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Developmental and social constraints on early reproduction in an asocial ground squirrel

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Abstract

For short-lived species, selection for early reproduction should be strong, yet females often delay their first reproductive bout. Delay in age of first reproduction due to developmental constraints, such as food availability, or social constraints, such as the inhibitory presence of breeding adults, has been documented for social mammals, but effects on asocial species are less well known. We evaluated the influence of developmental and social factors on early reproduction in a short-lived, asocial species, the golden-mantled ground squirrel (*Callospermophilus lateralis*). We found that females who reproduced as yearlings had been weaned earlier in their natal summer and experienced early snow melt during their yearling spring, suggesting the importance of access to high-quality food at critical stages. Females were more likely to reproduce as yearlings when there were more adult males present during the breeding season, possibly because exposure to males accelerates reproductive maturity. Maternal presence had no effect on yearling reproduction, but yearlings with a littermate sister present were only 22% as likely to reproduce as females without a sister present, suggesting the effect of sibling competition well past weaning. Furthermore, the negative effect of a sister's presence, but not the presence of other females, suggests that relatedness affects reproductive competition in this asocial species.

Introduction

The age at which females first reproduce is an important component of vertebrate life histories, with effects on individual fitness (Lewontin, 1965; Oli, Hepp & Kennamer, 2002), population dynamics (Cole, 1954; Tkadlek & Zejda, 1995; Dobson & Oli, 2001) and social organization (Armitage, 1981; Bekoff, Diamond & Mitton, 1981). Selection for early reproduction should be strong when lifespans are short (Stearns, 1992), because early maturing individuals are more likely than their later-maturing counterparts to successfully reproduce before they die, and this expectation is well supported among vertebrates (Saether, 1988; Scharf *et al.*, 2015), including mammals (Promislow & Harvey, 1990; Fisher, Owens & Johnson, 2001). However, considerable variation exists in timing of first reproduction even within short-lived species (Bronson & Rissman, 1986), and individual females may delay reproduction beyond what appears to be optimal (*sensu* Stearns, 1992). Despite substantial theoretical work in this field, our understanding of the proximate factors that may constrain optimal early reproduction is incomplete.

In small mammals, optimal early reproduction may be constrained by developmental or social conditions that delay reproductive maturity. Characteristics of the natal litter can slow the rate of juvenile development: individuals from larger litters tend to exhibit lower mass at weaning (Phillips, 1981), which may delay maturation, and females from male-biased litters, exposed to fetal androgens produced by their male siblings, tend to delay reproduction (Ryan & Vandenbergh, 2002). Development may also be affected by resource availability after weaning; in small mammals, the timing of reproductive maturity is controlled by the hypothalamic–pituitary–gonadal (HPG) axis, which is sensitive to energetic factors (Adkins-Regan, 2005), and limited energy availability may preclude ovulation (Bronson, 2000). This effect may be particularly important for species living in strongly seasonal environments. Among ground-dwelling squirrels, the Armitage (1981) model of sociality emphasizes the effects of limited energy available in highly seasonal environments on delayed reproductive maturity, and this link is supported by several studies of food availability and maturation in ground squirrels (Dobson & Kjelgaard, 1985; Ritchie & Belovsky, 1990; Neuhaus *et al.*, 2004). In addition to developmental effects, the timing of reproductive maturity in small mammals may be influenced by social factors (Adkins-Regan, 2005), and the presence of conspecific adults can inhibit (Whitten, 1959; Drickamer, 1977) or facilitate (Vandenbergh, 1967) female maturation.

Among long-lived, social ground-dwelling squirrels, male-bias in the natal litter has been implicated in delayed reproduction (e.g. yellow-bellied marmots, *Marmota flaviventris*, Monclús & Blumstein, 2012; Monclús *et al.*, 2014), and so has the presence of related females and adult males in the social environment (e.g. black-tailed prairie dogs, *Cynomys ludovicianus*, Shier, 2006; Cape ground squirrels, *Xerus inauris*, Pettitt & Waterman, 2011). However, the effects of developmental and social factors on the reproductive maturation of short-lived, asocial ground squirrels are poorly known.

