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Fitness consequences of variation in social group size are not population-specific but are associated with access to food in the communally breeding rodent, *Octodon degus*

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Abstract

Studies that concurrently investigate the functional benefits of group living in multiple populations of the same species are rare. Over a 3-year period (2014–2016), we examined two ecologically contrasting populations to test multiple hypotheses for the adaptive significance of group living in the communally breeding rodent *Octodon degus*. We quantified the size of social units (number of adults, number of adult females), edible vegetation at burrow systems, and per capita offspring weaned (PCOW) in each population. Contrary to expectations, we did not observe population-specific associations between group size and edible vegetation or PCOW nor universal benefits of group living. In one population, PCOW increased in mid-sized groups with more edible vegetation. However, this trend was not consistent across years. Notably, we observed a complete reproductive failure in one population during the first year of study, one that was characterized by low rainfall and no detectable edible vegetation. This result is important because reproductive failure occurred regardless of group size, suggesting that communal living may not buffer degus against the harshest of environmental conditions. Examining how social organization shapes individual reproductive success under extreme variation in food availability is an important step towards understanding how populations will respond to a changing climate.

KEYWORDS
group size, harsh environment, *Octodon degus*, reproductive success, sociality

1 | INTRODUCTION

The costs and benefits of group living can result from a combination of group size effects linked to the costs and benefits experienced from the presence of other individuals and cooperation (i.e., interactions of individuals acting together to attain mutual benefits) (Alexander, 1974; Krause & Ruxton, 2002). Beneficial group size effects include decreased predation risk by enhanced collective vigilance ('many eyes hypothesis', Powell, 1974) or dilution or risk (Ebensperger, 2001; Roberts, 1996) and collective defense of resources (Wrangham, 1980). Cooperative interactions among group members, such as social foraging (Beauchamp, 2005; Creel & Creel, 1995), allogrooming (Henazi & Barrett, 1999), huddling (Gilbert et al., 2010), coordinated digging of burrows (Ebensperger & Bozinovic, 2000), and communal care of offspring (Hayes, 2000) may contribute to increased survival and reproductive success (Erb & Porter, 2017; Smith et al., 2017). In species in which inter-group competition is high, individuals in highly cooperative groups may win contests for resources with individuals in neighboring or competitor groups (Koenig, 2002). Individuals are expected to maintain interactions with an increasing number of group members until the costs outweigh the benefits (Sueur et al., 2011). Fitness may be maximized in intermediate-sized groups (Chapman & Valenta, 2015; Lardy et al., 2015; Markham et al., 2015; Pride, 2005). If groups become too large, group living may result in net costs to group members through increased visibility to predators (Ioannou et al., 2009), enhanced exposure to pathogenic parasites (Hoogland, 1979) and within-group scramble or contest competition (Chapman et al., 1995; Koenig, 2002; Markham et al., 2015; Snaith & Chapman, 2007), and reproductive suppression (Alexander, 1974; Krause & Ruxton, 2002; Silk, 2007a, 2007b).

Populations in different regions within a species geographical range may experience different ecological conditions. Consequently, the costs and benefits of group living are likely population- or habitat-specific (Silk, 2007a, 2007b). Only a few studies on social mammals have examined how social unit size influences reproductive success in different populations and the conclusions have not been consistent (Clutton-Brock et al., 1999; Harrington et al., 1983; Solomon & Keane, 2018). Harrington et al. (1983) determined that litter size and pack size were inversely related and that pairs produced more surviving pups than did larger packs in a wolf (*Canis lupus*) population experiencing low prey abundance. In contrast, litter size and pack size were positively correlated in a population in which prey were relatively abundant. Clutton-Brock et al. (1999) observed that juvenile mortality was higher in small than in large meerkat (*Suricata suricatta*) groups in a national park (where predation risk was high), but lower in small groups than in large groups in a ranchland (where predation risk was low). In the same study, adult mortality declined in larger groups in both sites (Clutton-Brock et al., 1999). Solomon and Keane (2018) observed that social units were larger, and the proportion of prairie vole (*Microtus ochrograster*) social units that were groups was greater in an Indiana population compared to a population in Kansas. However, there were no measurable effects of the number of adult females per social unit on direct fitness in either population of prairie voles (Solomon & Keane, 2018). Species examined in this context are primarily cooperative breeders, meaning that non-breeding adults help raise the offspring of a few breeders in the group. To date, no one has examined group size-reproductive success relationships in multiple populations of a species that is predominantly a communal breeder where multiple females breed within each group.

