ORIGINAL ARTICLE

Food abundance and group size influence the phenology of reproduction in communally breeding *Octodon degus*

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Abstract

Socioecological conditions are expected to influence the timing, or phenology, of when adult females give birth to off-spring. Females may time reproduction such that offspring are born to maximize the length of the period that offspring have to forage during the growing season. In communal breeders, females may alter reproductive phenology to maximize benefits of group-living through synchronizing reproduction and improve offspring survival. We used an 11-year dataset on a population of communally breeding degus (*Octodon degus*) to test whether the (i) reproductive phenology was influenced by the abundance of food, social conditions, and the degree of masculinization of females and (ii) reproductive synchrony was influenced by similar access to food and degree of masculinization among females and communal litter size, in multi-female groups. The phenology of litter parturition (parturition day) was negatively associated with the abundance of food at burrow systems during winter (but not during spring) and was negatively associated with the number of adult females per social unit in the spring. Synchrony of litter production within communal groups increased in years with less available food. Our study suggests that degu females timed reproduction based the socioecological conditions likely to be experienced by their dependent offspring.

Significance statement

We hypothesized that females use socioecological cues, such as food abundance and number of conspecifics in a social unit to optimize the timing of mating and production of offspring. We found that *Octodon degus* females produced litters earlier in the austral spring when food abundance during the austral winter (i.e., mating time) was high. The timing of litter production was also negatively associated with the number of adult females per social unit during the austral spring. The extent of litter synchrony within groups was explained by the average availability of food to groupmates, but not anogenital distance, group size, or communal litter size. Our results suggest that females reproduce when resources are abundant and fine-tune offspring production based on the number of potential communal care givers in a social unit during the period of lactation.

Keywords *Octodon degus* · Litter · Parturition · Synchrony · Communal

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Introduction

Reproductive phenology influences offspring survival and maternal fitness (Plard et al. 2013; Rotella et al. 2016). Ultimately, ecological, social, and individual factors may influence when parturition occurs and should impact the individual fitness (Viblanc et al. 2022). Among ecological conditions, females typically produce offspring when food is abundant (Lack 1968; Daan et al. 1988; Arlettaz et al. 2001; Lof et al. 2012; Selonen et al. 2016; Neumann et al. 2020). Failing to gather adequate food or energy stores to support offspring care may result in mothers and offspring becoming more prone to nutritional deficits (Metcalfe and Monaghan 2001) and compromising offspring growth and survival (Dijkstra et al. 1990). Therefore, selection should favor mating when current food availability predicts later food availability for offspring (Lack 1968; Nager and van Noordwijk 1995). It is also possible that females could lengthen gestation, postponing the birth of offspring until sufficient food is available (Rachlow and Bowyer 1991; Speakman 2008). One aim of this study was to determine if food abundance impacts the timing of offspring births in a social rodent.

Social organization may also influence when offspring are born (Bertram 1975; Hemsworth 1982), including the size and composition of social groups and the nature of interactions among group members (Hayes 2000; Silk 2007; Kappeler 2019). For example, in communal breeders (species in which multiple females rear offspring together such as cooperative nesting birds), synchronizing litter production could reduce the negative effects of competition between offspring from different litters that are at different stages of development (Mennella et al. 1990; Hodge et al. 2009) or the probability of infanticide (Bertram 1975; Riehl 2016). Alternatively, asynchrony in age composition within communal litters could be advantageous to dominant females if their offspring gain more mass than younger offspring during development (Ebensperger et al. 2007; Dey et al. 2014). Social organization can vary considerably among communal breeders (Clutton-Brock 2013). Thus, understanding the fitness consequences of communal breeding requires an examination of how the number of adults and number of breeding females per social unit influence the timing of offspring production.

Female morphotype, such as the degree to which females were masculinized due to androgen exposure during prenatal development (vom Saal 1989), may be a proximate mechanism underlying mating and offspring production. Females exposed to relatively high levels of prenatal androgens are morphologically characterized by long distances between the anus and genitals, i.e. a long anogenital distance index (AGD; Ryan and Vandenbergh 2002). Prenatal exposure to androgens also shapes other morphological, physiological, and behavioral traits (Zielinski et al. 1992; Ryan and Vandenbergh 2002; Monclús et al. 2012; Correa et al. 2013; Buijs et al. 2016). AGD is associated with numerous reproductive traits potentially linked to the timing of offspring births (Ryan and Vandenbergh 2002). For example, female mice (*Mus musculus*) with long AGDs exhibit delayed puberty (vom Saal 1989), longer estrous cycles (vom Saal et al. 1991) and are less sexually attractive to males (vom Saal 1989) than females with short AGDs. Female mice with long AGDs also mate or are impregnated later than females with short AGDs (vom Saal 1989). Similar reproductive differences are observed in other female mammals (gerbils: Clark et al. 1993; swine: Rohde et al. 1990; rabbits: Bánszegi et al. 2012; humans: Wainstock et al. 2017).