We used 21 years of demographic data from a high elevation, free-living population of golden-mantled ground squirrels (*Callospermophilus lateralis*) to evaluate the developmental and social factors that may constrain early reproduction in a short-lived, asocial ground squirrel in a strongly seasonal environment. The golden-mantled ground squirrel is a hibernating species that reproduces once per year, and life expectancy of females in our population is 1.6 years (Hostetler *et al.*, 2012). As is typical of small-bodied (200–300 g) ground squirrels, female golden-mantled ground squirrels usually reach reproductive maturity at age 1 year (Armitage, 1981). However, they are less likely to do so in high-elevation environments with a short growing season (Bronson, 1979), suggesting the influence of developmental constraints. If exposure to fetal androgens *in utero* or neonatal competition for maternal resources affected female development, we expected that females that were born into male-biased litters, or that had a low mass at weaning, would be less likely to breed as yearlings. Juveniles are weaned midway through a short vegetative growing season, hence limited time for growth could also constrain development. Golden-mantled ground squirrels are primarily herbivorous, and availability of green vegetation for food begins at weaning and ends at the first killing frost during late summer (Van Vuren & Armitage, 1991); further, summer rainfall may reduce aboveground activity, hence limiting foraging opportunities (Kneip *et al.*, 2011). Consequently, we expected that females that were weaned later than other females, experienced extensive summer rainfall, or encountered an early killing frost, would be less likely to breed at age 1 year. Finally, because growth of vegetation the following spring is initiated by snow melt, delayed snow melt when females emerge from hibernation as yearlings could reduce the likelihood of reproduction.

Female golden-mantled ground squirrels tend to live solitarily, but can be in close proximity to both unrelated and related females (Wells & Van Vuren, 2017). In rodents, the presence of adult females can delay reproductive maturation in young females, with the presumed effect of reducing reproductive competition (Drickamer, 2007). However, it is unclear whether it is related females, particularly the mother, or unrelated females that suppress reproduction: in some species the presence of female kin inhibits reproduction of young females (Clark & Galef, 2001; Pettitt & Waterman, 2011), and in other cases it does not (Wolff, Dunlap & Ritchhart, 2001; Schradin & Pillay, 2014). We expected that the presence of either related or unrelated females would reduce the likelihood of golden-mantled ground squirrels reproducing at age 1. In addition, due to substantial variation in annual population density (Kneip *et al.*, 2011), female golden-mantled ground squirrels may be exposed to many or few potential male mates. The presence of adult males has been shown to accelerate reproductive maturity in female mice (Drickamer & Mikesic, 1990) and voles (Batzli, Getz & Hurley, 1977; Carter *et al.*, 1980). If a scarcity of males can delay female reproduction, either by delaying reproductive maturity or by decreasing the likelihood of conception, we expected that in years of low density of adult males, or a low ratio of adult males to females, yearling females would be less likely to reproduce.

Materials and methods

Study area

We studied golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory (2900 m), in the East River Valley, Gunnison County, Colorado (38°58′N, 106°59′W), from 1995 to 2015. Vegetation in the valley consisted mostly of subalpine meadows, aspen (*Populus tremuloides*) woodlands and spruce (*Picea* spp.) forests. The 13-ha study site was characterized by meadows that supported golden-mantled ground squirrels, interspersed with groves of aspen and spruce (McEachern *et al.,* 2011). We live-trapped squirrels using traps (Tomahawk model 201) baited with black-oil sunflower seeds and peanut butter, and we marked individuals with numbered eartags for permanent identification and a unique pattern of black dye (Nyanzol D, Greenville Colorants, Greenville, SC, USA) on the dorsal pelage for visual identification. At capture, we recorded mass (to the nearest g) with a Pesola spring scale, location and reproductive status (positive for females with swollen nipples and for males with scrotal testes). We censused the population each year beginning in late May, after squirrels emerged from hibernation in April and May (emergence dates varied by year), and continued for several weeks until all individuals were identified and marked. Males emerge from hibernation in breeding condition, but females may take 2–3 weeks from emergence to become sexually receptive (Bartels & Thompson, 1993); it is behavioral interactions with males during this period that we expect could influence reproductive maturity. Females give birth to a single litter per year after a month-long gestation, and nurse pups underground for approximately 30 days (Phillips, 1981) until the litter emerges from the natal burrow. Litter sizes range from 1 to 8 pups, with an average of 4.8 (Kneip *et al.*, 2011), and typically average an even 1:1 sex ratio (Bartels & Thompson, 1993; Wells & Van Vuren, 2017). We trapped litters within 2 days of their emergence aboveground at weaning during late June and July, and recorded emergence date, mass and sex of each pup. We attempted to trap and weigh all squirrels each month until squirrels immerged for hibernation during August and September. All trapping procedures were approved by the institutional animal care and use committees of the University of California at Davis and the Rocky Mountain Biological Laboratory, and met guidelines set by the American Society of Mammalogists (Sikes, 2016).