The degu (*Octodon degus*) is a communally breeding rodent endemic to central-north Chile. Adults live in social units of varying size and adult sex composition, but most commonly multi-female groups with and without males (~60% of social units; (Hayes et al., 2009; Hayes et al., 2019). Individuals in groups share multiple burrow systems (visualized as interconnected burrow openings from aboveground), which provide refuge from predators and places to rear offspring. Although group membership changes between the periods of mating (May–July) and offspring care (Sept-Nov), group composition within the period of offspring care (the period of observation in this study) is stable (Ebensperger et al., 2016, 2019). During the daytime, degus forage in groups that may consist of members of their social group as well as other individuals from different social groups (Ebensperger & Wallem, 2002). Current field studies are quantifying the kinds of social interactions that occur between members of different social units. Degus are prey to numerous predators including foxes and several birds of prey (Ebensperger et al., 2002; Ebensperger et al., 2006). Group-size benefits of group living include reduced predation risk (Ebensperger & Wallem, 2002), reduced energetic costs due to huddling (Nuñez-Villegas et al., 2014) and reduced per capita digging costs (Ebensperger & Bozinovic, 2000). Although we know that social foraging enhances time spent feeding (Ebensperger et al., 2006), we do not know the extent to which social group size enhances access to or increases collective defense of food resources near burrow systems. Females communally rear offspring (Ebensperger et al., 2002) and the number of adult females per social unit is a predictor of the potential for communal care (Ebensperger et al., 2014). Degu groups lack kin structure in two populations (Davis et al., 2016; Quirici et al., 2011) and under laboratory conditions, reproductive success of communally rearing sisters is not different from that of unrelated females (Ebensperger et al., 2007). Thus, to maximize inclusive fitness, females should engage in strategies that maximize direct fitness.

Our understanding of the fitness consequences of group living is informed by a long-term study (>15 years) of degus in one population in central-north Chile (Ebensperger et al., 2014; Hayes et al., 2019). An emergent theme from this long-term study is that socioecological conditions influence the reproductive consequences of group living in complex ways. The relationship between social unit size and direct fitness of females is influenced by the composition and stability of social units (Correa et al., 2021; Ebensperger et al., 2016, 2019; Hayes et al., 2019) as well as rainfall, population density, and food availability (Ebensperger et al., 2014). Evidence that per capita offspring weaned (PCOW) increases with increasing number of adult females per social unit years when mean food abundance at burrow systems during the austral spring is low (Ebensperger et al., 2014) supports the hypothesis that communal breeding is most advantageous when mean ecological conditions are harsh. Although we know that social unit composition varies within and between populations (Ebensperger et al., 2012; Hayes et al., 2019; Sobrero et al., 2016), we do not know if the reproductive consequences of group living differ between populations experiencing different socio-ecological conditions.

The aim of this study was to determine if the costs and benefits of group living are contingent upon local environmental conditions in a communal breeder. Since group-living is common in degus, we focused on how variation in group size influences fitness. Previous studies on degus revealed linear fitness relationships (Ebensperger et al., 2014; Hayes et al., 2009; Hayes et al., 2019). Thus, we did not anticipate nor predict non-linear relationships indicating optimal group sizes. Over a three-year period, we quantified relationships between social unit size and (i) abundance of food at burrow systems and (ii) per capita reproductive success (PCOW) of adult females in two degu populations characterized by different ecological conditions in Chile. Using linear mixed models (LMM) to control for year and population effects, we tested five hypotheses for the costs and benefits of group living (Table 1). We tested the hypothesis that regardless of local food abundance, group living enhances access to or defense of food (H1) or result in depleted resources (H2). Group living could enhance fitness in multiple ways. Females may experience increased fitness in large groups, including both adult males and females, because of group-size effects (e.g., increased access to food) or cooperation (e.g., cooperation defense of food) (H3). Females living in large multi-female groups may benefit from communal care, which could enhance the number of offspring that females successfully wean (H4). Based on arguments that (i) group living may have evolved in harsh environments in birds (Jetz & Rubenstein, 2011) and mammals (Firman et al., 2020) and (ii) PCOW is positively associated with group size during harsh years in one degu population (Ebensperger et al., 2014), we also tested the hypotheses that group living enhances access or defense of resources (H5) or communal offspring care (H6) in the harshest environments or years. Predictions for these hypotheses are presented in Table 1. Given the relatively small range in group sizes, we did not expect benefits to be greatest in intermediate group sizes as one might expect in species that live in larger groups (Chapman & Valenta, 2015).

2 | METHODS

2.1 | Study populations

This study was conducted in two degu populations in Chile over a 3-year period (2014–2016): (i) Estación Experimental Germán Greve Silva (33°23′S, 70°31′W; EEGGS) and (ii) Parque Nacional Bosque Fray Jorge (30°38′S, 71°40′W; PNBFJ). EEGGS is a semi-arid site approximately 30 km west of Santiago (central Chile) with a mean monthly rainfall of 12.6, 15.0, and 18.2 mm in 2014, 2015 and 2016, respectively. The landscape at EEGGS is a mix of open savanna with very limited shrub cover and uniformly distributed herbs and forbs, a primary food source for degus (Meserve & Martin, 1983; Quirici et al., 2010). These conditions might favor increased within-group scramble competition and thus, decreasing

TABLE 1 Levels of support for hypotheses and predictions tested in this study.

