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Female kin density affects offspring sex ratio in an asocial mammal, the golden-mantled ground squirrel, *Callospermophilus lateralis*

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Evolutionary theory predicts that parents should bias investment in offspring towards the sex that will yield the higher fitness returns, and one outcome may be biased offspring sex ratios. Bias in offspring sex ratios has been proposed to vary with specific social, maternal and environmental conditions that alter the fitness returns of each sex, but empirical evidence is conflicting both within and across taxa. We used 18 years of pedigree and demographic data to investigate variation in offspring sex ratios in a population of golden-mantled ground squirrels. Despite overall parity in offspring sex ratio, we found predictable changes in offspring sex ratio in response to female density at the population level: squirrels produced more daughters when female density was low and more sons when female density was high. At the individual level, females adjusted litter sex ratios similarly, but only in response to high densities of kin, and not in response to density of nonkin. This effect was reversed for older females (≥3 years) in dense kin neighbourhoods, which were more likely to produce daughters, perhaps because older females had the behavioural dominance necessary to recruit daughters at high densities. By contrast, litter sex ratios did not vary with maternal condition or food availability. Our results support the local resource competition theory of offspring sex allocation for this species. Knowledge of female relatedness revealed patterns of sex ratio adjustment that otherwise would have been obscured, highlighting the importance of interactions with kin in an asocial species.
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Variation in offspring sex ratio is often observed in natural populations, but debate continues over whether this variation is adaptive (Cockburn, Legge, & Double, 2002; West, 2009). Evolutionary theory predicts (Charnov, 1982), and recent evidence supports (Thogerson et al., 2013), fitness benefits to parents who are able to bias offspring sex ratios towards the sex with the higher reproductive value. The conditions under which parents bias offspring sex ratios are poorly known for most species, but several influential theories have been advanced. Trivers and Willard (1973) proposed that offspring sex ratios might vary according to maternal condition, hence females should vary the sex of their offspring according to their ability to physically invest in their offspring. In polygynous species, when maternal body condition positively affects offspring body condition, and when body condition influences variation in male reproductive success, females in good condition should produce sons and females in poor condition should not.

The Trivers and Willard (1973) theory focuses on the ability of offspring to compete for mates, but offspring fitness may also be affected by competition for resources, especially among female mammals (Stockley & Bro-Jørgensen, 2011). Natal philopatry in female mammals generates the potential for competition for resources between mothers and daughters, as well as other female kin (local resource competition; Clark, 1978). By contrast, because male mammals tend to disperse away from their natal territory (Greenwood, 1980; Mabry, Shelley, Davis, Blumstein, & Van Vuren, 2013), production of sons does not create the same potential competition for resources such as food and territory. Thus, mammalian mothers may gain from adjusting offspring sex in favour of daughters when local density is low and resources are abundant. At low densities, when there are available territories in which to settle, the philopatric sex should yield the highest fitness returns (Armitage, 1987; Michener, 1980). At high densities, when resources are scarce, females may benefit from producing more of the dispersing sex (sons) (Clark, 1978).

Density alone, however, is a coarse measure of competition, because access to resources often varies with dominance and kinship (Moses & Millar, 1994; Stockley & Bro-Jørgensen, 2011). The reproductive consequences of competition have been well studied in group-living species, where female dominance is positively correlated with access to resources and offspring survival (Clutton-

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Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). By contrast, researchers are just beginning to investigate how spatial proximity might facilitate dominance and kin-directed behaviours in females of relatively asocial species, in which philopatry results in spatial overlap among females, both kin and nonkin (Hatchwell, 2010; Innes et al., 2012; Jones et al., 2013; McEachern, Eadie, & Van Vuren, 2007). Furthermore, competition may differ among female kin as opposed to nonkin, and it is not yet clear which is more intense (Clutton-Brock & Huchard, 2013). On the one hand, competition with nonkin may be more intense because interactions are not complicated by trade-offs between direct and inclusive fitness (Hamilton, 1964; but see West, Pen, & Griffin, 2002). On the other hand, competition with kin may be more intense because members of a matriline may be competing for resources (e.g. burrows) within their shared natal range (Queller, 1994). Despite evidence that kin presence can play an important role in sex ratio adjustment (West, Shuker, & Sheldon, 2005), there have been few mammal studies of offspring sex ratios that explicitly incorporate the effects of kin (Aars, Andreassen, & Ims, 1995; Armitage, 1987; Lambin, 1994; Nunn & Pereira, 2000).