We used an 11-year dataset (2009–2019) to test alternate hypotheses to explain variation in reproductive phenology and within-group litter synchrony in the degu (*Octodon degus*), a communally breeding rodent endemic to central-north Chile (Di Castri and Hajek 1976). Adult lifespan under natural conditions is typically 1–2 years. The reproductive cycle is relatively long and includes a period of mating during the austral winter (May-June), a 3 month-long period of gestation, and a ~1 month-long period of lactation during the austral spring (September-October) (Woods and Boraker 1975). Degu females rarely survive more than one year and only produce 1–2 litters of (1–11 offspring) during their reproductive lifetime (Veloso 1997; Ebensperger et al. 2002, 2013). Degu offspring are precocial and begin to eat solid food within a week of birth (Long and Ebensperger 2010). The main peak of births in degus generally takes place during the late austral winter through early spring (September-October), the period with the greatest growth of herbaceous vegetation (Gastó and Contreras 1972; Veloso and Bozinovic 2000). However, birth timing varies both geographically (Ebensperger and Hurtado 2005; Previtali et al. 2010) and annually (Correa et al. 2016). Degus face strong seasonal variation in ecological conditions, including the quality and abundance of preferred food (Ebensperger and Hurtado 2005; Quirici et al. 2010), and periods of low food abundance during spring negatively impact individual survival and female reproductive success (Hayes et al. 2009). Available food during winter (i.e. at the time of mating) is a predictor of permanent changes in female social unit composition recorded from winter through spring (Ebensperger et al. 2021), suggesting the possibility that food availability during mating predicts environmental conditions during lactation, and that mothers may time reproduction to provide offspring with ample time to nurse while food conditions are abundant. Females using burrows with relatively low

Table 1 Level of support for hypotheses explaining why females can produce offspring early in the austral spring

Hypothesis	Prediction	Support?
H1: A minimum amount of food is necessary to initiate mating	Negative association between date of offspring production and food abundance during the winter	Negative association in full model ($P = 0.06$); statistically significant negative association in reduced model $P = 0.046$)
H2: Abundant food in spring supports litter production and lactation	Negative association between date of offspring production and food abundance during the spring	Not supported
H3: Large multi-female groups enhance the capacity to produce offspring early in the spring	Negative association between the date of offspring production and number of adult females per social group during the spring	Statistically significant negative association ($P < 0.01$)

Table 2 Levels of support for hypotheses of factors influencing litter synchrony within multi-female groups

Hypothesis	Prediction	Support?
H4: Females with access to abundant food produce litters at about the same time because they are in similar reproductive condition	Negative association between the difference in parturition day of females with the first and last litters in a group and mean food abundance of those females.	Statistically significant negative association ($P = 0.023$)
	Positive association between the difference in parturition day of females with the first and last litters in a group and the difference in abundance of food between those females	Not supported
H5: The benefits of homophilic associations include litter synchrony	Negative association between the difference in parturition day between females with the first and last litters in a group and the difference in AGD between those females	Not supported
H6: Litter synchrony reduces costs of large communal litter size to offspring	The difference in parturition dates between females with the first and last litters decreases within increasing communal litter size	Not supported

nearby food may delay reproduction until food resources have improved or they have had sufficient time to forage.

Adult degus organize into different types of social units, including solitary and female-male units and groups of varying size (2–8 adults; Hayes et al. 2009, 2019). The most common social unit consists of multiple breeding females (with and without males) (~60%; Hayes et al. 2009, 2019). In multi-female groups, females indiscriminately care for offspring in communal litters (Ebensperger et al. 2007). Female reproductive success is positively associated with the number of adult females per social unit during years with low food abundance, suggesting that benefits of communal breeding group-living are greatest when environmental conditions are harsh (Ebensperger et al. 2014). However, laboratory evidence indicates that birth asynchrony within communal litters decreases the number and quality of offspring weaned by the females under limited food conditions (Ebensperger et al. 2007). Adult social unit composition is unstable, with most social units changing adult composition between the austral winter (mating) and austral spring (lactation) (Ebensperger et al. 2016). The number of offspring weaned by females is enhanced by the number and stability of relationships with other females in a social unit (Wey et al. 2013; Ebensperger et al. 2014, 2016). The amount of time that degus spend foraging increases with increasing foraging group size (Ebensperger et al. 2006b), suggesting a possible benefit of increased food intake.