Hypothesis	Prediction(s)	Model	Level of support
Group living enhances access to or defense of food (H1)	(i) a positive association between the biomass of edible vegetation and total number of adults per social unit, (ii) a positive association between per capita offspring weaned and the biomass of edible vegetation, and (iii) no random effect of population.	1, 2	No random population effect
Large groups deplete food resources (H2)	(iv) negative association between the biomass of edible vegetation and the total number of adults per social unit, (v) a negative association between per capita offspring and the total number of adults per social unit, and (vi) no random effect of population.	1	No random population effect
Fitness is enhanced by large group size (H3)	(vii) positive association between per capita offspring and number of adults per social unit and (viii) no random effect of population.	2	No random effect of population
Fitness is maximized by communal care by females (H4)	(ix) positive association between per capita offspring and total number of adult females per social unit and (x) no random effect of population.	3	No random effect of population
Group living enhances access or defense of resources when conditions are harsh (H5)	(xi) biomass of edible vegetation increases with increasing number of adults or adult females in years and populations with lowest biomass of edible vegetation, and (xii) random effect of year or population.	2, 3	Random effect of year
Communal care helps overcome costs of offspring rearing in harsh environments (H6)	(xiii) per capita offspring is greatest in social units in which the biomass of edible vegetation increases with increasing number of adults or adult females (interaction) and (xiv) random effect of year or population.	3	Random effect of year

benefits of large social group size (Koenig, 2002) but not foraging group sizes (Ebensperger et al., 2006). PNBFJ is a semi-arid site approximately 400 km northwest of Santiago (northcentral Chile) with strong inter-annual variation in rainfall (Armas et al., 2016; Previtali et al., 2010) and a mean monthly rainfall of 3.8, 13.3, and 10.2 mm in 2014, 2015 and 2016, respectively. PNBFJ is a predominantly cactus and shrubland plant community interspersed with herbaceous ground cover and bare, sandy areas, and where shrubs provide a potential secondary source of food (Meserve et al., 1984). These conditions might favor increasing benefits of large group sizes if degus from different groups compete for resources (Koenig, 2002). Overall, based on these ecological differences in rainfall and edible ground vegetation, we consider the environmental conditions at PNBFJ to be harsher for reproduction than conditions at EEGGS.

2.2 | Data collection

In all 3 years of the study, we quantified relationships between social unit size (number of adult females, number of adults), biomass of edible vegetation at burrow systems used by social units, and per capita number of offspring weaned (PCOW (Ebensperger et al., 2014). Two teams conducted concurrent studies with coordinated methods at each site, accounting for the differences in the timing of degu pregnancy and offspring production between sites (PNBFJ: September–November; EEGGS: August–November). We used a combination of live-trapping and radiotelemetry to collect data needed to determine social group membership.

2.3 | Live trapping

Between August and early November (period of late pregnancy, lactation), burrow systems were trapped for 59–68 days per year in EEEGS and 35–62 days per year in PNBFJ. Methods of burrow trapping were similar in both sites. Eight to ten Tomahawk live-traps (model 201, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) and locally produced traps (similar to Sherman live traps [H. B. Sherman Traps, Inc., Tallahassee, FL] in design) were set in the early morning before sunrise (06:00–07:00). The traps were left open for 1–2 h after sunrise, allowing us to capture animals as they emerged from underground burrows. We recorded the location, identity, sex, body mass of all individuals, and the reproductive condition of females (pregnant or lactating). Each degu was identified with unique ear tags (Monel 1005-1, National Band and Tag Co., Newport, KY) on each ear at first capture. Each year, trapping ended when less than 5% of captured offspring were new individuals. Regarding STRANGE framework (Webster & Rutz, 2020), the use of multiple trap types (Burger et al., 2009) in both sites likely minimized sampling bias. The work in EEGGS was part of a long-term study. Thus, it is possible that degus in EEGGS were more acclimated to us than in PNBFJ.

