

Determinants of multiple paternity in a fluctuating population of ground squirrels

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Received: 18 July 2016 / Revised: 9 January 2017 / Accepted: 13 January 2017 / Published online: 27 January 2017
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Abstract

Multiple paternity is common in vertebrates that produce several offspring in the same reproductive bout, but the rate often varies among and within populations. Three primary explanations for this variation have been advanced: null models based on encounter rate of mates, socioecological models dependent on the ability of males to monopolize females, and age- or condition-dependent models of female choice. We used 18 years of genetic and demographic data to examine the mating system and patterns of multiple paternity in a free-living population of golden-mantled ground squirrels (*Callospermophilus lateralis*). The mating system was polygynandrous, but opportunity for sexual selection was lower for females than for males. Annual reproductive success of males was low for yearlings and new immigrants and increased with breeding tenure in the population. Multiple paternity was evident in 62% of litters. In accordance with the socioecological model of male monopolization, rates of multiple paternity decreased with female spatial clustering, unless male–male competition, as indicated by male

density, was also high. From Bateman gradients, we found no direct fitness benefit of multiple paternity for females. Though not statistically significant, multiple paternity appeared to decrease with maternal age and peri-oestrous mass, in possible support of the female choice model. Together, our results suggest that variation in the rate of multiple paternity in golden-mantled ground squirrels was determined by density and the active strategies of males and females.

Significance statement

Since the advent of molecular parentage assignment several decades ago, we have known that females of many species produce offspring with different fathers. Several theories have been developed for why females produce multiply-sired clutches or litters, but rarely are we able to identify the environmental, social, or individual conditions under which they do so. In this study, we genotyped offspring produced in one population of ground squirrels over 18 years, and found that the frequency of multiple paternity varied considerably from year to year, that density of female kin interacted with male density to influence multiple paternity, and that older and heavier females tended to be less likely to produce multiply-sired litters. These results demonstrate how dynamic population and individual characteristics of breeding males and females contribute to mating system variation in the same population over time.

Communicated by E. Korpimäki

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Keywords Multiple male mating · Density · Polygynandry · Mating system variation · Male reproductive success · *Callospermophilus lateralis*

Introduction

Female vertebrates often mate with multiple males, resulting in multiple paternity within their clutch or litter (Jennions and

Petrie 2000; Slatyer et al. 2012). While rates of multiple paternity appear quite stable in some species (e.g., Murie 1995; Naim et al. 2011; Thonhauser et al. 2014; Sommaro et al. 2015), other species show substantial variation among populations (Dean et al. 2006) or among years within populations (Schwagmeyer and Brown 1983; Jones et al. 2012). Several explanations have been proposed for within-population variation in multiple paternity, both environmental and social, but the causes remain poorly understood (Solomon and Keane 2007).

Multiple mating by females may be simply a matter of opportunity, varying with the rate at which females encounter potential mates. Both increases in male density and increases in male-bias in the operational sex ratio (number of adult males per adult female, Emlen and Oring 1977) increase the number of males that females might encounter (Kokko and Rankin 2006), and barriers to male movement during the breeding season, such as spring snowfall, may decrease that number (Michener and McLean 1996; Bergeron et al. 2011; Martin et al. 2014). This scenario, in which the rate of multiple mating scales with encounter rate, has been considered the null model of multiple mating (Kokko and Rankin 2006); we will refer to it as the “encounter rate” model (Table 1). Additionally, multiple paternity may result from the active mating strategies of males or females. Males may attempt to maximize paternity by monopolizing receptive females; if so, multiple mating by females is expected to be the most common when they are the least monopolizable, such as when females become spatially dispersed (Emlen and Oring 1977), their receptivity becomes temporally clustered (Isvaran and Clutton-Brock 2007), or both (Emlen and Oring 1977; Shuster and Wade 2003). We will refer to this scenario as the “male monopolization” model. On the other hand, females may seek multiple paternity according to the costs and