The degree of masculinization, indicated by anogenital distance (AGD), influences degu reproduction. Masculinized (i.e. long AGD) females produce heavier offspring than feminized females (Correa et al. 2016) and females in communal groups with more masculinized females wean more offspring than females in groups with more feminized

females (Correa et al. 2021). Masculinized females have a higher social rank than less-masculinized females (Correa et al. 2013), which may influence differences in access to food resources between females of different AGD lengths. Thus, it is possible that variation in the AGD of females within multi-female groups could impact litter synchrony.

We do not know the extent to which socioecological conditions influence the timing of litter production and litter synchrony in degus under natural conditions. The first aim of this study was to determine how socioecological conditions including food abundance and group size impact the timing offspring production by individual females within the same year. The second aim of this study was to determine how socioecological conditions influence litter synchrony within multi-female groups. We tested three hypotheses for both the timing of offspring production and litter synchrony (Tables 1 and 2), which we detail below. We assumed that (i) females benefit from timing reproduction such that offspring have the most time to forage on green vegetation before the onset of the summer, when high quality food is very limited and (ii) litter synchrony reduces the costs of competition among offspring within communal litters.

Hypotheses for the timing of offspring production

The impact of socioecological conditions on the timing of offspring production likely differs between the austral autumn-winter, when mating occurs, and the austral spring,

when offspring are produced and reared. In the winter, a minimum abundance of food likely is required for females to initiate mating (H1; Table 1). Additionally, females with abundant food during the austral spring will be able to advance the production of litters because they are in good condition and have the resources necessary to sustain lactation (H2; Table 1). Enhanced foraging associated with large group size (Ebensperger et al. 2006b) and benefits of communal care in large multi-female groups under harsh conditions (Ebensperger et al. 2014) could improve the capacity of females to produce offspring early in the spring (H3; Table 1). Previously, we observed that females with relatively long AGDs give birth later in the reproductive season (Correa et al. 2016). Thus, we included female AGD in statistical models to control for this influence on reproductive phenology.

Hypotheses for litter synchrony

Since degu groups are characterized by instability in group membership between seasons (Ebensperger et al. 2016), we expected that current socioecological conditions during spring would have the greatest impact on litter synchrony within multi-female groups. We hypothesized that females with access to abundant food are likely to be in a relatively similar reproductive condition and thus, produce offspring at about the same time (H4; Table 2). We also examined how two components of the social environment might influence litter synchrony. Degu females that associate with similarly masculinized females (based on AGD) have the greatest reproductive success (Correa et al. 2021) and are not socially hierarchical (Correa et al. 2016). It is possible that similarly masculinized females share similar benefits of group-living, including reduced competition among offspring associated with litter synchrony (H5; Table 2; Mennella et al. 1990). Competition among different-aged offspring in communal litters may be costly to some offspring (Mennella et al. 1990). To reduce this cost, females may adjust the production of litters based on the presence of other offspring in a communal group (H6; Table 2). Predictions to these hypotheses are in Table 2.

Methods

We conducted a long-term study (2009–2019) on a naturally occurring population of degus at the Estación Experimental Germán Greve Silva (33°23′ S, 70°31′ W, altitude 495 m), a field station of the Universidad de Chile. Specifically, we conducted live-trapping and determined radio-telemetry locations of individually identified degus during the austral winter (May-June) and spring (September-October)

months, which correspond to the periods of mating and late pregnancy/lactation, respectively. All individuals were regularly weighed, sexed, and given ear tags—1 per ear— with a unique identification code upon first capture (Hayes et al. 2009, 2019; Ebensperger et al. 2014; Correa et al. 2021). Pregnancy status was determined by abdominal palpations and lactation status by the expression of milk. It was not possible to record data blind because our study involved focal animals in the field.