Statistical analysis

We defined 'early reproduction' in this study as positive reproductive status at 1 year of age, the earliest age at which reproduction has been reported for this species (Armitage, 1981). Reproductive status was based on swollen nipples in late May or early June. In most cases (83%, $n = 40$), reproduction was subsequently confirmed by the emergence of a litter at the female's burrow. However, we also scored as reproductive those females with swollen nipples who were killed by predators during lactation ($n = 4$), or who were alive but without an emerged litter ($n = 3$), which we suspected was due to predation of the litter underground by weasels (*Mustela* spp.). We excluded females for which reproductive status as a yearling was uncertain (e.g. yearling females who died or dispersed before reproductive status could be assessed). We included immigrant females who settled as juveniles at the end of their natal summer and could be aged by body mass. No juvenile females survived their first hibernation in 1999 and 2001, so those years are not represented in the dataset. We used the yearly census data to determine number of adult males, number of breeding females and adult sex ratio (number of breeding females per adult male). We reasoned that if exposure to the sight or smell of males affected reproductive maturity, then a higher number of adult males would predict early reproduction, whereas if additional mating opportunities increased likelihood of conception, a lower ratio of females to males (i.e. an increase in the relative number of males) would predict early reproduction. We used litter data to determine litter sex ratios, mass at weaning, and female kin relationships (mother-daughter, littermate sisters) of yearling females. We further used litter data to construct matriline pedigrees and thereby identify all female kin present in the same locality as each yearling female. All females that were part of the same matriline pedigree (e.g. non-littermate sisters born to the same female in different years, aunts, nieces, grandmothers, granddaughters, cousins, etc.) were categorized as female relatives; females present in the same locality but not part of the same matriline pedigree were categorized as unrelated (Wells & Van Vuren, 2017). Because some male golden-mantled ground squirrels mate with multiple females (Wells *et al.*, 2017), it is possible that yearling females may also be in the presence of female kin related through the paternal line. To assess this possibility, we used the program ML-Relate (Kalinowski, Wagner & Taper, 2006) to estimate pairwise relatedness from female multilocus genotypes in a subset of years (2008–2015, Wells *et al.*, 2017). Estimates of genetic relatedness confirmed most unrelated pairs (17/20 $r = 0$), but 3/20 'unrelated' pairs appeared related at $r = 0.09$–0.13, equivalent to the level of third-order relatives. When we re-categorized these females as relatives, the results of our social-environment model (see below), were unchanged.

To explore the effect of growing season duration on subsequent reproduction, we obtained weather records for the Rocky Mountain Biological Laboratory (weather station GTH161, http://www.epa.gov/castnet). We defined the first hard freeze as the first date on which minimum air temperature fell below −2°C on 2 consecutive days, and we totaled the amount of rain (mm) that fell between emergence of each female from the natal burrow and the date of the first hard freeze.

To model likelihood of early reproduction (0 or 1), we fit Bayesian generalized linear mixed-effects models (bglmer, package bmle, Dorie, 2015; R 3.0.2, R Core Team 2013), with a binomial error structure and logit link. We did not have complete data for all females, so for each group of hypotheses (developmental constraints, social environment), we constructed an *a priori* model of factors affecting yearling reproduction. For developmental constraints, we modeled likelihood of yearling reproduction as a function of mass at emergence from natal burrow (g), natal litter sex ratio (ratio of male/female pups), date of emergence from natal burrow, natal summer rainfall (mm), date of first hard freeze and onset of spring the next year (defined as first date of bare ground in the yearling spring). Dates were entered into the model as integers corresponding to the number of days after April 30. We lacked data on late-summer mass for sufficient females to be able to include pre-hibernation mass as a fixed effect in our developmental model. However, to determine if females weaned late could compensate with higher growth rates, we calculated growth rate beginning at weaning for a subset of juvenile females for which we did have both emergence mass and pre-hibernation mass ($n = 26$, measurements taken in late August or early September). We calculated the average growth rate for these females (g day^{-1}), and fit a linear model to determine how rate of mass gain varied with date of natal emergence. To determine if late-weaned females ended the summer at lower mass than early weaned females, we also fit a linear model of pre-hibernation mass on date of natal emergence ($n = 32$).

