 1.06–2.08), respectively, implying no biases during parameter estimation. A total of 55 females and 27 males provided replicates for these analyses

Model set	Submodel	Fixed effects	Degrees of freedom	AIC _c	AIC _{difference}	Akaike weight
1	1.1	Intercept-only	4	493.958	28.046	0.000
	1.2	Sex + SFGC + NF _{spring} + NF _{winter}	8	487.833	21.921	0.000
	1.3	Sex + SFGC + NF _{spring} + NF _{winter} + (Sex*NF _{spring}) + (Sex*NF _{winter}) + (SFGC*NF _{spring}) + (SFGC*NF _{winter})	14	494.756	28.844	0.001
	1.4	Sex + SFGC + NF _{spring} + NF _{winter} + (Sex*SFGC) + (Sex*NF _{spring}) + (Sex*NF _{winter}) + (SFGC*NF _{spring}) + (SFGC*NF _{winter}) + (Sex*SFGC*NF _{spring}) + (Sex*SFGC*NF _{winter})	15	465.912	0.000	0.999
2	2.1	Intercept-only	4	493.958	2.475	0.126
	2.2	Sex + SFGC + NM _{spring} + NM _{winter}	8	492.122	0.639	0.317
	2.3	Sex + SFGC + NM _{spring} + NM _{winter} + (Sex*SFGC) + (Sex*NM _{spring}) + (Sex*NM _{winter}) + (SFGC*NM _{spring}) + (SFGC*NM _{winter})	14	491.483	0.000	0.436
	2.4	Sex + SFGC + NM _{spring} + NM _{winter} + (Sex*SFGC) + (Sex*NM _{spring}) + (Sex*NM _{winter}) + (SFGC*NM _{spring}) + (SFGC*NM _{winter}) + (Sex*SFGC*NM _{spring}) + (Sex*SFGC*NM _{winter})	15	494.045	2.562	0.121
3	3.1	Intercept-only	4	493.958	28.702	0.000
	3.2	Sex + SMGC + NF _{spring} + NF _{winter}	8	476.615	11.359	0.003
	3.3	Sex + SMGC + NF _{spring} + NF _{winter} + (Sex*SMGC) + (Sex*NF _{spring}) + (Sex*NF _{winter}) + (SMGC*NF _{spring}) + (SMGC*NF _{winter})	13	487.711	22.455	0.000
	3.4	Sex + SMGC + NF _{spring} + NF _{winter} + (Sex*SMGC) + (Sex*NF _{spring}) + (Sex*NF _{winter}) + (SMGC*NF _{spring}) + (SMGC*NF _{winter}) + (Sex*SMGC*NF _{spring}) + (Sex*SMGC*NF _{winter})	15	465.256	0.000	0.997
4	4.1	Intercept-only	4	493.958	21.348	0.000
	4.2	Sex + SMGC + NM _{spring} + NM _{winter}	8	472.610	0.000	0.865
	4.3	Sex + SMGC + NM _{spring} + NM _{winter} + (Sex*SMGC) + (Sex*NM _{spring}) + (Sex*NM _{winter}) + (SMGC*NM _{spring}) + (SMGC*NM _{winter})	14	477.048	4.438	0.094
	4.4	Sex + SMGC + NM _{spring} + NM _{winter} + (Sex*SMGC) + (Sex*NM _{spring}) + (Sex*NM _{winter}) + (SMGC*NM _{spring}) + (SMGC*NM _{winter}) + (Sex*SMGC*NM _{spring}) + (Sex*SMGC*NM _{winter})	15	478.690	6.080	0.041

Dependent variables were assumed to follow a Poisson distribution and modelled with the use of a log link function (Zuur *et al.* 2009). Overdispersion was assessed by means of parametric bootstrapping as recommended by Harrison (2014). We calculated VIF (variance inflation factor) values to assess the extent of collinearity. Following Miles (2005), VIF values below 10 would indicate low to moderate collinearity, while VIF values above this value would require variable exclusion or a change in model specification. We used three diagnostic techniques to rule out potential outliers or influential observations. First, we used Cleveland plots between each covariate and the response variable (Zuur, Ieno & Elphic 2010). Secondly, we calculated Cook's distances with formulas proposed for GLMM (Xiang, Tsea & Lee 2002; Pinho, Nobrea & Singerb 2015). Thirdly, we conducted an influential-cases analysis to quantify the extent to which model parameters are affected by removal of observations (Van der Meer, Te Grotenhuis & Pelzer 2010). All three analyses – Cleveland plots, Cook's distances and influential analyses – did not reveal potential outliers in the data set (Data S1).