Socioecological conditions

The social environment was indexed by the number of adult females (FGS) per social unit during each season (Hayes et al. 2009, 2019; Ebensperger et al. 2014). Degus typically use multiple burrow systems, which are usually more than 5 m apart. Social unit assignments for the austral winter and austral spring were based on the degree of nightly overlap (during burrow trapping and night telemetry) at the same burrow systems during May-June and September-October, respectively. Complete details of how we quantified social unit membership are reported in Supplemental materials (Methods Supplemental S1).

To estimate food abundance, we quantified the biomass of dried green herbs at burrow systems during the austral winter and spring, following methods detailed in the Supplementary materials (Methods Supplemental S2). Thus, all burrow systems in our study site were assigned a food abundance value during both seasons. Since adult females in the same social unit do not always overlap in the same burrow systems, we used an index of food abundance that was weighted based on where females were located during the nighttime (Hayes et al. 2009). Abundance of food for all females was indexed by the average biomass of dried green herbs of females across burrow systems in which they lived during May-June and September-October (Ebensperger and Hurtado 2005; Hayes et al. 2009; Ebensperger et al. 2014).

Adult female morphotypes

The degree of masculinization was assessed through anogenital distance (AGD), the distance between the ventral anus commissure to the base of the genital papilla (Vandenbergh and Hugget 1994), during both seasons. We measured the AGD of adult females exhibiting a non-perforated vagina with a digital caliper (precision 0.1 mm) at every capture event. All AGD measurements were taken by the same observer (LAC). We calculated the average AGD of all measurements for each female, resulting in a single AGD estimate per female (Bánszegi et al. 2012).

Parturition date and litter synchrony

During trapping of adult female degus in spring, signs of reproductive status (pregnant, lactating) were recorded during handling. The dates of first observations of pregnancy and lactation for females were used to establish females' pregnancy day and first day of lactation (hereafter, lactation day), respectively. We estimated parturition day in the spring from the sum of pregnancy day and half the difference between the pregnancy and lactation day (Eq. 1).

$$
\begin{aligned}
\text{Parturition day} = &\ \text{pregnancy day} \\
&+ ((\,\text{lactation day} - \text{pregnancy day}\,)\,/\,2)
\end{aligned}
\tag{1}
$$

Within-group litter synchrony was indexed as the absolute value of the number of days between the earliest and latest day of parturition in groups consisting of two or more breeding females, hereafter difference in parturition day (Riehl and Strong 2018; Eq. 2).

$$
\begin{aligned}
\text{Difference in parturition day} \\
=\ &\text{absolute value of the earliest parturition day} \\
&- \text{latest parturition day}
\end{aligned}
\tag{2}
$$

To assess the influence of socioecological and physical conditions of females within the same group on litter synchrony, we also estimated absolute differences in food abundance estimates and AGD measurements between females with the earliest and latest parturition days.

Statistics

All statistical analyses were run in R 4.0.2 software (R Development Core Team 2020) using the RStudio 1.3.1093 integrated development environment (RStudio Team 2020). To test hypotheses 1–3 for litter parturition (Table 1), we used a linear mixed-effect model with year as a random effect and food abundance in the austral winter, food abundance during the austral spring, and number of adult females per social unit in the austral spring as predictor variables. Anogenital distance was included as a covariate in this model. The linear mixed-effect model was fitted using functions in library lme4 1.1–27.1 (Bates et al. 2014). Marginal and conditional R^2 values are reported as measures of goodness-fit (Nakagawa and Schielzeth 2013; Johnson et al. 2015).

To test hypotheses 4–6 for variation in litter synchrony (Table 2), we ran a series of linear regressions with differences in groupmates' food abundance and anogenital distance and communal litter size. Separate models were necessary due to small sample sizes and used the functions in library stats 4.0.2 (Fox and Weisberg 2011).

Akaike Information Criteria (AIC; Akaike 1974) were used to determine the best-fit models model types (linear mixed-effect model vs. linear regression) for each response variable and respective dataset, using function in library stats 4.0.2. Model selection was based on relative comparisons of AIC values and models yielding the smallest AIC value with >2 units difference from the others were considered best-fit to test predictions. Models within 2 AIC units of the lowest AIC were considered for tests of predictions (Burnham and Anderson 1998, 2002). Marginal and conditional R^2 values, and r^2 values for linear models, are reported as measures of effect size for linear-mixed models (Nakagawa and Schoelzeth 2013; Johnson et al. 2015). All libraries were accessed during March 2024.

We conducted a post-hoc test to determine if individual female food abundance in winter predicted individual female food abundance in spring. To do this, we used LMER to model this fixed effect with year and degu ID as random effects.