For our social-environment analysis, we used population level factors for male presence (total number of adult males, adult sex ratio for the population), because males are not territorial during the breeding season and roam throughout the entire study site (C.P. Wells, unpublished data). We used local level factors for female presence, because females are thought to be territorial (Michener, 1983) and at our study site occur in six distinct localities containing persistent burrow systems. Localities contained both related and unrelated females, with 1–6 breeding females per locality (Wells, 2016; Wells & Van Vuren, 2017). We modeled likelihood of yearling reproduction as a function of the number of adult males (2 years and older; yearling males rarely breed, Wells *et al.*, 2017), adult sex ratio, maternal presence, littermate sister presence, number of related breeding females and number of unrelated breeding females. We specified 'year' as a random effect in both models, to account for cohort effects and unspecified interannual variation in environmental conditions.

Results

Overall, 44% of 93 yearling female golden-mantled ground squirrels became reproductive. We found no significant effect of mass at emergence from the natal burrow ($x_{repro} = 74.3 \pm 2.0$ g, $x_{non\text{-}repro} = 70.9 \pm 2.5$ g, $\beta = 0.06 \pm 0.04$, $z = 1.64$, $P = 0.102$) or natal sex ratio ($x_{repro} = 38.5 \pm 2.9\%$ male, $x_{non\text{-}repro} = 37.6 \pm 3.5\%$ male, $\beta = -0.90 \pm 0.64$, $z = -1.42$, $P = 0.157$) on the

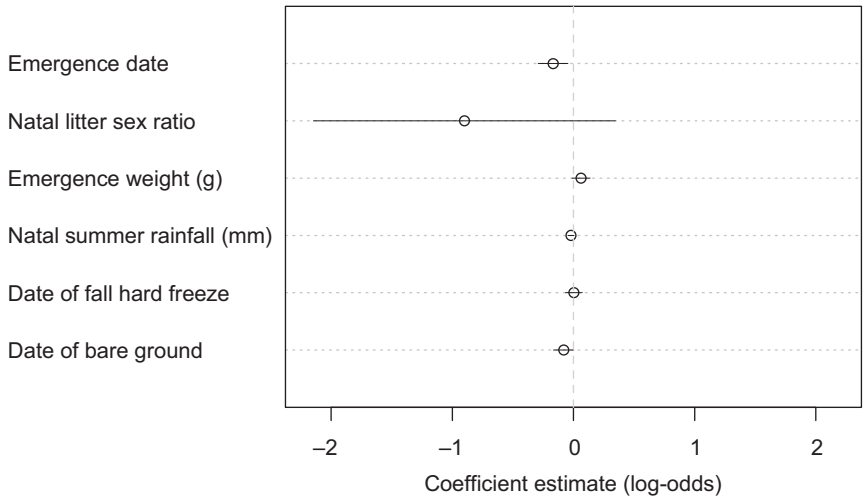

Figure 1 Plot of coefficients for fixed effects in the developmental constraints model of early reproduction in female golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, Colorado. Dots represent point estimates and lines represent 95% confidence interval (2 SE). Positive values indicate increase in log-odds of a female reproducing as a yearling, negative values indicate a decrease in log-odds of a female reproducing as a yearling.