All statistical analyses were performed in R 3.2.3. Generalized linear mixed models were fitted using package LME4 (Pinheiro & Bates 2000; Bates *et al.* 2015). Akaike weights were estimated with functions included in the MuMIN, version 1.15.6 library (Barton 2009). Influential analyses were examined using package INFLUENCE.ME, version 0.9.2 (Nieuwenhuis, te Grotenhuis & Pelzer 2012).

Results

VARIATION IN GROUP SIZE, SOCIAL STABILITY AND REPRODUCTIVE SUCCESS

Overall, 82 adults (55 females, 27 males) had well-known membership to winter and spring groups and were used as replicates in statistical analyses. These individuals were members of 36 social groups during spring that were linked to 16 groups during winter. In spring, groups averaged 2.9 adults (SD = 1.9) and ranged from 1 to 5 adults. During winter, groups consisted of 2.6 adults (SD = 1.9) and ranged from 1 to 9 adults.

Comparisons between winter and spring social groups allowed the quantification of stability in female and male group composition. We recorded that only 2.7% (1/36) of spring social groups examined showed no changes in group composition during the breeding season. Twenty-five percentage (9/36) of these groups were the consequence of breaking up of previously larger winter groups. Together, social groups examined experienced 2.0 (SD = 2.1; range: 0–7) and 1.5 (SD = 1.3; range: 0–5) changes in female and male group composition, respectively, between winter (mating time) and spring (lactation time). Changes in female group composition involved 1.7 (SD = 2.1; range: 0–7) losses per group (i.e. due to emigration or presumed mortality) and 0.3 (SD = 0.6; range: 0–3) gains per group (i.e. immigration from known or unknown social groups). Changes in male group composition involved 1.1 (SD = 1.1; range: 0–4) losses per group and 0.5 (SD = 0.6; range: 0–2) gains per group. Thus,

relatively low female or male stability generally involved the loss of former group members.

Individual females weaned an average of 5.3 (SD = 2.5, median = 5.0) offspring, a figure that ranged from 0 to 11 offspring. The number of offspring sired by individual males averaged 6.6 (SD = 8.7, median = 3.0) and ranged from 0 to 32. The number of offspring weaned by females that survived to breeding age averaged 0.8 (SD = 1.0, median = 0) and ranged from 0 to 4. The number of offspring sired by males that survived to breeding age averaged 1.1 (SD = 2.0, median = 0) and ranged from 0 to 8 offspring. Male and female histograms of these two fitness measures are provided in the Fig. S1.

GENERAL FINDINGS

Two models that were examined supported our hypothesis that stability in group composition modulated the effects of sex and group size on the number of offspring weaned (sired). Specifically, we recorded statistically significant modulating effects of stability in female (model set 1) and male (model set 3) group composition (Table 1). One additional model (model set 4, Table 1) revealed only main positive effects of sex and of stability in male group composition on the number of offspring weaned (sired). Model set 2 did not discriminate a best supported model (Table 1).

None of the models examined supported stability in group composition modulated the effects of sex and group size on the number of offspring weaned (sired) that survived to breeding age. Model sets 5, 6, 7 and 8 did not discriminate a best and well-supported model (Table 2).

EFFECTS OF SOCIAL STABILITY BASED ON FEMALE GROUP COMPOSITION ON THE NUMBER OF OFFSPRING WEANED (SIRE)

The effect of the number of females in winter social groups on the number of offspring weaned (or sired) was modified by stability in female group composition and the sex of adult group members (Table 3; submodel 1.4; Fig. 1a,b).

Females

Submodel 1.4 (Table 3) revealed that the number of offspring weaned by each female increases with the number of females in winter groups experiencing high stability in female group composition (Fig. 1a).

Males

Regarding male degus, submodel 1.4 (Table 3) revealed that the number of offspring sired by each male generally increased with the number of females in winter groups experiencing low female stability (Fig. 1b).