Mechanistically, the availability of food resources may underlie the production of biased offspring sex ratios. During gestation, female embryos may be more vulnerable to excessive maternal glucose levels, generating male-biased offspring sex ratios when food is abundant (Cameron, Lemons, Bateman, & Bennett, 2008). Conversely, during lactation, male offspring may be more vulnerable to maternal food stress, generating female-biased offspring sex ratios when food is scarce (McClure, 1981). Sex-biased resorption of embryos during gestation has been documented to simultaneously reduce litter size and litter sex ratio (Huck, Pratt, Labov, & Lisk, 1988); hence, a strong relationship between these two components suggests that sex-biased mortality may underlie the observed bias in offspring sex. Effects of food availability and diet composition on offspring sex have primarily been investigated in laboratory populations of rodents (Alexenko et al., 2007; Dama, Singh, & Rajender, 2011; Fountain et al., 2008), with little work done on mammals in the wild.

In this paper, we test predictions about offspring sex allocation using data from a long-term study of free-living golden-mantled ground squirrels. First, we ask whether mothers who are able to invest more in offspring, invest more in sons than daughters (Trivers & Willard, 1973). Second, we ask whether mothers adjust offspring sex ratio in response female density or local competition (Clark, 1978), either with kin or nonkin. Third, we ask whether changes in food availability for mothers at the time of conception contribute to variation in offspring sex ratio (Cameron, 2004).

METHODS

Study Site and Species

We conducted this study at the Rocky Mountain Biological Laboratory (2900 m), located in the East River Valley, Gunnison County, Colorado, U.S.A. (38°58′N, 106°59′W). We studied one population of golden-mantled ground squirrels at this site over an 18-year period (1995–2012). Golden-mantled ground squirrels, about 200–300 g in size, are considered to be a solitary, asocial species (Armitage, 1981; Michener, 1983). Adults are thought to establish distinct home ranges (Ferron, 1985; Jesmer, Van Vuren, Wilson, Kelt, & Johnson, 2011; Michener, 1983), and interactions among adults are primarily agonistic, potentially even among adult kin (Ferron, 1985; Michener, 1983). At our 13 ha study site, squirrels generally inhabited dry meadows and rocky slopes adjacent to stands of aspen or spruce; habitat characteristics and vegetation are further described in McEachern, Van Vuren, Floyd, May, and Eadie (2011). Females emerged from hibernation in April or May, mated soon after, and weaned their pups from mid-June to mid-July; gestation in golden-mantled ground squirrels is 28 days (Cameron, 1967) and weaning occurs when pups reach 30 days of age (Phillips, 1981). Adults began to immerge for hibernation in early August, and all squirrels remained below ground by October.

We censused this population of ground squirrels each year in May, after adults emerged from hibernation and began mating. We captured squirrels with Tomahawk live traps (Model 201) baited with black oil sunflower seeds and peanut butter, set in areas of squirrel activity and checked at 30 min intervals. At capture, we recorded sex (anogenital distance), reproductive status (colour and swelling of nipples for females) and body mass to the nearest 1 g. We attached a numbered metal tag to each ear for permanent identification and applied a unique dye mark to the dorsal pelage for individual identification during behavioural observations. Daily trapping continued until all adults were identified and marked and later as necessary to replace eartags when they had been lost, or to renew dye marks when squirrels moulted.

Adult ($\geq$1 year old) density varied several-fold in this population over the study period, from a minimum of 0.9 squirrels/ha in 1999 to a maximum of 3.2 squirrels/ha in 2005 (Kneip, Van Vuren, Hostetler, & Oli, 2011). Additionally, adult females were heterogeneously distributed across the study site, with six discrete localities of female activity centred in suitable rocky, dry meadow habitat patches containing burrow systems that are occupied long term. Hence, in addition to population density (squirrels per ha across the study area), we considered local density (squirrels per locality). In the year of highest population density (2005), local density of breeding females ranged from one to six females per locality. Competition at high densities seems likely; female golden-mantled ground squirrels maintain exclusive use of a core area around their burrow system within a larger home range (Jesmer et al., 2011), and the reduced survival of females following high-density years is likely due to increased occupancy of poor-quality habitats that are not sufficient to sustain long-term survival (Kneip et al., 2011).