2.4 | Radiotelemetry

Night-time telemetry was used to track individuals to burrow systems used exclusively (solitary social organization) or shared with members of a given social unit, which could include pairs or groups of varying size and adult composition. Individuals weighing more than 110 g were fitted with 5 g radiocollars (BD-2C; Holohil Systems Limited, Carp, Ontario, Canada) and individuals weighing more than 150 g were fitted with 7 g radiocollars (PD-2C; Holohil Systems Limited, Carp, Ontario, Canada) with unique frequencies. During September and October at EEGGS, and September, October and November in Fray Jorge (depending on the year), radio-collared degus were tracked to their burrow system once per night approximately 1 h before sunrise or 1 h after sunset using an FM-100 receiver (for transmitters tuned to 164.00–164.999 MHz frequency; Advanced Telemetry Systems, Isanti, MN, USA) and a hand-held three element Yagi antenna (AVM instrument Co., or Advanced Telemetry Systems). We tracked radiocollared degus for 22.4 ± 1.0 (mean ± SE) nights and 20.9 ± .6 nights at EEGGS in 2014 and 2015, respectively. We tracked degus for 18 ± 0 nights and 20.2 ± 1.5 nights at PNBFJ in 2014 and 2015, respectively. In 2016, we tracked radiocollared degus for 18.9 ± .5 nights at EEGGS and 35 ± 2.1 days at PNBFJ. Radiocollars do not negatively impact the survival and reproductive success of adult degus (Ebensperger et al., 2021).

2.5 | Social unit identification

Social units occupy multiple burrow systems (i.e., the area encompassing multiple burrow openings in which degus overlap during the night-time). The main criterion used to assign adult degus to social units (solitary, male–female pairs, groups of varying size and composition) was the sharing of burrow systems during the period of late pregnancy and lactation (August–October) (Ebensperger et al., 2014). We used a combination of live-trapping at burrow systems and radio-tracking of adults to burrow systems prior to emergence in the early morning to identify adults sharing the same burrow system. Previous work confirmed that degus do not move between burrow systems during the night-time (Ebensperger et al., 2004). Thus, each night represents a single data point and multiple nights of overlap are needed to assign individuals to social units. The composition of groups changes between seasons and years, in part due to high mortality rates of adults and social instability between seasons (Ebensperger et al., 2011, 2016; Hayes et al., 2009). However, social unit membership is stable during the period of late pregnancy/early lactation (Ebensperger et al., 2016). Thus, it is appropriate to index social unit membership based on sampling within a season as we have done here. Details of how we determined social unit membership are described in Figure S1.

2.6 | Ecological sampling

During the austral winter, degu ranges overlap areas with abundant herbs (Quirici et al., 2010), a low fiber food and preferred dietary component (Bozinovic, 1995). We used the abundance of food at burrow systems as an index of food availability. We quantified the abundance of edible vegetation on the ground (herbs, forbs) at burrow systems by placing a 250×250mm quadrat on the ground at three meters and nine meters from a burrow system in one of the cardinal directions, randomly selected for each distance at each burrow system. All green herbs in the quadrant were removed and immediately stored in 2kg paper bags. We oven-dried each sample at 60°C for 72h to determine its dry biomass of edible vegetation on the ground available to degus. Following Hayes et al., 2007, we averaged the sampling points from three meters and nine meters and standardized to grams per square meter. Measurements at these distances gave us information about food abundance in areas in which degus likely feed initially upon emergence. Degus in the same social unit often use multiple burrow systems. Thus, for all individuals in both populations, we calculated a weighted average of biomass of food on the ground based on the different values of biomass of food at burrow systems and the number of times individuals were caught in these burrow systems. Based on these values, we calculated the per capita biomass of food on the ground available to all members of social units.

2.7 | Reproductive success

The number of offspring weaned by social units was determined by quantifying the number of offspring captured for the first time at active burrow systems used by a social unit between September and November (Hayes et al., 2009). Subsequently, the per capita number of offspring weaned (PCOW) was determined by dividing the number of offspring captured at burrow systems by the number of adult females known to live in the social unit using these same burrow systems (Ebensperger et al., 2014). This index relies on two assumptions: (i) first captures of offspring reflect the burrow systems in which they were born or raised before weaning and (ii) direct fitness is shared equally among all females in the same social unit. This index has been used as a measure of direct fitness used in previous studies on degus e.g., (Hayes et al., 2009) and correlates positively with estimates based on maternity analyses ($r^2 = .51$, $p < .0001$; Figure S2; Ebensperger LA. & Hayes, LD, unpublished data).

2.8 | Statistical analysis

We conducted our statistical analyses based on 96 social units. We developed three distinct mixed linear regression models (LMM) to test hypotheses in Table 1. The first LMM was used to test the hypotheses that the abundance of food at burrow systems (ground_food) increases (hypothesis 1) or decreases (hypothesis 2) with total group size (Model 1: Ground_food = Population + Year + TGS). In the event of a random year or population effect, we could evaluate if large group size increases access to or defense of food under harsh conditions (hypothesis 4). The second LMM model tested the hypothesis that per capita offspring weaned (PCOW) was influenced by the number of adults per social unit (TGS) and abundance of food on the ground (both fixed factors, with year and populations considered as random effects (Model 2: PCOW = Population + Year + ground_food + TGS + ground_food*TGS). The third model tested the hypothesis that per capita offspring weaned (PCOW) was influenced by the number of adults females per social unit with year and populations considered as random effects (Model 3: PCOW = Population + Year + ground_food + FGS + ground_food*FGS). The interaction between ground_food and FGS or TGS was included in models 2 and 3, respectively, to test for context-text dependent benefits of living in groups (Ebensperger et al., 2014).