likelihood of early reproduction. However, emergence date from the natal burrow had a significantly negative effect on the likelihood of early reproduction ($\beta = -0.17 \pm 0.06$, $z = -2.67$, $P = 0.008$, $n = 47$; Fig. 1): the mean ($\pm$SE) date of emergence for females who would later reproduce as yearlings was 5 July ($\pm$1.8 days), compared to 12 July ($\pm$1.8 days) for females who would not reproduce. The amount of rainfall during the natal summer ($\beta = -0.02 \pm 0.01$, $z = -1.59$, $P = 0.113$) did not significantly affect likelihood of early reproduction, and neither did the date of the first hard freeze ($\beta = 0.00 \pm 0.04$, $z = 0.11$, $P = 0.915$). However, the effect of the first date of bare ground in the yearling spring was negative and approached statistical significance ($\beta = -0.08 \pm 0.04$, $z = -1.89$, $P = 0.059$). Rate of mass gain during the natal summer declined significantly with later emergence from the natal burrow ($\beta = -0.05 \pm 0.01$, $F_{1,24} = 18.07$, $P < 0.001$, $R^2 = 0.43$, $n = 26$; Fig. 2), and so did pre-hibernation mass ($\beta = -2.54 \pm 0.44$, $F_{1,30} = 33.56$, $P < 0.001$, $R^2 = 0.53$, $n = 32$).

The number of adult males present during the breeding season ranged from 3 to 13 per year, and the number of adult females ranged from 5 to 29, resulting in an annual adult sex ratio that varied from 0.63 to 3.22. Number of adult males present during the yearling's first breeding season had a significantly positive effect on likelihood of early reproduction ($\beta = 0.33 \pm 0.25$, $z = 2.20$, $P = 0.028$, $n = 83$; Fig. 3), but adult sex ratio had no significant effect ($\beta = 0.49 \pm 0.51$, $z = 0.95$, $P = 0.340$). Maternal presence ($\beta = 0.32 \pm 0.66$, $z = 0.49$, $P = 0.624$), number of related breeding females ($\beta = 0.15 \pm 0.25$, $z = 0.57$, $P = 0.566$) and number of unrelated breeding females ($\beta = -0.10 \pm 0.21$, $z = -0.47$, $P = 0.640$) had no significant effect. However, the local presence of a littermate sister had a strong negative effect on the likelihood of early reproduction ($\beta = -1.52 \pm 0.70$, $z = -2.15$, $P = 0.031$).

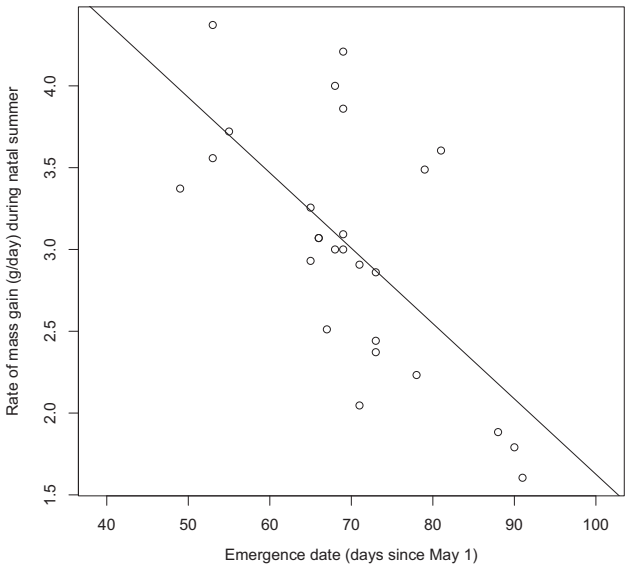

Figure 2 Linear regression of date of emergence from the natal burrow on rate of mass gain (fall mass-emergence mass/days between measurements) for juvenile female golden-mantled ground squirrels in their natal summer at the Rocky Mountain Biological Laboratory, Colorado.

Discussion

In our population of golden-mantled ground squirrels, fewer than half of females first reproduce as yearlings, and this reproductive timing appears to be influenced both by developmental and social constraints. Characteristics of the natal litter might affect early reproduction, but neither of the characteristics we tested – individual mass at weaning or litter sex ratio