benefits of multiple mating. Females may choose to mate multiply to gain direct (Wolff and MacDonald 2004; Hoogland 2013) or indirect benefits (Eberhard 1996; Zeh and Zeh 1997; Jennions and Petrie 2000) that enhance reproductive success. One of the proposed direct benefits of multiple mating, enhanced fertility, should be particularly important for species in which the costs of reproductive failure are high, such as those who face a short breeding season, produce only one litter, or have low survival probability. Additionally, the costs and benefits of mate choice, including multiple mating, likely vary according to a female’s age or physical condition (Cotton et al. 2006). Young females with higher associated reproductive value may be more selective than older females (Kodric-Brown and Nicoletto 2001; Atwell and Wagner 2014), and hence reduce multiple mating. Additionally, females in poor physical condition may reduce multiple mating in order to minimize the costs associated with mating, such as disease transmission or enhanced vulnerability to predation (Daly 1978; Magnhagen 1991). This scenario, in which multiple paternity varies with maternal characteristics, we call the “female choice” model.

Multiple paternity has the potential to shape the strength of sexual selection. The opportunity for sexual selection is determined by intrasexual variation in the number of offspring produced; the strength of sexual selection is often defined as the slope of the linear relationship between offspring produced and number of mates obtained, known as Bateman’s gradient (Bateman 1948; Jones et al. 2002). In vertebrates, it is assumed that sexual selection acts more strongly on males (Andersson and Iwasa 1996). However, this may not be the case if variation in reproductive success is similar between the sexes. Specifically, if females gain direct benefits from multiple mating, in the form of higher reproductive success

Table 1 Predictions of hypotheses posed to explain variation in multiple paternity

Hypothesis	References	Predictions
Encounter rate, “Null model”	An increase in the rate at which females encounter male mates will increase multiple paternity Kokko and Rankin 2006	1. Increased male density or male-bias in operational sex ratio will increase multiple paternity 2. Weather conditions that impede male ability to locate females will decrease multiple paternity
Male monopolization	Male monopolization of females will decrease multiple paternity Emlen and Oring 1977 Shuster and Wade 2003	1. Increased spatial clustering of females will decrease multiple paternity 2. Increased breeding synchrony will increase multiple paternity
Female choice	Multiple paternity varies with female age and condition because of the following: A. Reproductive value is positively associated with strength of mate choice, and/or B. Mating is costly Cotton et al. 2006 Daly 1978	A1. Young females will decrease multiple paternity B1. Females in poor condition will decrease multiple paternity

(Jennions and Petrie 2000; Munroe and Koprowski 2011; Hoogland 2013), then high rates of multiple paternity can produce strong and potentially divergent selection on mating tactics of males and females (Munroe and Koprowski 2011).

Female vertebrates appear to mate multiply under many systems of social organization. Social monogamy is typical in avian species, yet female birds frequently produce multiply-sired clutches (Arct et al. 2015), and female mammals of socially monogamous species mate with multiple males as often as those of socially polygynous species (Solomon and Keane 2007). Among mammals, multiple paternity is common in ground-dwelling squirrels, and small-bodied ground squirrels in particular exhibit polygynandrous (sensu Shuster and Wade 2003) mating systems in which males mate with multiple females and females mate with multiple males (Munroe and Koprowski 2011; Schwanz et al. 2016). We used data from a long-term study of golden-mantled ground squirrels (*Callospermophilus lateralis*) to investigate intrapopulation variation in rate of multiple paternity. The mating system of golden-mantled ground squirrels is unknown, but limited spatial overlap among home ranges of adult females (Jesmer et al. 2011) suggests that potential for polygyny is low (Emlen and Oring 1977). Nonetheless, spatial clustering of females appears to increase with population density (Wells 2016), potentially generating interannual variation in mating patterns with changes in density.

We characterized the mating system of golden-mantled ground squirrels in order to estimate the opportunity for sexual selection and Bateman gradient for each sex, quantify the rate of multiple paternity, and assess factors influencing the frequency of multiple paternity. We tested two predictions based on encounter rate, that multiple paternity would increase when male density or operational sex ratio (OSR) was high and decrease when weather conditions at mating were unfavorable. We tested two predictions about the effect of male monopolization, that multiple paternity would decrease when female breeding synchrony was high, and when female density, and thus presumably spatial overlap of females, was high. We tested two predictions based on female choice, that multiple paternity would be higher for older mothers than mothers at the age of first reproduction (1 year) and also higher for mothers in better condition.