Table 3. Fixed main and interactive effects of best and well-supported models highlighted in Table 2. Parameter estimates were attained with the use of generalized linear mixed models (GLMM). Random component variance estimates (year of study, degu winter and spring group ID) not shown. Factor estimates (and standard error), z-values, *P*-values and estimates of overdispersion (VIF) are shown. Bold-typed *P*-values highlight significant 3-factor interactions in best and well-supported models from Table 1. A total of 55 females and 27 males provided replicates for these analyses

Submodel	Fixed effects	β (standard error)	Z-value	<i>P</i> -value	VIF
1-4	Sex (male)	0.955 (0.452)	2.114	0.0345	1.267
	SFGC	-0.06 (0.166)	-0.363	0.7167	3.639
	NF _{spring}	-0.373 (0.148)	-2.517	0.0119	1.582
	NF _{winter}	0.402 (0.133)	3.011	0.0026	4.549
	SFGC*NM _{spring}	0.01 (0.038)	0.267	0.7893	
	Sex*SFGC	-0.997 (0.417)	-2.388	0.0169	
	Sex*NF _{spring}	0.331 (0.415)	0.799	0.4244	
	SFGC*NF _{winter}	-0.033 (0.024)	-1.365	0.1722	
	Sex*NF _{winter}	-0.713 (0.181)	-3.928	0.0001	
	Sex*SFGC*NF _{spring}	0.174 (0.261)	0.667	0.5046	
	Sex*SFGC*NF _{winter}	0.242 (0.054)	4.492	< 0.001	
	Sex (male)	1.691 (0.519)	3.258	0.0011	1.263
	SMGC	0.828 (0.279)	2.974	0.0029	1.031
3-4	NF _{spring}	0.154 (0.204)	0.755	0.4504	1.496
	NF _{winter}	0.238 (0.13)	1.835	0.0665	1.404
	SMGC*NM _{spring}	-0.095 (0.168)	-0.564	0.5730	
	Sex*SMGC	-0.896 (0.262)	-3.424	0.0006	
	Sex*NF _{spring}	-0.273 (0.401)	-0.679	0.4971	
	SMGC*NF _{winter}	-0.12 (0.073)	-1.642	0.1007	
	Sex*NF _{winter}	-0.371 (0.146)	-2.534	0.0113	
	Sex*SMGC*NF _{spring}	0.092 (0.201)	0.459	0.6462	
	Sex*SMGC*NF _{winter}	0.262 (0.076)	3.457	0.0005	
	Sex (male)	0.4306 (0.118)	3.636	0.0002	1.496
	SMGC	0.496 (0.113)	4.392	<0.001	2.589
	NM _{spring}	-0.222 (0.120)	-1.858	0.0632	1.763
	NM _{winter}	-0.269 (0.144)	-1.859	0.0630	2.229
4-2					