Results

General findings

In total, we examined the parturition days of 103 adult females and within-group litter synchrony of 14 pairs of female groupmates with the earliest and latest litter parturition days in their spring social group. Median parturition day of all recorded degu litters in the austral spring occurred on September 8 (median = day 251, range 236–274, $N = 103$) out of 365. Mean food abundance at burrow systems available to females was 26.85 ± 3.65 (mean $\pm$ SE) g/m^2 in June (winter) and 99.15 (± 5.11) g/m^2 in September (spring). Food abundance in winter was not strongly associated with food abundance in spring ($r = -0.037$). The mean AGD for females was 2.24 (± 0.05) mm during mating. Parturition day of females varied among the eleven years of study, with significant differences between some years but not others (Table S1, Fig. S1). Thus, year was included as a random variable in the linear mixed-effect model (Bates et al. 2014). Degu social units varied in the number of females per unit (range 3–6), with a mean ($\pm$ SD) number of adult females per social unit of 3.0 (± 0.2) in winter and mean number of adult females per social unit of 2.5 (± 0.1) in spring. The mean difference in parturition day of female groupmates with the earliest and latest -born litters was 6.8 (± 1.0, $N = 23$) days, and they differed 0.30 (± 0.05) mm in AGD length on average. Females weaned 4.7 (± 0.2, $N = 103$) pups with a mean communal litter size of 9.6 (± 0.7, $N = 23$) pups. The mean difference in food abundance available to females was 1.5

(± 0.9, $N=23$) g/m^2 in the autumn and 5.6 (± 1.7, $N=14$) g/m^2 in the spring.

Predictors of parturition day

Complete data were available for 71 out of 103 females with assigned parturition days. Analyses were based on these 71 females. As autumn food biomass increased, birth dates became earlier, though the pattern only approached significance (Table 3; Fig. 1). Parturition day was negatively associated with the number of adult females per social unit in the spring (slope=-1.95, CI = [-3.37 – -0.52], $p=0.007$) (Fig. 2) but was not associated with individual females' anogenital distance (Table 3). To further evaluate the influence of females' food abundance during winter on parturition day, we ran a simplified model with other variables removed. In this bivariate analysis, parturition day of females ($N=103$) was negatively associated with food abundance during the austral winter ($r^2=0.252$; $p<0.001$; Table S2, Fig. S2).

Predictors of within-group litter synchrony

The difference in parturition day between the females with the first and the last litter produced within multi-female groups ($N=14$) was negatively associated with mean food abundance (spring) of females ($r^2=0.360$, $p=0.023$; Fig. 3). Neither the difference in food abundance of females ($r^2=0.056$, $p=0.417$) nor the difference in their AGD ($r^2=0.109$, $p=0.250$) predicted the difference in parturition day of females in the same multi-female groups. The difference in parturition day between females with the first and the last litters in multi-female groups was also not influenced by communal litter size ($r^2=0.00$, $p=0.961$).

Discussion

Timing of litter parturition

Degu females with abundant food resources during the austral winter produced litters earlier in the spring. This biologically meaningful trend is consistent with other studies on birds (Daan et al. 1988; Komdeur 1996; Davies and Deviche 2014) and mammals (Wade and Schneider 1992; Dubost and Henry 2017; Ortega et al. 2021), indicating that in some species the timing of parturition is in response to food availability experienced during mating. Food availability during the spring did not impact when degus produced litters. Therefore, the abundance of food during winter, but not spring, plays a moderate role in females' ability to produce offspring as early as possible in the spring. There are several explanations for the observed negative association between

Table 3 Results of a linear mixed-effect model for the effects of food abundance, social unit size, and anogenital distance on parturition day. Significant P-values are bolded

Predictor	Estimate	CI	P
(Intercept)	258.28	246.91–269.64	**< 0.001**
Abundance of food in winter	-0.07	-0.14–0.00	0.062
Abundance of food in spring	-0.03	-0.07–0.02	0.233
Number of adult females per social unit	-1.95	-3.37 – -0.52	**0.007**
Anogenital distance	1.05	-2.76–4.85	0.590
Random effects			
σ^2	49.67		
$\tau_{00\ Year}$	20.10		
ICC	0.29		
N_{year}	10		