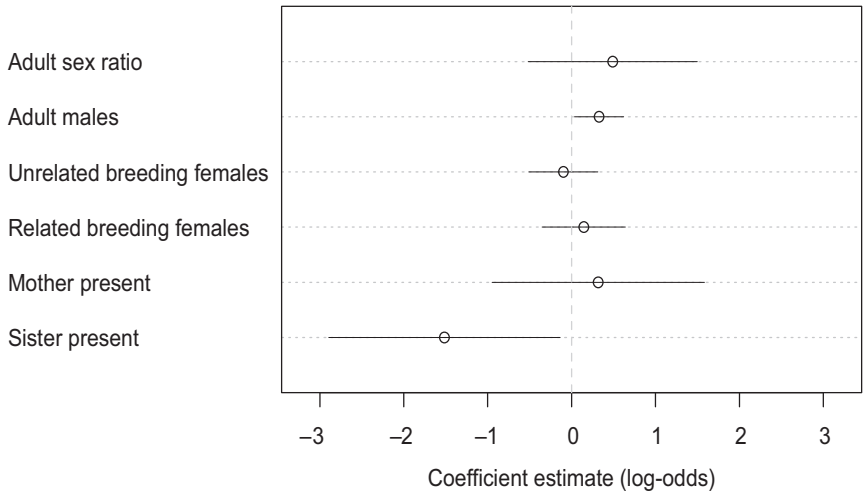

Figure 3 Plot of coefficients for fixed effects in the social-environment model of early reproduction in female golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, Colorado. Dots represent point estimates and lines represent 95% confidence interval (2 SE). Positive values indicate increase in log-odds of a female reproducing as a yearling, negative values indicate a decrease in log-odds of a female reproducing as a yearling.

– had a significant effect. Growth rates among juveniles in the same litter are variable (C.P. Wells, unpublished data), hence perhaps the mass differential at weaning was inconsequential by the time of entry into hibernation. Evidence from laboratory rodents shows that natal sex ratio affects development by influencing the local uterine environment; females can become 'masculinized' via exposure to the androgens produced by adjacent male fetuses (Ryan & Vandenbergh, 2002). The lack of an effect in golden-mantled ground squirrels may be due to variation in intrauterine position, which we did not measure: a female fetus developing between two brothers will experience a more androgen-rich local environment, with greater 'masculinizing' consequences, than will a female with one or no adjacent brothers (Ryan & Vandenbergh, 2002).

In free-living rodents, female reproductive maturity depends at least in part on food availability: for example supplemental feeding accelerates reproductive maturity in female tropical mice (*Peromyscus mexicanus*, from 219 to 109 days, Duquette & Millar, 1995) and Columbian ground squirrels (*Urocitellus columbianus*, from 2 years to 1 year, Dobson & Kjelgaard, 1985). Food availability may be limited for golden-mantled ground squirrels living at high elevations, where the vegetative growing season is short and green forbs (which make up much of their diet, McKeever, 1964) begin to senesce by late summer. Hence, the number of days available for foraging before winter may determine the amount of food available for developing juveniles in their natal summer (Armitage, 1981; Ritchie & Belovsky, 1990). Female Columbian ground squirrels exposed to longer periods of plant growth were more likely to reproduce as yearlings (Ritchie & Belovsky, 1990). Consistent with this expectation, we found that early emergence from the natal burrow had a strong positive effect on the likelihood of early reproduction in golden-mantled ground squirrels. Furthermore, late-emerging females were unable to compensate with higher growth rates, and in fact showed lower growth rates and lower pre-hibernation mass than early emerging females, perhaps because of lower quality of forage as the season progressed. Hence, delayed emergence from the natal burrow results in both less time to forage and potentially reduced forage quality, thereby delaying development and reproductive maturity until after the yearling spring.

Contrary to our expectation, amount of rainfall during the period of independent foraging did not reduce the likelihood of yearling reproduction. This result appears inconsistent with that of Kneip *et al.* (2011), who found a negative effect of summer rainfall on reproduction the next year for yearling females in the same population. However, the differing outcomes likely result from the different time periods examined by each study; Kneip *et al.* (2011) considered only early season rainfall, during June and July. Perhaps early season rainfall affects reproduction of young females indirectly, by affecting their mothers during lactation. Lactation in ground squirrels is fueled by daily food intake (Kenagy, Stevenson & Masman, 1989), and heavy rains that limit foraging during lactation may reduce the amount of energy available to nursing pups, which in turn might influence the subsequent timing of reproductive maturity (Lindstrom, 1999). However, our results indicate that this effect did not extend to pups after weaning.