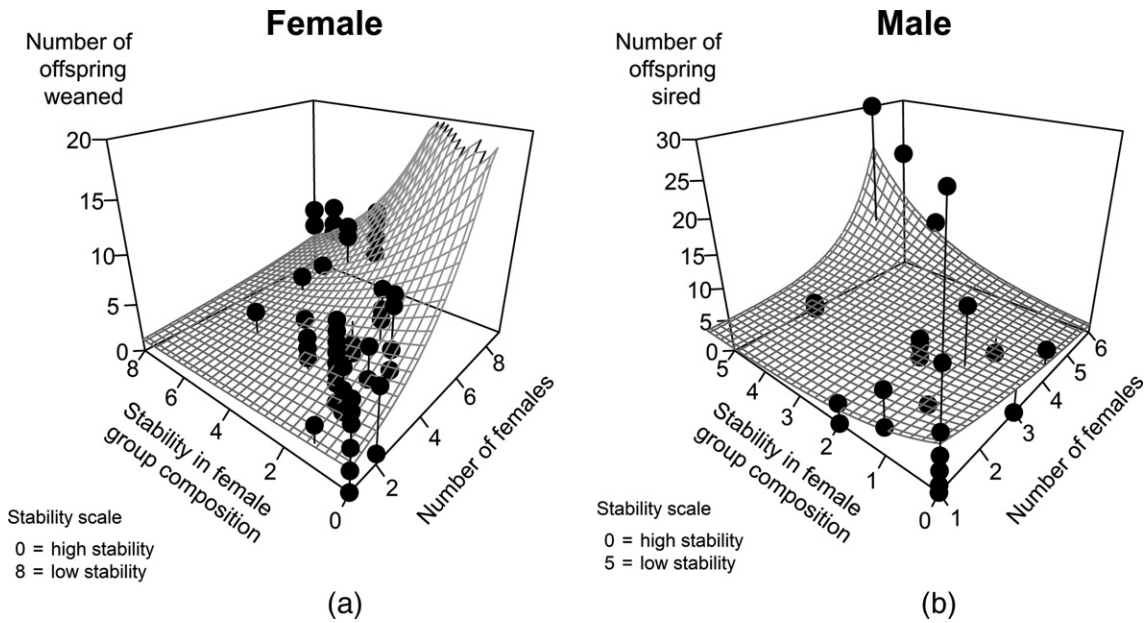


Fig. 1. Three-factor interaction effect between sex of adults, stability in female group composition and number of adult females in winter social groups on the number of offspring weaned by females (a) and sired by males (b), as revealed by model 1 in Table 2. On the stability axis, a value of 0 represents the highest social stability. Social stability decreases with increasing values on the stability axis. Black circles represent observed data higher and lower than model expectations represented by the surface. A total of 55 females and 27 males are shown in (a) and (b). Discrepancies between these numbers and the data points shown in the figure are due to data point overlap.

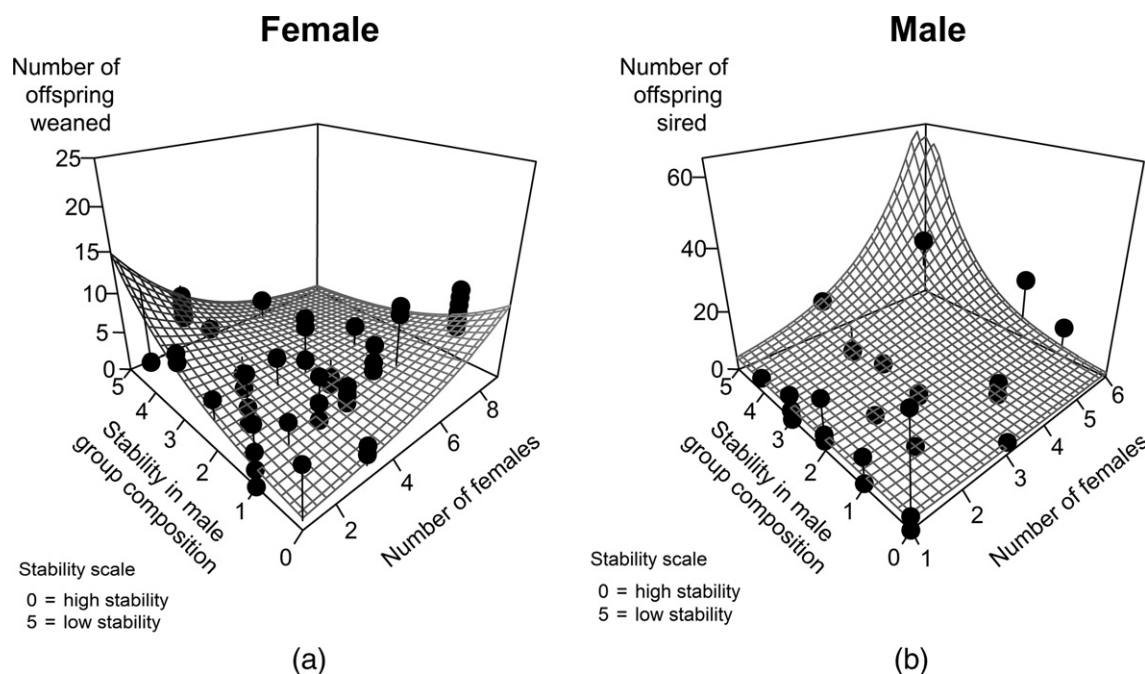


Fig. 2. Three-factor interaction effect between sex of adults, stability in male group composition and number of adult females in winter social groups on the number of offspring weaned by females (a) and sired by males (b), as revealed by model 3 in Table 2. On the stability axis, a value of 0 represents the highest social stability. Social stability decreases with increasing values on the stability axis. Black circles represent observed data higher and lower than model expectations represented by the surface. A total of 55 females and 27 males provided replicates in (a) and (b). Discrepancies between these numbers and the data points depicted are due to data point overlap.