Methods

Study site and species

We studied golden-mantled ground squirrels in the East River Valley of Gunnison County, Colorado (38°58'N, 106°59'W), at the Rocky Mountain Biological Laboratory (2900 m), from 1996 to 2015. Golden-mantled ground squirrels are a small-sized (150–300 g) diurnal species, and are considered asocial

(Michener 1983; Ferron 1985; Bartels and Thompson 1993). At our study site, adult (≥ 1 year old) squirrels were active above ground between late April and early September. The breeding season began shortly after females emerged from hibernation in April or May and encountered scrotal males; breeding ended usually by late May. Females gave birth to a single litter per year, after approximately 28 days gestation (McKeever 1964). Litters emerged from their natal burrows at weaning (approximately 30 days after birth, Phillips 1981), in June or July. Juvenile dispersal, which was male-biased, began in August; adult immigrants of both sexes appeared in all months of the active season. Adults reduced aboveground activity beginning in August, juveniles in September, and all squirrels were below ground for hibernation by October. Female activity was generally concentrated on rocky slopes and in dry meadows, in one of six localities containing persistent burrow systems (Wells 2016). Density of adults at our 13-ha site ranged from 1 to 3 squirrels/ha among years (Kneip et al. 2011), with 1–6 breeding females per locality (Wells 2016).

We captured squirrels using live traps (Tomahawk Model 201) set in areas of squirrel activity and baited with peanut butter and sunflower seeds; our trapping protocol was approved by Animal Care and Use Committees of the University of California, Davis, and the Rocky Mountain Biological Laboratory, and adhered to guidelines approved by the American Society of Mammalogists (Sikes and Gannon 2011). It was not possible to record data blind because our study involved focal animals in the field. We attempted to capture adults monthly. Pups were captured at weaning as they emerged from their natal burrows from mid-June to mid-July, and again before immergence in September; mothers typically were trapped with their pups as the litter emerged. Immigrants were captured as they appeared in the population, and again before immergence in September. At capture, we recorded body mass (to the nearest 1 g), sex (anogenital distance), and reproductive status. Age was known for individuals who were born into the population, or who immigrated into the population as juveniles. We marked each squirrel with a numbered metal eartag in each ear for permanent identification, and with black fur dye for identification during behavioral observations. We plucked hairs from the rump of each animal and stored the hairs in a dry envelope at room temperature until the end of the field season, when they were transferred to a chest freezer (-18°C) until genetic analysis.

DNA extraction and genotyping

Squirrels captured 1996–2005 were genotyped as described in McEachern et al. (2011). Usable DNA could not be obtained from hair samples collected in 2006 and 2007. Squirrels captured for 2008–2015 were genotyped according to the

following protocol. Hairs were individually inspected for the presence of a tissue bulb, and DNA was extracted from ten hairs per individual using the DNA IQ system with Hair and Tissue kit (Promega Corp., Madison, WI, USA), following manufacturer instructions. Hair samples were stored up to 6 years before extraction. Six microsatellite loci, previously verified to amplify in this species (McEachern et al. 2011), were amplified for 445 individuals. Forward primers were fluorescently labeled with 6-FAM (ST7, Bib36), NED (Bib18, Sgs17), or VIC (Bib4, Sgs14), and reverse primers were unlabeled (all primers Applied Biosystems, Foster City, CA, USA).