Observations 71

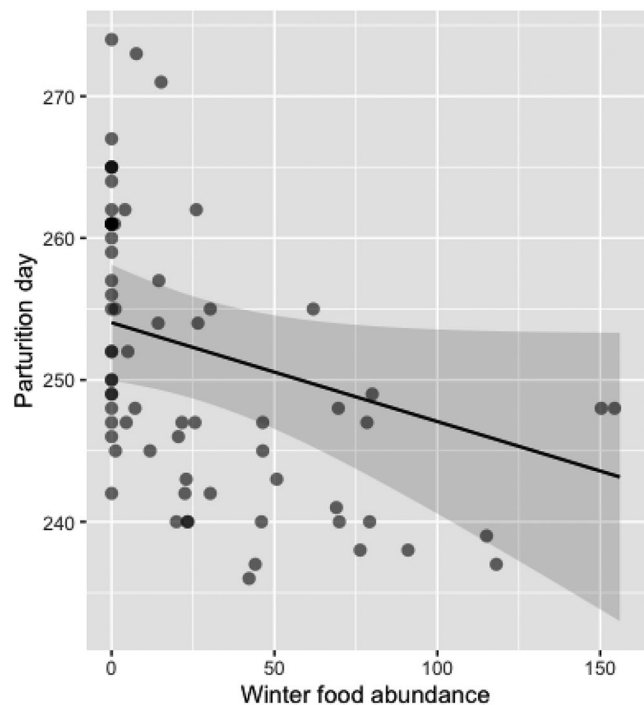Marginal R^2 / Conditional R^2 0.193 / 0.426

Fig. 1 Negative relationship between parturition day and food abundance during the austral winter. Regression line is for the fixed effect component ($N=71$ females). Shaded areas indicate 95% confidence intervals

food abundance in winter and timing of litter production. Females may require sufficient food to support the energetic demands of mating behavior (Gittleman and Thompson 1988). Females that do not ingest enough food may experience reduced sexual motivation (Schneider et al. 2013) and delays or failed mating efforts (Temple et al. 2002; Pierce
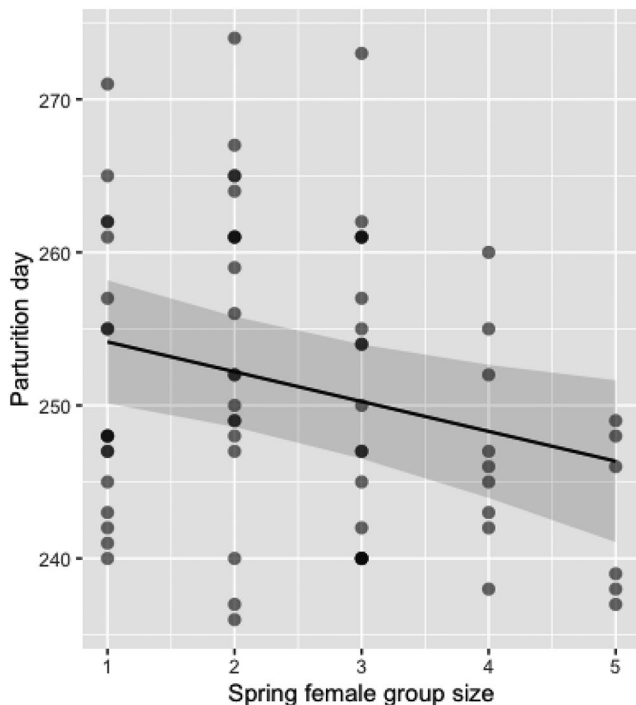
Fig. 2 Negative relationship between parturition day and FGS (female group size) during the austral spring. Regression line is for the fixed effect component ($N=71$ females). Shaded areas indicate 95% confidence intervals
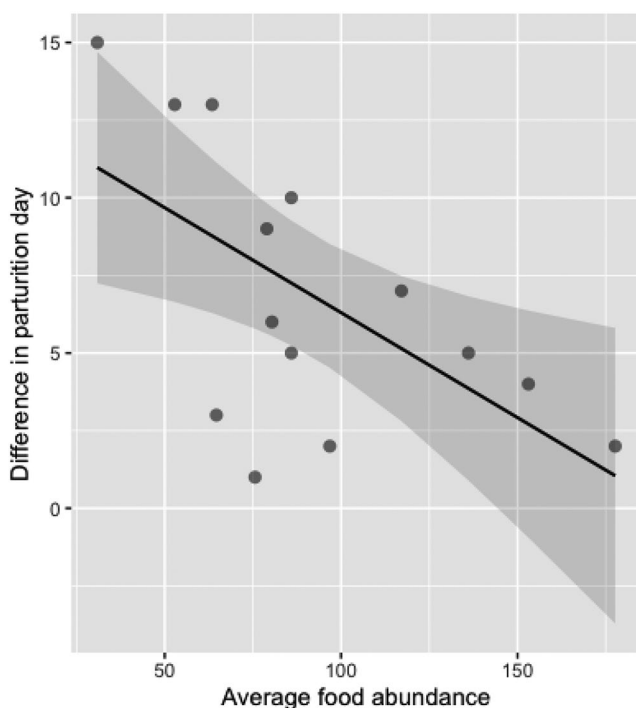