EFFECTS OF SOCIAL STABILITY BASED ON MALE GROUP COMPOSITION ON THE NUMBER OF OFFSPRING WEANED (SIRE)

The effect of the number of females in winter social groups on the number of offspring weaned (or sired) was modified by stability in male group composition and the sex of adult group members (Table 3; submodel 3.4; Fig. 2a,b).

In addition, main effects of sex and stability in male group composition were detected as revealed by submodel 4.2 (Table 3). Specifically, this submodel revealed that males sired more offspring than females and that both females and males weaned (sired) more offspring in groups with increasing stability in male group composition.

Females

Submodel 3.4 in Table 3 revealed that the number of offspring weaned by each female increased with the number of females in winter groups experiencing high stability in male group composition, but decreased with the number of females in winter groups experiencing low stability in male group composition (Fig. 2a).

Males

Submodel 3.4 in Table 3 also revealed how the number of offspring sired by individual males increased with the number of females in winter groups experiencing low stability in male group composition (Fig. 2b).

Discussion

MAIN FINDINGS

Variation in adult composition of social groups in *O. degus* was extensive during the main breeding season: 35 of the 36 (i.e. 97%) social groups determined during spring revealed permanent changes in female and/or male group composition since the previous winter. These changes were caused by a relatively high frequency of group members disappearing (due to mortality) or leaving their group, and a relatively smaller frequency of individuals joining other groups. To some extent, the movement of adults, leaving or joining other groups, paralleled the relatively high frequency of natal dispersal of female and male offspring known to occur from late spring through summer (Ebensperger *et al.* 2009; Quirici *et al.* 2011b). During a previous two-year study, we further reported how only 31% of degu social groups present during spring persist to the subsequent year in *O. degus* (Ebensperger *et al.* 2009). Persistence of groups is mostly the result of previous female offspring exhibiting natal philopatry, and secondarily, the result of adult females remaining in a group (Ebensperger *et al.* 2009). Collectively, these two studies indicate social groups of *O. degus* are variable in terms of group composition within the breeding season, and relatively short-lived across years.

This study on degu highlights how factors driving fitness effects of group living can be sex specific as shown recently in two other social species. For instance, males of