We amplified markers by polymerase chain reaction (PCR), conducted in 10 μ l reactions, using 1 μ l template DNA (approx. 2 μ g/ μ l), 0.15–0.4 μ l forward and reverse primers, 1 μ l BSA (100 μ g/ μ l), 0.15 μ l FastStart Taq DNA polymerase, 1 μ l FastStart buffer, 0.8 μ l dNTP (all Sigma-Aldrich Co., St. Louis, MO, USA), and 5.6–5.9 μ l H₂O. We used a touch-down thermal profile for PCR, consisting of one denaturation cycle at 94 °C for 5 min, 15 cycles at 94 °C for 30 s, 65 °C (stepped down by 1 °C each cycle) for 90 s, and 72 °C for 60 s; 15 cycles at 94 °C for 30 s, 55 °C for 90 s, and 72 °C for 45 s; ending with 10 min at 72 °C for final extension. We used a nested PCR protocol, involving two rounds of PCR, to increase amplification for five of the six loci (all but Sgs14). The first round was conducted as above using 1 μ l extracted DNA, and the second (“nested”) round replaced the 1 μ l DNA with 1 μ l PCR product from the first round to increase the number of template copies for amplification. Amplification was sufficient for locus SGS14 without the nested protocol, using 2 μ l extracted DNA, 0.5 μ l each forward and reverse primer, and 4.05 μ l H₂O (other reagents stayed the same). We loaded 1 μ l PCR product with 8.7 μ l formamide and 0.3 μ l 600LIZ internal size standard to visualize PCR fragments on an ABI 3730xl DNA Analyzer (Applied Biosystems Inc., Foster City, CA, USA). Alleles were scored using GeneMapper software (v4.0, Applied Biosystems, Inc.) and were confirmed by visual inspection of electropherograms.

Paternity analysis

We used Cervus 3.0.7 (Kalinowski et al. 2007) to assign paternity to offspring with known mothers. We simulated the likelihood of paternity assignment separately for each year to determine critical delta values. Simulations used allele frequencies from genotypes of all squirrels in the population for that year; parameters were set to simulate 100,000 offspring from all known mothers and 75% of potential fathers (all potential fathers ranged from 4 to 20 males per year), with 90% of loci typed (minimum observed value) and 2% genotyping error (empirically determined, averaged across all loci from a minimum of 40 replications for each locus).

We used mother–father–offspring trios that were assigned at the 80% confidence level or higher. For some litters, particularly those born for 1996–2005, not all offspring in a litter could be definitively assigned to specific males; however, if one pup in a litter was assigned to a male at 80% or higher confidence, and that male was not among the top two candidate fathers for an unassigned sibling, we considered that litter was multiply sired. Litters for which no fathers could be confidently assigned were excluded from analysis. For 2002–2005, limitations of gel electrophoresis made scoring unreliable for some loci, resulting in poor paternity assignment. For each of those years, we used genotype matching of known maternal–offspring pairs in Cervus to determine error rates and excluded the locus with the highest error rate. For 2002, this was locus ST7 (4 mismatches out of 8 parent–offspring pairs, 55.8% error rate), and locus Sgs14 in 2003 (5 mismatches/31 pairs, 13.8%), 2004 (12 mismatches/67 pairs, 16.3%), and 2005 (18 mismatches/72 pairs, 22%). For 2005, locus Sgs17 was found not to be in Hardy–Weinberg equilibrium and was also excluded. After these loci were excluded, observed error rates dropped to 7% or lower for those years, and paternity assignment was possible for some offspring. We excluded any assignments that were based on fewer than three loci.

Mating and opportunity for sexual selection

For a subset of years ($n = 30$ litters, 168 pups from 2008 to 2015), we were able to assign paternity for 84% of pups. For each of those years, we tallied the number of pups sired by each male and the number of pups born to each female. We used these values for all reproductive adults (males that sired at least one pup, and females that produced at least one pup) to calculate the opportunity for sexual selection for each sex (I) according to the equation: $I = V_o/O^2$, where V_o is the variance in offspring numbers and O^2 is the squared average in offspring numbers (Shuster and Wade 2003; Munroe and Koprowski 2011). We also calculated the difference in opportunity for sexual selection between the sexes ($\Delta I = I_{\text{male}} - I_{\text{female}}$), to describe the difference in strength of selection between the sexes (Shuster and Wade 2003). To determine Bateman’s gradient (β_{ss}) for each sex, we tallied the number of mates for each male and each female and combined these data with the above offspring values for all reproductive adults (Andersson and Iwasa 1996). We fit a linear model for each sex, with total offspring produced per individual modeled as a function of number of mates.