We used the restricted maximum likelihood method (REML) to test the effects of fixed factors, utilizing the "lmer" function from the R package "lme4". To balance model complexity and goodness-of-fit, we used AIC (Akaike Information Criterion) as a criterion for model comparison. Additionally, the impact of random factors was assessed through Likelihood Ratio Tests (LRT tests), comparing models with and without random effects. All statistical analyses were carried out in R version 4.3.1, and a $p < .05$ was considered statistically significant. R code for all three models is in Appendix S1.

3 | RESULTS

3.1 | Descriptive data and tests of random effects

Across years, social units consisted of 2.0 ± .11 (mean, SEM) adult females and 3.1 ± .16 adults. Annual differences in the size and adult sex composition of social units in EEGGS and PNBFJ are shown in Figure 1. The number of adult females per social unit was greater in EEGGS than PNBFJ (2-way ANOVA: $F_{1,90} = 4.20$, $p = .04$), but did not vary between years (2-way ANOVA: $F_{2,90} = .41$, $p = .66$). There was not a statistically significant interaction between population and year (2-way ANOVA: $F_{2,90} = 1.73$, $p = .18$). There was a statistically significant interaction between year and population on total number of adults per social unit (2-way ANOVA: $F_{2,90} = 3.30$, $p = .04$). Post-hoc Tukey's tests indicated that total group sizes in EEGGS were greater than total group sizes in PBNFJ in 2015 (difference = 2.2, $p = .003$) and 2016 (difference = 1.6, $p = .02$).

The biomass of edible vegetation at each site is summarized in Table 2. At PNBFJ, there was no edible vegetation on the ground in 2014 and edible vegetation increased to the highest level of both populations in 2016. In contrast, edible vegetation on the ground at EEGGS decreased annually between 2014 and 2016. In terms of edible vegetation, the models that included the random effect

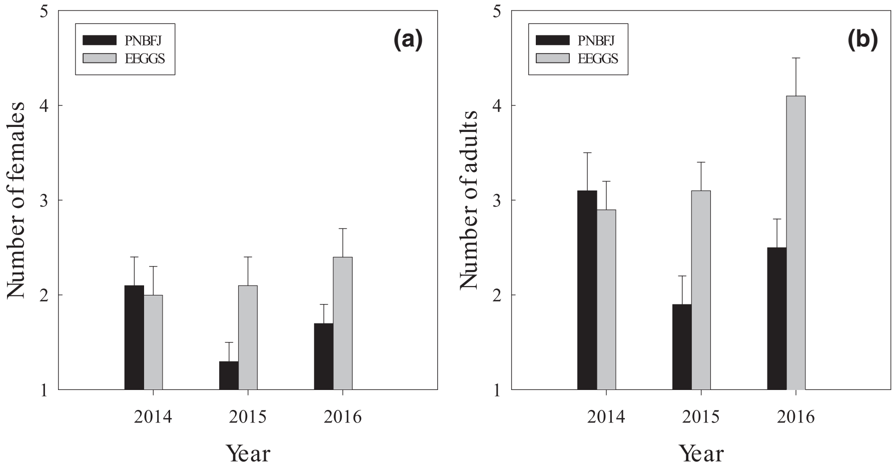

FIGURE 1 Mean (SE) number of adult females (a) and total number of adults (b) in social units in the two study sites, separated by year.

TABLE 2 Biomass of edible vegetation on the ground at PNBFJ and EEGGS.

Population	Year	Biomass of edible vegetation (mean ± SE, g)
PNBFJ	2014	.0 ± .0
	2015	53.5 ± 12.8
	2016	184.9 ± 49.3
EEGGS	2014	140.4 ± 10.9
	2015	115.7 ± 9.9
	2016	99.7 ± 12.0