We calculated local breeding female density as the number of reproductively active females in each locality. Females were categorized as reproductive if they exhibited swollen nipples during gestation or chewed nipples during lactation. Rarely, a female was observed to use more than one locality; in these cases, she was counted in the breeding female density of each locality, and the breeding female density assigned to her was the sum of females in both localities.

Beginning in June of each year, we monitored reproductive females for indications that their litters would soon emerge and searched their home ranges daily for the emergence of pups. Litters were trapped within 1–2 days of emergence from the natal burrow, and emergence date was recorded as the day on which the first pup was seen aboveground. Each pup was weighed, and sexed by anogenital distance. Maternity was determined through a combination of spatial, temporal and behavioural data: assignment was suspected when a litter emerged within a female's core area of activity and was confirmed when she directed affiliative behaviours (e.g. nose-greeting; Ferron, 1985) towards the pups in the days following emergence. Mothers were almost always trapped with their pups on the day of weaning. The few litters for which maternity could not be definitively assigned (e.g. when natal burrows were close and pups intermingled before trapping was complete) were excluded from analysis.

Maternal Investment

We defined maternal investment in a pup as the pup's weight at weaning (weight measured within 48 h of litter emergence from

the natal burrow). We defined total maternal investment as the litter mass (aggregate mass of pups at weaning; Broussard, Dobson, & Murie, 2005; Gedir & Michener, 2014). We were able to calculate litter mass for a subset ($N = 32$) of litters. We tested relative investment in sons versus daughters in three ways. First, we tested whether male pups weighed more than their sisters at weaning, using a paired t test of mean male weight versus mean female weight within each litter. Second, we modelled relative investment in male pups versus female pups (aggregate mass of male pups at weaning, divided by aggregate mass of female pups, for each litter) as a function of total maternal investment (litter mass) in a generalized linear mixed model (GLMM), with maternal identity and year fitted as random effects. Third, we modelled relative investment in male pups versus female pups (mean mass of male pups at weaning, divided by mean mass of female pups, for each litter) in a boosted generalized linear mixed model (bGLMM; Tutz & Groll, 2010) with the same set of predictors.

Female Density and Local Competition with Kin and Nonkin

At the population level, we calculated offspring sex ratio as the percentage of male pups produced out of the total pups each year. Rarely, pups were killed by predators before they could be trapped and sex could be determined; these pups were excluded from analysis. To assess the effect of female density on offspring sex ratio at the population level, we fitted a linear model of the percentage male pups on breeding female density.

We used maternal identity to reconstruct the relatedness of females born within the study area. Females that immigrated into the study site, whether as juveniles or adults, were assumed to be unrelated to resident females; thus, their only relatives were direct descendants (daughters, granddaughters). Kin density was calculated as the number of related breeding females (those with coefficient of relatedness $\geq$0.125) using the same locality as the focal female. Nonkin density was calculated as the number of unrelated breeding females using the same locality as the focal female. Both kin and nonkin densities were treated as categorical variables (1, 2, 3 or 4 female kin; 1, 2, 3 or 4+ female nonkin) to investigate nonlinear effects. Maternal age, categorized as yearling, 2 or $\geq$3 years old, was known for females born in the study area and was estimated for females that immigrated as juveniles or yearlings based on body mass.

To explore the effect of local density on litter sex ratio, calculated as the proportion of male pups in each litter, we fitted linear multilevel models (GLMMs) with a binomial error structure and logit link. We specified kin density and nonkin density as fixed effects. We also included maternal age, and the interaction between maternal age and kin density, as fixed effects because age might confer dominance, hence competitive ability. We incorporated female identity as a random effect, to control for multiple litters produced by individual females. We also included year as a random effect, to control for annual stochasticity in environmental conditions that may have affected sex ratios. Parameter estimates β ($\pm$SE) are reported in the logit form.