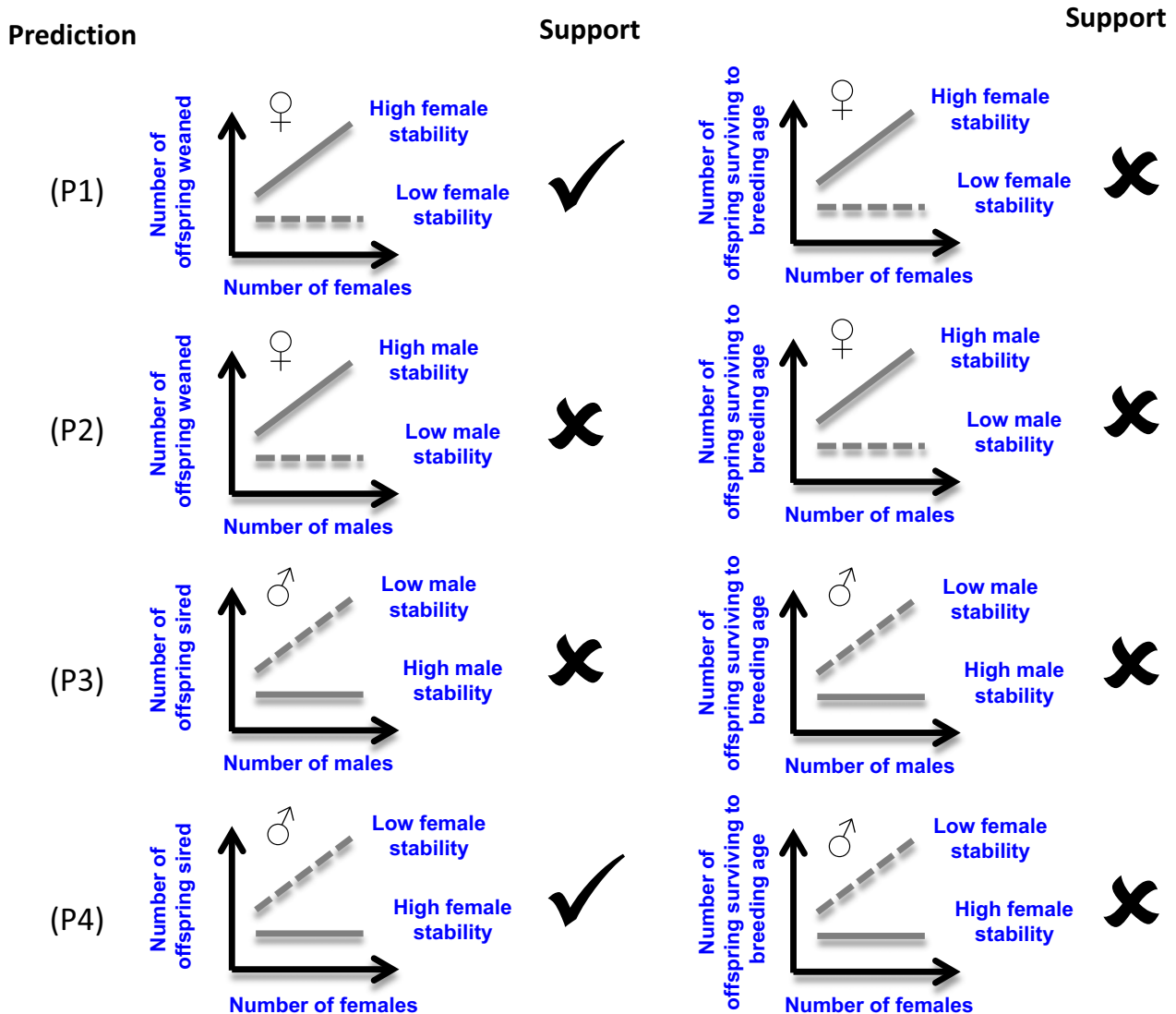


Fig. 3. Predicted modulating effects of social stability on the reproductive success of adult females and males (P1–P4). Reproductive success (model response) was quantified in females (♀) as (i) number of offspring weaned and number of offspring weaned that survived to breeding age, and in males (♂) as (i) number of offspring sired and (ii) number of offspring sired that survived to breeding. Check marks indicate support for the model predictions, whereas (✗) indicates lack of support.

the social and promiscuous fruit bat *Cynopterus sphinx* attain direct reproductive benefits, while females obtain both direct and possibly indirect kin benefits (Garg *et al.* 2015). Among rodents, the number of males in the group contributes the most to variation in Alpine marmot (*Marmota marmota*) male direct fitness, whereas the number of females contributed the most to variation in female direct fitness, implying social benefits are driven by the number of same-sex subordinates present in the group (Lardy *et al.* 2015). Our current study showed how group size dependent benefits are modulated differently in males and females by variation in social stability. In particular, increasing social stability was often beneficial to the fitness of females. However, decreasing social stability was generally fitness enhancing to the males. An intriguing, major implication of these patterns is the possibility of a sex conflict over immigration or emigration of male and female members

during breeding time. Our findings further revealed how the modulating role of social stability in group composition materializes mostly through winter group-size effects on the number of offspring produced. These results are supportive of the hypothesis that the reproductive success of female and male degus depends on social interactions in winter, when mating activity is at a peak.