Fig. 3 Negative association between difference in parturition day of females with first and last litters and average food abundance (spring) of females in multi-female groups ($N=14$ multi-female groups). Shaded areas indicate 95% confidence intervals

et al. 2005). Thus, degu females may initiate mating behavior in response to prevailing food conditions. Alternatively, selection could favor mating strategies that ensure females have sufficient energy to sustain the costs of gestation (in degus, ~1/3 of a lifetime; Woods and Boraker 1975), birthing (Gittleman and Thompson 1988) and parental investment, including the very high costs of lactation (Bronson 1985; Wade and Schneider 1992; Naya et al. 2008; Speakman 2008). Offspring that do not receive sufficient parental investment may experience developmental deficiencies (Metcalfe and Monaghan 2001) leading to fitness costs later in life (Rickard et al. 2010; Monclús et al. 2014). Thus, degu females may time reproduction so that offspring are born when food is abundant in the spring (e.g. Cumming and Bernard 1997; Holekamp et al. 1999; Visser et al. 2006). Since food abundance in winter was only weakly associated with food abundance in spring, it is unlikely that females are able to 'forecast' future conditions based on prevailing food conditions as has been observed in other animals (Lind et al. 2020). Determining whether energetic demands of mating behavior or of gestation and lactation either individually, or in combination underlies degu reproduction requires further studies. Specifically, we need to (i) to determine how energetic costs of mating interactions may limit subsequent pregnancy and lactation in the field (Bozinovic et al. 2004) and (ii) whether food availability during mating reliably predicts food availability during offspring rearing and weaning (di Bitetti et al. 2000; Lind et al. 2020). Our observation that food abundance during mating does not predict food abundance during the period of offspring production and weaning is consistent with our previous observation that similarity of socioecological conditions across consecutive breeding events was variable across years (Ebensperger et al. 2021). This suggests that current conditions were not appropriate for forecasting future conditions.

Parturition day was negatively associated with the number of adult females per social unit in the spring (Fig. 2), supporting the hypothesis that living in large multi-female groups enhances the likelihood of females to producing offspring early in the spring (H3; Table 1). In large multi-female groups, females may advance the production of offspring because of the fitness benefits associated with communal care (Roulin and Heeb 1999; Hayes 2000), particularly when food abundance is low (Ebensperger et al. 2014). Living in large multi-female groups may also enhance access to resources (Ebensperger et al. 2006b), ensuring that females have enough food to support lactation and offspring have more time to forage before the onset of summer (when abundance of high-quality food is low; Quirici et al. 2010). The increased cumulative risk of predation to offspring in large communal litters that are weaned early in the spring may be offset by the reduced risk of predation associated

with large female group size during foraging (Ebensperger and Wallem 2002; Ebensperger et al. 2006b; Lagos et al. 2009). Interestingly, degu females experiencing low food conditions during winter have a high propensity to change social units (Ebensperger et al. 2021). A future analysis should determine if these changes in social organization impact female group size and the timing of litter production in the spring.

The level of masculinization, indexed by AGD, is an important factor potentially underlying different components of degu fitness, including the birth weight of offspring (Correa et al. 2016) and reproductive success of males (Correa et al. 2018). Previously, we observed a positive association between AGD and parturition day (Correa et al. 2016), an observation supporting the inclusion of AGD as a proximate mechanism influencing parturition day and covariate in model 1. The lack of an association between AGD and parturition day in this study suggests that the degree of masculinization of females does not influence when females produced offspring during the period of study under investigation. Differences in results in this study and Correa et al. (2016) may have occurred because our dataset included more years of study and because our analysis included different socioecological factors as predictor variables. Future analyses should examine potential associations between AGD and physiological mechanisms (e.g., hormonal pathways) that underlie social interactions and sexual maturation.