Food Availability at Conception

Golden-mantled ground squirrels are primarily herbivores (McKeever, 1964), and green herbaceous vegetation in our study area becomes available immediately after melting snow exposes bare soil (Van Vuren & Armitage, 1991). Hence, we used date of snow melt as the indicator of the onset food availability each year to evaluate glucose-driven effects on offspring sex ratio (Cameron, 2004; Helle, Laaksonen, Adamsson, Paranko, & Huitu, 2008). We expected females to have low levels of circulating glucose before snow melt and thus gestate litters that were female-biased; litters conceived after snow melt would be male-biased. We estimated the date of conception for each litter by subtracting 58 days (length of gestation + lactation) from the date of litter emergence. We then subtracted date of conception from date of snow melt to yield an estimate of food availability at the time of conception; we used this estimate of food availability as a predictor of litter sex ratio in a GLMM with a binomial error structure and logit link. As before, maternal identity and year were included as random effects. Additionally, we used a one-way ANOVA to determine whether smaller litters were more biased than larger litters, as would be expected if litter sex-bias was generated by sex-specific mortality.

Data were analysed using R version 3.0.2 (R Core Team, 2013). We used the packages lme4 (Bates, Maechler, Bolker, & Walker, 2014) and rethinking (McElreath, 2014) to fit multilevel models.

Ethical Note

The golden-mantled ground squirrel is not endangered or threatened and is common in the East River Valley of Colorado, where this study population occurs. Our methods were conducted according to protocols approved by the Animal Care and Use Committees of the University of California, Davis (Protocol No. 19642) and the Rocky Mountain Biological Laboratory (Protocol No. 21), permitted by Colorado Parks and Wildlife (Colorado Scientific Collecting Permit No. TR334) and followed guidelines approved by the American Society of Mammalogists (Sikes, 2016). Squirrels were live trapped, handled, tagged and dye-marked by trained researchers and released at point of capture. Mortality rate as a result of trapping was 0.16%, with no additional injuries associated with trapping.

RESULTS

We recorded 127 litters that were weaned within the study area from 1995 through 2012; of these, litter size, sex ratio at weaning and maternity were known for 101 litters, born to 64 females. Across all litters in all years, the sex ratio of weaned pups was 48.7% male, which was not significantly different from the null hypothesis of 50% males (exact binomial test: two-tailed $P = 0.545$). By year, the percentage of male pups produced varied from 18.2% (in 2000) to 60.5% (in 1995).

Maternal Investment

There was no relationship between total litter mass (a proxy for total maternal investment) and litter sex ratio ($F_{1,30} = 0.108$, $P = 0.744$). Within a litter, sons were not heavier than daughters (paired t test: $t_{31} = -0.162$, $P = 0.872$). After controlling for maternal identity and year, relative investment in sons did not vary with total maternal investment (GLMM effect of litter mass: $\beta = -0.001 \pm 0.002$, $t = -0.673$, $P = 0.500$; Fig. 1). The ratio of average mass of sons to average mass of daughters also did not vary with maternal investment (bGLMM effect of litter mass: $\beta = 0.0001 \pm 0.0002$, $t = 0.624$, $P = 0.532$).

Female Density and Local Competition with Kin and Nonkin

The number of breeding females (log transformed) present in the population was a significant predictor of offspring sex ratio ($F_{1,16} = 17.36$, $P < 0.001$, $R^2 = 0.52$; Fig. 2). At the individual female level, local density of total breeding adult females was not significantly related to litter sex ratio ($F_{1,99} = 2.04$, $P = 0.156$, $R^2 = 0.01$). However, litter sex ratio was significantly affected by the density of the type of breeding female. Solitary females, defined as those not