EFFECTS OF STABILITY IN GROUP COMPOSITION: THE FEMALE PERSPECTIVE

We hypothesized that stability of group composition during the breeding season, a salient feature of degu social behaviour, modulates the effects of group size and that this modulating effect is sex specific. Given that degus exhibit cooperation in the form of communal rearing of offspring (Ebensperger, Veloso & Wallem 2002; Ebensperger *et al.*

2004; Jesseau, Holmes & Lee 2009), we expected female reproductive success to increase with the number of females (i.e. the number of caregivers) in groups experiencing higher stability in female group composition (P1, Fig. 3). Our results supported this prediction in terms of offspring weaned (Fig. 1a), but not offspring surviving to maturity. Together, these findings are consistent with the hypothesis that benefits of communal rearing in terms of offspring weaning are modulated by group stability and that changes in female group composition during winter (mating time) may interfere with efficiency of this cooperative behaviour, as implied previously (Champagne & Curley 2009; Cirulli *et al.* 2010). At least three factors may have contributed to a lack of modulation of stability at the time of offspring sexual maturation. First, this finding may represent a numerical effect due to the relatively low number of offspring surviving to breeding age in the study population. Secondly, offspring survival from weaning to reproductive age might be more affected by the size and short-term dynamics of foraging groups and group-size effects on predation risk (e.g. through social vigilance or dilution; Ebensperger & Wallem 2002). Alternatively, the modulating role of group stability at this life-history stage may affect offspring quality rather than quantity. Given the prominent role of social familiarity in influencing the nature of social interactions in degus (Jesseau, Holmes & Lee 2009; Villavicencio *et al.* 2009), subsequent studies are needed to determine how variation in the stability of group composition based on traits other than sex of adults might add to these reproductive effects on the females. For example, the loss of individual members exhibiting strong social bonds with other group members may have highly negative effects on the reproductive success of remaining group members (Silk, Alberts & Altmann 2003; Cameron, Setsaas & Linklater 2009). In the extreme, the loss of breeders in singular breeders, where breeding is monopolized within the group, may result in complete group dissolution (Borg *et al.* 2015). Similar effects due to a change in composition of breeding group membership are less likely in plurally breeding degus. Most adult degu females breed when reaching their first year of age (Ebensperger *et al.* 2013), implying that females within groups are less dependent on the breeding and/or parental effort of other members compared with the females of singularly breeding societies. However, reproductive success of female degus increases with equality (homogeneity) of social interaction in social networks (Wey *et al.* 2013), suggesting that changes in group composition altering this aspect of social environment may have further fitness consequences.

The role of other attributes of group composition in influencing the fitness modulatory role of social stability seems less important in degus. On the one hand, degus rarely survive beyond one year of age (Ebensperger *et al.* 2013). As a consequence, social groups typically are composed of similarly young breeding males and females, implying that age-linked changes in group composition are unlikely to differ considerably from those based on

sex composition examined here. Likewise, studies of two populations indicate degu groups lack kin structure (Quirici *et al.* 2011a; Davis *et al.* 2016), suggesting that changes in group composition affecting kin or non-kin would not result in fitness effects.

Contrary to prediction 2 (P2, Fig. 3), reproductive success of females did not increase with the number of males in groups experiencing high male stability in group composition. Instead, breeding females also weaned more offspring in winter groups with more breeding females that experienced increasing stability in male group composition (Fig. 2a). This observation further supported prediction 1 (P1, Fig. 3) and suggests that benefits of communal rearing to the females may be disrupted by previous changes in male group composition. Alternatively, social females that form stable associations with one or a few males may benefit from experiencing less sexual or other social harassment compared with females in groups where male composition changes frequently, as recorded in baboons, *Papio cynocephalus* (Nguyen *et al.* 2009). Stable relationships between females and single males in feral horses (*Equus caballus*) enhance female reproductive success, presumably through reducing male aggression directed towards females (Kaseda, Khalil & Ogawa 1995; Linklater *et al.* 1999). However, strong territoriality where males exclude non-group members from main burrows or areas of activity used by group members does not seem conspicuous in degus. Ongoing work indicates male and female degus mate multiply, including mating with non-group members. Thus, further studies are needed to examine how stability in male group composition influences polygyny and its potential effects on fertilization success. Taken together, our results indicate how stability in female and male group composition are important modulators of social benefits to the females, an effect that extends to the time of offspring weaning.