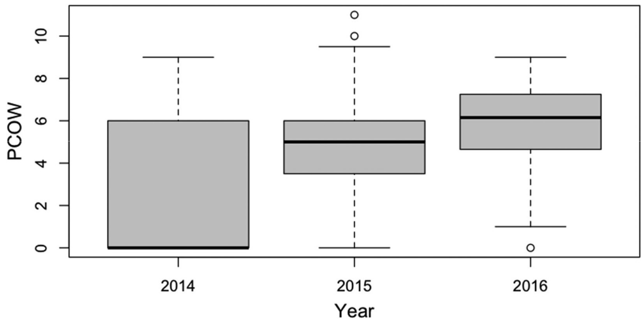

FIGURE 2 Box plot showing distribution of per capita offspring weaned (PCOW) by year for the two study sites combined. Visually, PCOW is lowest in 2014 due to the lack of offspring production at Parque Nacional Bosque Fray Jorge (PNBFJ). There was a statistically significant random effect of year in models 2 and 3, indicating that fixed effects should be evaluated within each year. The total number of social units examined across both study sites were 29 in 2014, 31 in 2015, and 36 in 2016.

of population or year did not yield different results compared with the models without such effects (Table S1), indicating these effects were not important (AIC = 1179 without random effect; AIC = 1181, $p=.9999$ with population as random effect; AIC = 1179.6, $p=.2374$ with year as random effect).

PCOW varied from 0 to 11 offspring per female, with no successful breeding in PNBFJ in 2014 and two unsuccessful units in PNBFJ in 2015. In both models 2 and 3, there was a statistically significant random year effect on PCOW (Table S1; Figure 2). Thus, any fixed effects in these models were assessed separately within years. There was not a statistically significant population effect in models 2 (AIC = 468 without random effect; AIC = 470, $p=.9999$ with population as random effect) and model 3 (AIC = 474 without random effect; AIC = 475, $p=.9999$ with population as random effect), implying that PCOW did not differ significantly between populations (Table S1).

3.2 | Tests of fixed effects

In model 1, there was not a statistically significant association between the biomass of edible vegetation and the number of adults per social unit (estimate = −6.73; $p=.36$). In model 2, there were negative associations between PCOW and the total number of adults per social unit (estimate = −1.10, $p=.002$) and the biomass of edible vegetation (estimate = −.01, $p=.02$). However, there was a statistically significant interaction between biomass of edible vegetation and the total number of adults per social unit (estimate = .008, $p=.001$; Figure 3). Comparisons were separated by year because of the statistically significant random effect of this factor (Figure 2). Visual inspection of Figure 3 indicated that (i) PCOW was generally greater in mid-sized groups (3–5 adults) with increasing biomass of edible vegetation and (ii) this trend was most clear in 2014 and 2015. Since no females bred in PNBFJ in 2014, this relationship was observed in EEGGS, only. This relationship was less apparent in pairs ($n=2$ adults) or groups exceeding 5 adults. There were not enough groups with 6–8 adults ($n=3$) to assess relationships within each year. Solitary individuals with more edible vegetation tended to have lower fitness across years.

In model 3, there were negative associations between PCOW and the number of adult females per social unit (estimate = −1.13, $p=.009$), but not between PCOW and the biomass of edible vegetation on the ground (estimate = −.005, $p=.29$). However, there was a statistically significant interaction between the biomass of edible vegetation and the number of adult females per social unit (estimate = .007, $p=.03$; Figure 4). Comparisons were separated by year because of the statistically significant random year effect (Figure 4). Visual inspection of

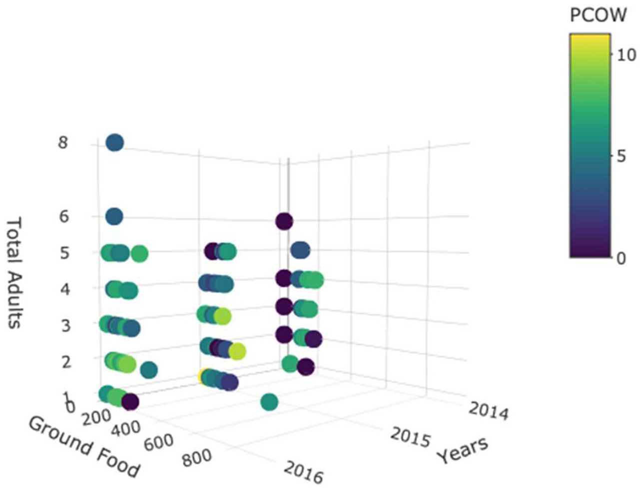

FIGURE 3 Per capita offspring weaned (PCOW) by females (for the two study sites combined) as a function of the interaction between biomass of edible vegetation (ground food, g/m^2) and the total number of adults per social unit, split by the random effect of year. On the color scale, high PCOW is indicated by green-yellow and low PCOW is indicated by dark blue-purple tones. The outlier point (>800 food) is a unit of two adults in 2016. Guidance for interpreting 3-D figures and supplemental 2-D figures are provided in Appendix S1.