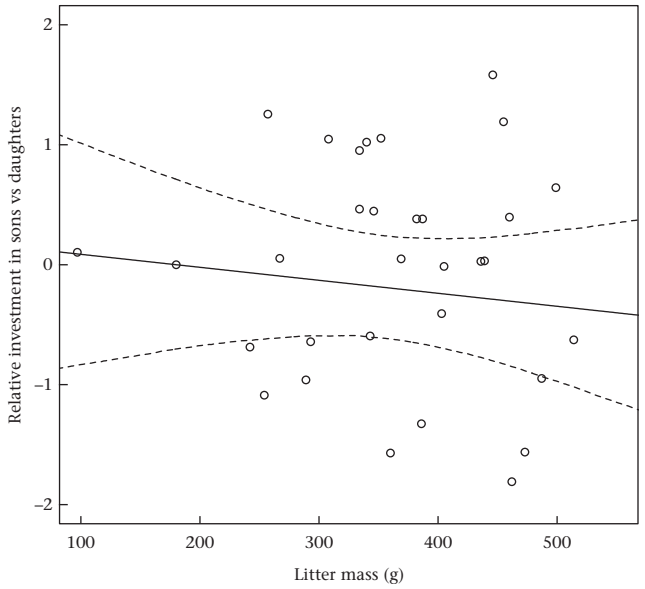

Figure 1. Relative investment in sons versus daughters (log (total mass of sons/total mass of daughters)) within a litter, as a function of maternal investment (litter mass). Positive values represent increased investment in sons; negative values represent increased investment in daughters. Points indicate observed values. The solid line represents the maximum likelihood estimate of the mean relative investment by litter mass, after controlling for maternal identity and year; the dashed lines represent the 95% prediction interval.

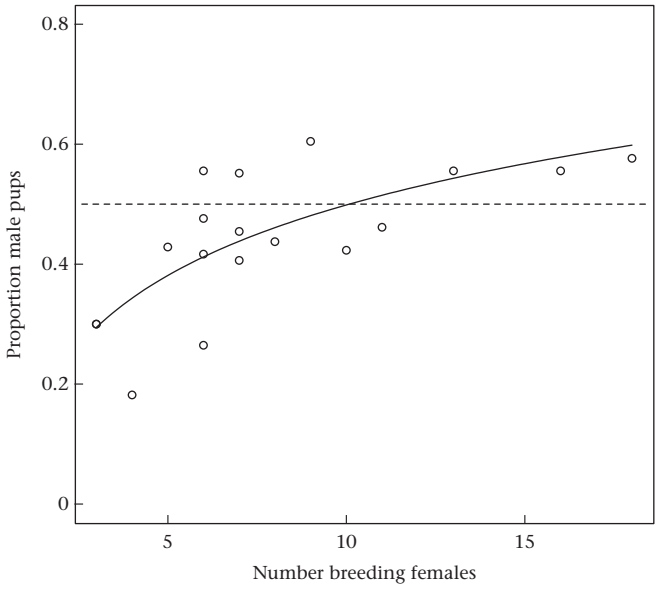

Figure 2. Proportion of male pups out of total pups produced each year, predicted by the number of breeding females present in the population that year. Dashed line represents null expectation of 50% males.

in the presence of female kin or nonkin, produced litters that were 40% male (95% CI = 26.5–55.97% male). Density of breeding kin predicted a shift towards production of sons at densities above two kin, although the effect was significant only at the highest density (four kin: $\beta = 3.08 \pm 1.5$, $Z = 2.03$, $P = 0.042$; Fig. 3). By contrast, there was no significant effect of density of nonkin breeding females on litter sex ratio (Fig. 3). Additionally, although maternal age did not affect offspring sex ratio ($\beta = 0.04 \pm 0.09$, $Z = 0.48$, $P = 0.635$; Fig. 3), there was an interaction between maternal age and kin density, where older females (≥3 years) surrounded by many breeding kin shifted towards production of daughters ($\beta = -1.45 \pm 0.73$, $Z = -1.96$, $P = 0.050$); yearling females surrounded by many breeding kin produced more sons (Fig. 4).

Food Availability at Conception

At the individual female level, timing of conception in relation to food availability had no significant effect on litter sex ratio ($\beta = 0.01 \pm 0.01, Z = 1.05, P = 0.293$; Fig. 5). Females who conceived litters after snow melt did not produce more male-biased litters than females who conceived litters before snow melt. Litter size ranged from one to eight pups, with an average litter size of 5.05 ± 1.39 pups. Litter size did not vary in relation to conception date (GLMM effect of conception date: $\beta = -0.02 \pm 0.01$, $Z = -1.20$, $P = 0.229$). Litter sex ratio did not vary significantly by litter size ($F_{7,93} = 1.48$, $P = 0.185$, $\eta^2 = 0.10$).