EFFECTS OF STABILITY IN GROUP COMPOSITION: THE MALE PERSPECTIVE

Contrary to prediction 3 (P3, Fig. 3), reproductive success of males did not change in groups with other males that were subjected to changes in male composition. In contrast, the number of offspring sired by the males increased with the number of females in winter social groups that experienced decreased stability in female group composition (Fig. 1b). Similar to the females, this effect did not extend to the number of weaned offspring that survived to breeding age. These findings are supportive of prediction 4, implying that mating opportunities of males are enhanced while in groups with an increasing number of females but facing low stability in female group composition (P4, Fig. 3). Further support of prediction 4 was provided by the observation that the number of offspring sired by the males increased with the number of females in groups subjected to changes in male composition (Fig. 2b). However, the mechanism explaining this additional effect to the males

remains unclear at this time. On the one hand, stable male–male familiarity (or partnership) early in the breeding season is not important for males to enhance mating opportunities under conditions of low male stability (Ryder *et al.* 2011; Wiszniewski *et al.* 2012). Possibly, changes in male group composition result in males losing paternity to incoming males when in multimale groups, but enhance paternity in multifemale groups. Currently, we are examining the extent to which offspring in communal litters are sired by multiple males from same and different social groups. Together, these results suggest modulation effects of stability in female and male group composition enhance reproductive success of males. Similar to the females, this social benefit extends to the time near offspring weaning.

SOCIAL STABILITY AND BENEFITS OF GROUP LIVING

Field-based studies on social birds and mammals have not shown consistent patterns in the effects of structural attributes of social groups (e.g. group size, number of females) on estimates of direct fitness (e.g. reproductive success, offspring survival; Cockburn 1998; Magrath 2001; Ebensperger, Rivera & Hayes 2012). These differential effects are explained in part by differences in major strategies of cooperation during breeding and by temporal and spatial variation in ecological conditions (Rubenstein 2011; Ebensperger, Rivera & Hayes 2012; Ebensperger *et al.* 2014). However, how factors intrinsic to the social groups other than group size contribute to these patterns had remained less clear. Results from this field study supported the hypothesis that social stability based on permanent changes in male and female group composition modulates the fitness effect of group size of a communal rearing species in sex-specific ways. Intriguingly, a recent field study revealed how one of the fitness components (i.e. the number of breeding events through lifetime) decreases similarly in male and female Alpine marmots with decreasing social stability (Lardy *et al.* 2015). While further examination on the modulating role of social stability is required in these marmots, our study and that of Lardy and colleagues support the possibility that social stability modifies fitness effects of group size in both singular and plural breeding species. Further studies are needed to examine how group stability modulates the fitness effects of other social attributes, including fitness effects of social status within the group or the propensity to cooperate with other group members. In a context of current climatic changes, a particularly relevant question to tackle is how the modulating role of social stability is in turn dependent on variation in ecological conditions. Reproductive success in female degus increases in larger social groups, but mostly during years with lower mean precipitation, lower mean food abundance and lower mean degu density (Ebensperger *et al.* 2014). The possibility that these long-term fitness effects are mediated through variation in group stability remains to be addressed.

Ethical standards

All observations and experiments carried out during this study complied with the current laws of Chile. This study was approved by the Institutional Animal Use and Care Committee at the Facultad de Ciencias Biológicas (DFCB-021/2008 and CBB-229/2012) and received the required authorization to live trap wild degus by the Servicio Agrícola y Ganadero (1-31/2009 [1956] and 2826/2013).

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Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.fh517> (Ebensperger *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Number of burrow systems, number of days that each burrow system was trapped, number of radiocollared degus, and mean ($\pm$ SD) number of night time telemetry locations per radiocollared degu during each season (winter, spring) and year of study (2009–2013) at Rinconada de Maipú.

Table S2. Total number of social groups and male and female group members monitored during winter and spring of each year.

Table S3. Means, standard deviation, and minimum number of degu captures recorded during each year and season.

Table S4. Total number ($n = 1006$) of genotyped adult and offspring degus (2009–2013).

Table S5. Sequence, annealing temperature (T_a), size, and number of alleles of 12 microsatellite loci used to genotype degu adults and offspring.

Table S6. Analysis of Hardy-Weinberg expectations for each locus within each study year (2009–2013).

Table S7. Number of genotyped offspring assigned to a candidate mother and father, assigned to a candidate mother only, assigned to a candidate father only, and unassigned (2009–2013).

Figure S1. Histograms of the number of offspring sired by each male (a) and weaned by each female (c).

Data S1. Data set used during statistical analyses.