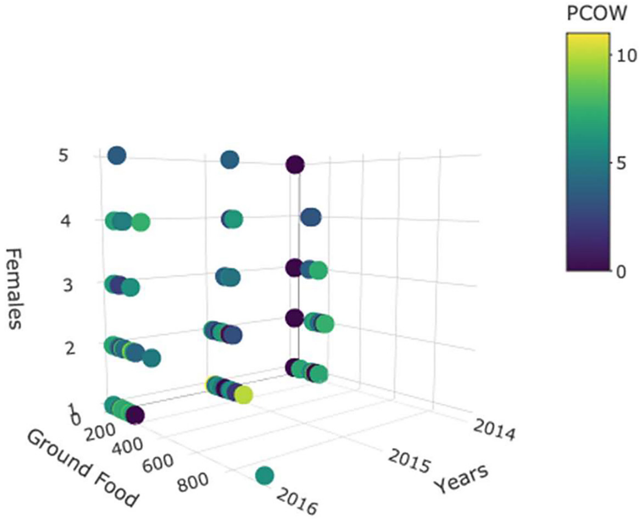

FIGURE 4 Per capita offspring weaned (PCOW) of females (for the two study sites combined) as a function of the interaction between biomass of edible vegetation (ground food, g/m^2) and the total number of females per social unit (Number of females), split by the random effect of year. On the color scale, high PCOW is indicated by green-yellow and low PCOW is indicated by dark blue-purple tones. The outlier point (>800 food) is a single female in 2016. Guidance for interpreting 3-D figures and supplemental 2-D figures are provided in Appendix S1.

Figure 4 indicated that PCOW was generally greater in social units with 1–3 adult females with increasing biomass of edible vegetation in 2014 and possibly in social units of 2 females with increasing biomass of edible vegetation in 2015. Since no females bred in PNBFJ in 2014, this relationship was observed in EEGGS, only. There were not enough groups with 5 females ($n=3$) to assess relationships within each year.

4 | DISCUSSION

4.1 | Summary of results and state of hypotheses

Our observation that the abundance of edible vegetation near burrow systems was not associated with the number of adults per social unit did not support the hypotheses that group living universally enhances access to or defense of food resources (hypothesis 1) nor that large groups deplete food resources (hypothesis 2). Although there was no random effect of population, we did not observe a positive association between PCOW and the number of adults or adult females, suggesting that group living and communal care do not enhance fitness regardless of environmental conditions (hypotheses 3 and 4). We also did not find the expected positive trends and population random effects in models examining PCOW and the number of adults and number of adult females per social unit, respectively. Thus, our study did not support the hypotheses that group living either enhances access or defense of food resources when conditions are harsh (hypothesis 5) or that communal care is most beneficial under harsh conditions (hypothesis 6; Ebensperger et al., 2014). The observed interactions in Figures 3 and 4 suggest that the benefits of group living are greatest in mid-sized groups in some years, suggesting a potential balance between social costs and benefits of group living. This observation supports similar reports of optimal group sizes in other social mammals (Lardy et al., 2015; Markham et al., 2015).

4.2 | Context-specific benefits and costs

Adults in mid-sized groups that had more edible vegetation on the ground near their burrow systems had the greatest per capita reproductive success in 2 of 3 years of study. On the surface, these suggests an important benefit of optimal groups sizes and is consistent with evidence of optimal group sizes in some social birds (Williams et al., 2003) and mammals (Lardy et al., 2015; Markham et al., 2015; VanderWaal et al., 2009). Females in mid-sized groups with the most food may have experienced reduced intragroup competition for resources (Hintz & Lonzarich, 2018; Terborgh & Janson, 1986), foraging costs (Stevenson & Castellanos, 2001), or lower overall physiological costs (Markham et al., 2015; Pride, 2005) than adults in other social units. Evidence of a random year effect, but not a random population effect, suggests that these benefits are dependent on annual environmental conditions but do not vary between populations.

Overall, the observed patterns need to be interpreted with caution for several reasons. First, our measures of social unit size and food abundance were based on data collected at burrow systems in which degus overlap during the nighttime (Hayes et al., 2009). Degu ranges overlap areas of herbs during the winter (Quirici et al., 2010).

Thus, food abundance at burrow systems is a reasonable index for our purposes. However, the size of daytime foraging groups may have a greater impact on how much degus eat (Ebensperger et al., 2006). Future work needs to examine how both components of degu social organization – social groups based on nighttime associations vs. daytime foraging groups – independently or interactively influence food availability and reproductive success of degus. Second, due to small sample sizes and random year effects, it is difficult to make definitive conclusions about the significance of our observation. Large groups were rare, precluding us from examining potential optimal group size effects. Finally, Figures 3 and 4 suggest that solitary females with the most edible vegetation have relatively low reproductive success (excluding the outlier point) in 2016, possibly because they must spend more time foraging to consume additional food and sustain lactation. A similar trend was detected in 2015 in Figure 3 (total group size) but not in Figure 4 (only females), even though the same females are represented in both figures. This difference might be due to the negative influence of males on females (Hayes et al., 2019). Ultimately, understanding these effects may require long-term datasets.