Longer growing seasons have been associated with increased body mass and population growth of yellow-bellied marmots (Ozgul *et al.*, 2010), and early age of reproduction in golden-mantled ground squirrels at low elevations (Bronson, 1979). We tested two factors that influence growing season length, and hence duration of food availability: date of the first hard freeze in the natal summer, and date of the first bare ground in the yearling spring. Interestingly, only the latter was associated with early reproduction. Although a later hard freeze in the natal summer should increase the number of days that vegetation is available to growing juveniles, a decline in vegetation quality late in the season may cancel out that benefit. In

contrast, earlier onset of vegetation growth in the yearling spring, when vegetation quality is high, may allow young females to gain additional mass immediately after hibernation and reach reproductive maturity with enough time left in the season to reproduce.

High density of breeding males could contribute to the early reproduction of females by advancing reproductive maturity or by increasing the likelihood of conception. The presence of breeding males has been shown to accelerate reproductive maturity in female rodents (Batzli *et al.*, 1977; Carter *et al.*, 1980; Drickamer & Mikesic, 1990), through exposure to the sight or scent of males (Drickamer, 2007). In prairie voles (*Microtus ochrogaster*), female inhalation of chemosignals in male urine triggers an increase in leutenizing hormone, bringing females into estrus (Carter *et al.*, 1980). In golden-mantled ground squirrels, we found that the number of adult males had a positive effect on reproduction by yearling females, but the ratio of males to females did not. During the breeding season, adult males routinely leave scent marks within female home ranges (C.P. Wells, pers. obs.), and chemosignals from these marks or from urine may accelerate reproductive maturity in females. In addition, though it remains unknown whether golden-mantled ground squirrels are induced or spontaneous ovulators, it is possible that physical stimulation from males may increase yearling female fertility. Alternatively, yearling females may fail to reproduce because of limited mating opportunities, and indeed a scarcity of males can contribute to breeding failure in yellow ground squirrels (*Spermophilus fulvus*, Vasilieva & Tchabovsky, 2015). However, yearling females in our population often mate with multiple males, even in years when the adult sex ratio is female-biased (Wells *et al.*, 2017), suggesting that accelerated maturity resulting from male abundance could underlie early reproduction in this species.

Social inhibition of reproduction is widespread among group-living species, where dominant females reduce competition by suppressing the reproduction of subordinate females (Stockley & Bro-Jorgensen, 2011), often including their own daughters (Wasser & Barash, 1983; Shier, 2006; Pettitt & Waterman, 2011). Conversely, maternal facilitation of reproduction may occur in other species, where adult females can advantage their daughters by protection or cooperation. In Columbian ground squirrels, for example, maternal presence was associated with higher reproductive output of the mother's early maturing daughters (Neuhaus *et al.*, 2004). Female golden-mantled ground squirrels tend to be philopatric, and hence are often found in close proximity to their mother. However, maternal presence did not affect the likelihood of early reproduction in golden-mantled ground squirrels, neither delaying nor advancing the timing of daughter reproduction, and neither did the density of related or unrelated females. Instead, it was the local presence of a littermate sister that inhibited early reproduction: yearling females with a sister present were only 22% as likely to reproduce compared to yearling females without a sister present. Competition among neonate siblings for limited maternal resources is assumed to be universal in polytocous species (Drummond, 2006; Bautista *et al.*, 2015), and may persist even after weaning: young female voles housed with littermate sisters, or simply exposed to their scent, grew more slowly than females housed with littermate brothers or females reared in isolation (Batzli *et al.*, 1977). If sisters remain in close proximity in their natal range, developmental delays, whether due to competition for resources or physiological suppression, may extend to delays in reproductive maturation.

In summary, we found that both developmental and social factors influence the timing of first reproduction in female golden-mantled ground squirrels. Developmentally, earlier emergence from the natal burrow and early snow melt the following spring promoted early reproduction, suggesting the importance of access to high-quality vegetation at those stages. Socially, the positive effect of more breeding males suggests that the presence of males stimulates female reproduction, perhaps through visual or olfactory cues. Somewhat surprisingly, the negative effect of a littermate sister's presence, but not the presence of other females, suggests that relatedness affects reproductive competition in this asocial species. In golden-mantled ground squirrels, delaying reproduction beyond the yearling summer is costly, but may confer some benefit: waiting to reproduce until age 2 negatively affects individual fitness, but can increase daughter survival (Moore *et al.*, 2016). Hence, constraints on early reproduction may affect population dynamics for multiple generations.

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