DISCUSSION

In this population of golden-mantled ground squirrels, variation in offspring sex ratio did not conform to predictions from the maternal condition theory of sex allocation (Trivers & Willard, 1973) or a proposed mechanism (sex-specific embryonic mortality; e.g. Larson, Kimura, Kubisch, & Roberts, 2001) of offspring sex ratio bias (Cameron, 2004).

The Trivers–Willard theory has been widely tested across mammalian taxa (Cockburn et al., 2002; West, 2009), but evidence from rodents remains equivocal; some studies report results that are consistent with predictions whereas others, including ours, report results that do not support the theory (Sikes, 2007). Inconsistent results might have several causes. One is that rodents are typically polytocous; mothers in polytocous species might manipulate litter size instead of sex ratio in response to maternal condition, potentially complicating predictions of sex ratio adjustment (Sikes, 2007; Williams, 1979). Another is the validity of the assumption that males in better condition enjoy higher reproductive success. Although male body size has been linked to mating success in many mammals (Lindenfors, Gittleman, & Jones, 2007), the assumption is not always verified for species tested under the Trivers–Willard theory, including golden-mantled ground squirrels. A third is that the ability of a female to invest in offspring may reflect extrinsic as opposed to intrinsic condition (Sikes, 1996). Ground squirrels appear to combine 'capital' and 'income' breeding strategies (Stearns, 1992), meaning that while maternal condition before conception may influence reproductive investment, the majority of resources invested in reproduction are acquired after parturition (Broussard et al., 2005). Lactation in ground squirrels is fuelled almost entirely by daily caloric intake (Kenagy, Stevenson, & Masman, 1989); thus, our measure of litter mass at weaning largely represents postnatal resource acquisition by the mother.

Food availability at conception has been proposed as a mechanism underlying biased offspring sex ratios in mammals (Cameron & Linklater, 2007; Cameron, 2004). Differential susceptibility of female embryos to circulating glucose levels ('glucose toxicity'; Larson et al., 2001) has been documented in rodents, including elevated female embryo mortality (Savchenko, Nazarova, & Evsikov, 2014) resulting in male-biased litters (Helle et al., 2008). While we did not measure maternal glucose levels in our study, we did not detect changes in sex ratio with timing of conception relative to the vegetation growing season. Furthermore, we did not detect a substantial effect of litter size on sex ratio: indeed, some of the largest litters contained exclusively female or exclusively male pups, suggesting that extremely biased sex ratios were not