4.3 | Does group living buffer against harsh conditions?

Research on numerous social animals, including our previous study of degus in EEGGS (Ebensperger et al., 2014), suggests that group living is most advantageous in harsh environments (Griesser et al., 2017; Komdeur & Ma, 2021; Rubenstein, 2011; Shen et al., 2017). Some have argued that these trends support the hypothesis that group living evolved to buffer breeders against harsh or unpredictable environmental conditions (Jetz & Rubenstein, 2011). However, recent studies of several cooperatively breeding birds and mammals suggest that this potential benefit is limited under very harsh conditions associated with climate change (birds: Borger et al., 2023; Bourne et al., 2020b; D'amelio et al., 2022; mammals: Rabaiotti et al., 2023) but see (Van de Ven et al., 2020). For example, in pied babblers (*Turdoides bicolor*), hot and drought conditions are associated with reduced incubation by non-breeders (Bourne et al., 2023) and reduced juvenile growth, adult body mass, and inter-annual survival, regardless of group size (Bourne et al., 2020b). Similarly, helpers seem unable to mitigate the negative effects of dry and hot weather on nestling mortality in social weavers (*Philetairus socius*) (D'amelio et al., 2022) and on the number of offspring produced per breeding group in Seychelles warblers (*Acrocephalus sechellensis*) (Borger et al., 2023). Mathematical simulations of cooperatively breeding African wild dog (*Lycaon pictus*) population dynamics predict that extinctions are associated with high temperatures, likely due to low offspring survival and reduced group augmentation (Rabaiotti et al., 2023).

Findings from our current study suggest that communal breeding may be unable to buffer degus against the harshest conditions associated with a changing climate. The reproductive failure in PNBFJ in 2014, an unexpected event given the effectively semelparous breeding strategy of degus (Ebensperger et al., 2013), occurred in a year with negligible rainfall and no detectable, edible vegetation on the ground (Table 2). We observed degus eating vegetation on shrubs and cactus blossoms that had fallen to the ground. Although degus are known to consume shrub leaves in PNBFJ, they generally consume a relatively high percentage of forbs during the austral spring, a period that corresponds with peak breeding (Meserve et al., 1984; Meserve & Martin, 1983). A complete shift to a diet consisting of shrubs exhibiting a higher fiber content may have had digestive costs (Veloso & Bozinovic, 1993). Therefore, we hypothesize that females likely did not assimilate sufficient energy to support the relatively high costs of reproduction (Bozinovic et al., 2004) and the initially high energetic content of milk their precocial offspring require (Veloso & Kenagy, 2005). Although females in PNBFJ compensated reproductively in 2015 and 2016 (see also Bourne et al., 2020a) the ongoing mega-drought in Chile (Garreaud et al., 2020) threatens the resilience of degu populations across Chile, regardless of social strategies. After this study, we observed a population crash in EEGGs in 2020. Preliminary analyses suggest that this crash was associated with a combination of high ambient temperature and low rainfall.

4.4 | Conclusions

The results of our study suggest that degu females could benefit from being in mid-sized groups, but that there are not population-specific benefits of group living. These findings do not support habitat-specific levels of cooperation and reciprocity. Understanding how group living affects fitness likely requires examinations of multiple components of the social system, including group size and social structure (Kappeler, 2019). Our observations of reproductive failure in one population add to a growing body of literature suggesting that social living may have a limited capacity to buffer individuals against the harshest environmental conditions associated with a changing climate. Long-term studies on social animals that examine yearly and population-specific patterns in group size, social interactions, resources, and reproductive success are needed to build theory on the resilience of social animals in a changing world. Following STRANGE recommendations (Webster & Rutz, 2020), we acknowledge that potential bias in our results may arise from the fact that degus in EEGGs, but not PBNFJ, were studied prior to this study.

AUTHOR CONTRIBUTIONS

Loren D. Hayes: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; project administration; supervision; resources. **Madeline K. Strom:** Investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; formal analysis; data curation. **Cecilia León:** Investigation; data curation; methodology; software. **Juan Ramírez-Estrada:** Investigation; methodology; software; data curation. **Sara Grillo:** Investigation; methodology. **Cuilan L. Gao:** Visualization; formal analysis. **Rodrigo A. Vásquez:** Funding

acquisition; investigation; writing – review and editing; resources. **Luis A. Ebensperger:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; resources.

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CONFLICT OF INTEREST STATEMENT

The authors do not declare any conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw data are available at DOI: 10.5061/dryad.vdncjsz3v.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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