Within-group litter synchrony

In a laboratory study in which food was restricted to degu females, early-born offspring to pairs of lactating females gained more mass and were more likely to survive than late-born offspring (Ebensperger et al. 2007). The costs to late-born offspring and their mothers are not trivial because females rarely breed more than once during a lifetime (Ebensperger et al. 2013) and live in social units with low kin structure (Davis et al. 2016). Based on these observations, we expected that litter synchrony would be associated with variation in socioecological conditions. Our analysis of factors influencing litter synchrony, however, was limited by a small sample size. Litter synchrony within multifemale groups was negatively associated with the average amount of food available to females during the austral spring (Fig. 3), but not with the difference in the amount of food of the first and last females producing litters in multi-female groups. This result is inconsistent with previous studies suggesting a positive association between food abundance and synchrony of offspring production in populations of boars (Maillard and Fournier 2004) and some ungulates (Sinclair et al. 2000). One interpretation of this result for degus is

that when groups have access to abundant food, pregnant females can adjust when they give birth to minimize the risks of infanticide and costs of inter-litter competition to their own offspring (Mennella et al. 1990; Ebensperger et al. 2007; Hodge et al. 2011). Alternatively, food may be so abundant that there is little competition among offspring. Since the risk of infanticide is low in degus (Ebensperger 2001), the costs of asynchrony more likely are associated with increased competition between and unequal development of different aged offspring (Ebensperger et al. 2007). Thus, the production of asynchronous litters during conditions of low average food abundance leads to inequality among communally breeding females during challenging conditions.

Our observation that females do not adjust offspring production to increase litter synchrony based on similarity in masculinization levels was surprising. Social groups consisting of dissimilarly masculinized females are characterized by high levels of aggression (Correa et al. 2013). Synchronizing litters under these conditions could effectively reduce inter-female aggression or enhance communal offspring care which in turn, could reduce differences in offspring development (Ebensperger et al. 2006a). Future work should examine homophilic associations and patterns of communal care.

Offspring in large communal litters likely experience elevated competition (Hodge et al. 2009). Costs of asynchrony to late-born offspring in degus (Ebensperger et al. 2007) and other mammals (Mennella et al. 1990; Hodge et al. 2011) likely increase with increasing communal litter size. Our study suggests that degu females do not synchronize litter production based on communal litter size. However, it is possible that females synchronize litters only when females have relatively large communal litters during periods of low food abundance. Under these conditions, synchrony would reduce inter-litter competition for limited resources. To test this hypothesis, we need a larger dataset that would allow us to model relationships between litter synchrony and communal litter size during periods of low and high food.

Concluding remarks

Reproductive phenology has important consequences for offspring and their mothers. Our study adds to a body of literature showing that mothers time reproduction based on prevailing food conditions (e.g. Lack 1968; Daan et al. 1988; Arlettaz et al. 2001; Selonen et al. 2016; Neumann et al. 2020). However, we also found that degus can adjust when offspring are produced based on social conditions in spring, suggesting that selection favors a multi-step strategy to ensure offspring are weaned when there is enough food to sustain development or to maximize the benefits

of communal care. This hypothesis aligns with evidence that breeding phenology often depends on climatic conditions during spring in some temperate mammals (Lane et al. 2012; Thompson et al. 2023). Although benefits of litter synchrony have been well established in other communally breeding mammals (Bertram 1975; Mennella et al. 1990; Hodge et al. 2011) and birds (Riehl 2016), we did not observe statistically significant relationships between litter synchrony and social conditions, likely due to small sample sizes. How other factors, such as male behavior during mating (Ebensperger and Hurtado 2005) and the effect of group membership changes (Ebensperger et al. 2016, 2021) influence reproductive phenology and litter synchrony remain to be examined.

Declarations

Ethical approval We adhered to the guidelines set forth by the American Society of Mammalogists (Sikes et al. 2011; Sikes and the IACUC committee 2016). This study was approved by the Institutional Animal Use and Care University of Louisiana at Monroe IACUC (2009–2011) Committee (IACUC) at the University of Tennessee at Chattanooga IACUC (2012–2019) as well as the P. Universidad Catolica de Chile Comité Ético Científico para el Cuidado de Animales y Ambiente (protocol #160819013). We received the required authorization to live trap wild degus by the Servicio Agrícola y Ganadero (1894, 3542/2008, 1–31/2009[1956], 2826/2013, and 2769/2017).

Conflict of interest We have no competing interests to declare that are relevant to the content of this article.

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