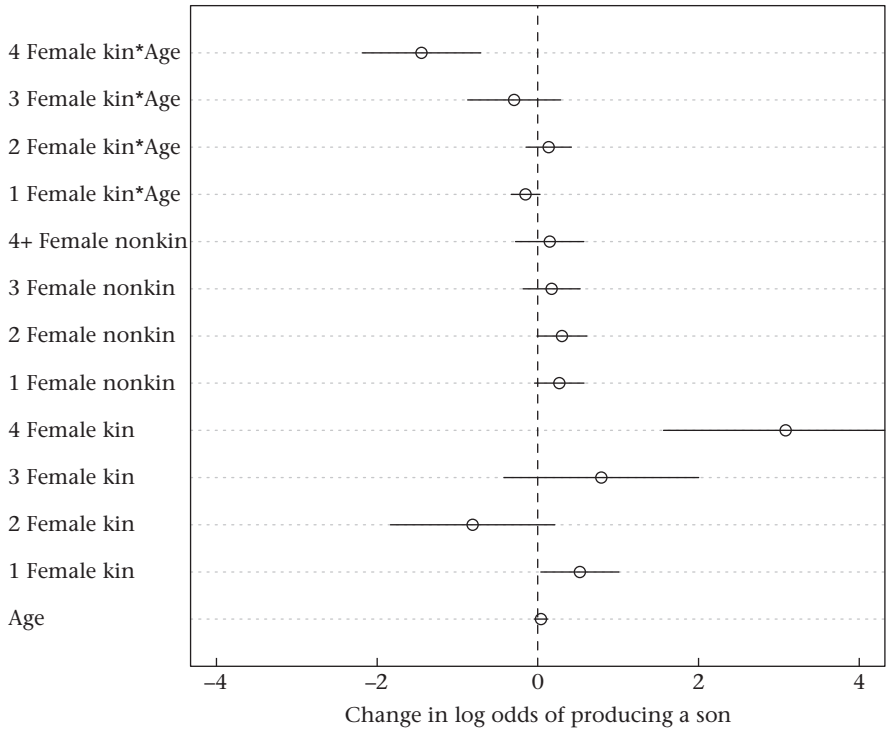

Figure 3. Coefficients from a GLMM of maternal age, density of related females, density of unrelated females, and an interaction between density of related females and maternal age; coefficients represent change in parameter compared to a solitary female (female kin = 0, female nonkin = 0). Density of related females ('Female kin') and unrelated females ('Female nonkin') were modelled as factors to explore nonlinear effects, and female identity was included as a random effect. Positive coefficients represent increased likelihood of producing a son; negative coefficients represent reduced likelihood of producing a son.

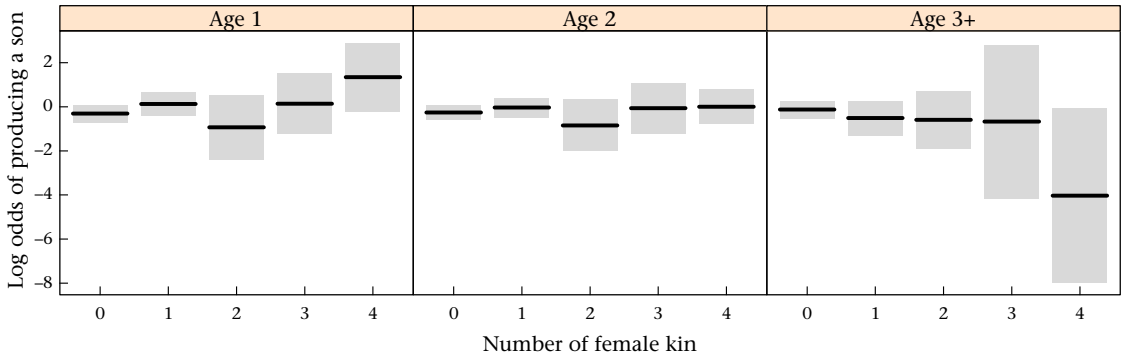

Figure 4. Modelled relationships between kin density and odds of producing a son for each birth, by maternal age. Effects were plotted with the additional factor (nonkin density) held constant at the mode (0). Black lines are estimates with shaded 95% confidence interval. Zero log odds indicates equal likelihood of producing a son or daughter; positive estimates represent increased likelihood of producing a son, and negative estimates represent reduced likelihood of producing a son.

accomplished through selective mortality that reduced overall litter size.

Density of breeding females appeared to influence offspring sex ratio. At the population level, more female offspring were produced in years of low density and more male offspring were produced in years of high density. This finding is consistent with theories of local resource competition (Clark, 1978; Silk, 1983), where females facing high competition for resources bias investment away from the philopatric sex (in this case, females). However, this density effect was expressed differentially at the individual level. Litter sex ratio did not vary in response to total density or nonkin density, but responded strongly to kin density. Furthermore, the effect of kin was nonlinear, as females in the presence of kin produced more sons than did solitary females only in particularly dense kin neighbourhoods. If density-dependent competition among breeding females is also nonlinear, four female kin may represent a threshold of habitat saturation beyond which additional daughters are unlikely to be recruited. The role of kinship in the behavioural interactions and spatial organization of golden-mantled ground squirrels has not been studied. However, even though the species is considered solitary and asocial, it possible that female kin are less agonistic towards each other than to nonkin and accordingly share space. Thus, competition with kin might be disproportionately intense, especially at high densities. Kin identification might be based on familiarity (Hare, 1998), self-referential scent matching (Mateo, 2010), or both (Holmes, 1995).

Interestingly, the effect of kin density was reversed for older females: in dense kin neighbourhoods, older (3 years or more) females were much more likely to produce daughters than sons. A negative relationship between sex ratio (sons produced) and

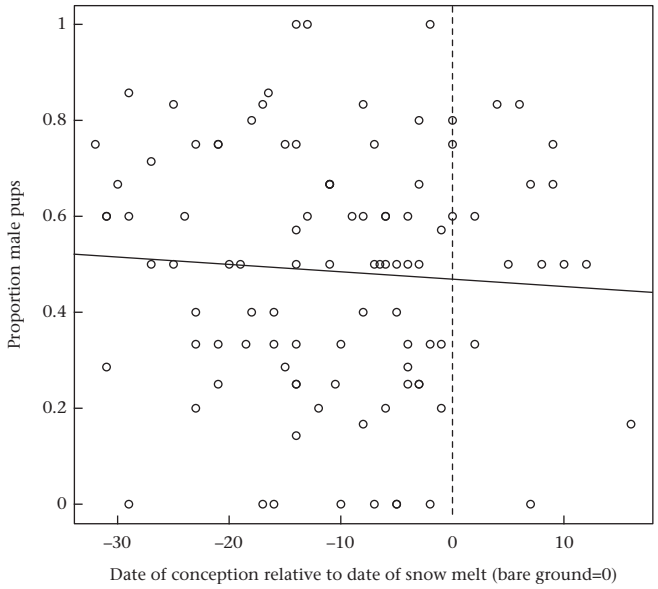

Figure 5. Litter sex ratio in relation to conception date, 1995–2012. Vertical dashed line at zero represents date of snow melt.

maternal age is expected when daughters remain philopatric, since daughters born late in a female's life will compete with her for fewer years than daughters born early (Clutton-Brock & Iason, 1986; Cockburn, Scott, & Dickman, 1985). However, in our study, offspring sex ratio was not affected by maternal age per se; another possibility is that the effect we detected was caused by female dominance within the matriline that is conferred by age. Dominant females may be more able to bear the costs that result from competition with additional philopatric daughters than are younger or subordinate females (Clark, 1978), or perhaps only dominant females are able to facilitate the recruitment of additional philopatric daughters, which provide greater fitness benefits than would dispersing sons. Female dominance is reliably associated with positive reproductive consequences in social species (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011) and may be in relatively asocial species as well.

Local resource competition has been invoked to explain changes in offspring sex ratio in a variety of mammalian taxa, including primates (Silk & Brown, 2008; Silk, 1983; van Schaik & Hrdy, 1991), ungulates (Hewison & Gaillard, 1999; Kruuk et al., 1999; Sheldon & West, 2004) and marsupials (Cockburn et al., 1985; Johnson et al., 2001; Schwanz & Robert, 2014). Our study found that support for local resource competition was most pronounced when females live in dense neighbourhoods of female kin. In other rodents, evidence for sex ratio adjustment in response to local density is mixed. The number of breeding females influenced offspring sex ratios in four species of *Acomys* mice, but the direction of the effect (male or female bias) differed by species (Nováková et al., 2010). Local female density increased the proportion of males born to Damaraland mole-rats, *Fukomys damarensis* (Lutermann, Cameron, Raihani, & Bennett, 2014), but did not affect offspring sex ratios of Richardson's ground squirrels, *Urocitellus richardsonii* (Gedir & Michener, 2014). Few studies have considered relatedness in calculations of local density. Local density of females did not affect offspring sex ratios of Townsend's voles, *Microtus townsendii*, nor did presence or absence of a matriline member (Lambin, 1994). Yellow-bellied marmots, *Marmota flaviventris*, did not alter offspring sex ratios according to local density, but young females produced female-biased litters in the presence of kin (Armitage, 1987). Inconsistent findings among species may result in part because the role of kinship was not considered in all studies. Alternatively, different findings among species may truly represent different effects of female density, resulting from differing social systems that alter the costs and benefits of producing sex ratios biased towards sons or daughters (Silk & Brown, 2008).

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