Male reproductive success

Male reproductive success, an important component of the mating system and opportunity for sexual selection, might be determined by several factors. We used the complete

paternity data from 2008 to 2015 to evaluate whether age, breeding tenure, breeding mass, or reproductive investment influenced male reproductive success. Age was known for almost half of adult males (47% of 71 males). Breeding tenure was the number of years the male was present during the breeding season. We used size of scrotal testes, measured as anogenital distance, to estimate reproductive investment (Schulte–Hostedde and Millar 2004).

We fit a series of generalized linear mixed-effect models (GLMMs) with male characteristics (age, breeding tenure, breeding mass, and reproductive investment; no interaction terms included) as fixed effects, to predict the following outcomes for each breeding season: likelihood of reproduction (yes/no, modeled with binomial error structure and logit link), number of mates (Poisson error structure), and number of offspring produced (Poisson error structure). We included male identity as a random effect in all models, to control for multiple records from males who were present in the breeding season of more than 1 year.

Multiple paternity

Unless otherwise stated, we modeled multiple paternity as a binary outcome variable (0/1) in generalized linear mixed-effects models (GLMMs), with binomial error structure and a logit link. We fitted maternal ID as a random effect, to control for multiple litters produced by individual females in different years. We also included year as a random effect, to control for unspecified annual variation in environmental conditions.

Encounter rate

The number of potential male mates may influence the frequency with which females mate multiply (Kokko and Rankin 2006, and citations therein). Increases in population density increase the absolute number of potential mates, while increased male-bias in adult sex ratios increases the relative number of potential mates that females are likely encounter (Kokko and Rankin 2006). Hence, we modeled multiple paternity as a function of male density and OSR. Male density was defined as the total number of adult (≥ 1 -year old) males resident in the population, and OSR was defined as number of adult males per adult female. Because the participation of 1-year old males in breeding was unknown, but potentially limited, we also tested for an effect of the density of males ≥ 2 -years old on multiple paternity.

Deep snow and spring storms can reduce mating activity in ground squirrels (Morton and Sherman 1978; Michener and McLean 1996), which may result in lower rates of multiple paternity (Bergeron et al. 2011; Martin et al. 2014). Golden-mantled ground squirrels often mate

before snowmelt, in some years when snow is quite deep (Wells 2016), and deep snow may impede male movement across the snow surface as they seek mates. Hence, we tested the prediction that deep snow or heavy precipitation reduce male mobility, impacting the likelihood that females will encounter multiple males during their estrous period, and therefore reducing the incidence of multiple paternity of their litters. We modeled multiple paternity of each litter as a function of snowpack and precipitation on date of estrous. Snowpack (depth of snow in cm) and precipitation (in cm) were measured daily, and date of estrous was estimated by subtracting 58 days (28 days for gestation, 30 days for lactation) from the observed date of litter emergence.

Male monopolization

We modeled multiple paternity as a function of breeding asynchrony and local density of breeding females. Breeding asynchrony, which we used as an estimate of temporal clustering of receptive females, was defined as the number of days between the emergence of the focal litter and the next litter closest in time (before or after): assuming a relatively fixed period of gestation + lactation, we reasoned that the number of days between the emergence of two litters should approximate the number of days between the conception of those two litters, and hence the temporal separation between mating of estrous females. However, because we excluded females who mated but did not conceive, or who conceived but lost their litter, our measure of breeding asynchrony may be an underestimate of temporal clustering. Local density of breeding females was defined as the number of reproductive females who produced a litter in the same one of the six localities as the focal female. This local density was further partitioned into local density of related females versus local density of unrelated females; there is some evidence that female kin tend to live in closer proximity (Wells 2016), thereby enhancing spatial clustering. Female relatedness was calculated by using pedigree data to construct matriline (Wells 2016); females were considered kin if estimated relatedness (r) was ≥ 0.125 , corresponding to first cousins or closer. Males should be attracted to clusters of females, and because increases in male–male competition may affect the ability of males to monopolize clustered females (Emlen and Oring 1977; Shuster and Wade 2003), we included male density in the model to test for an interaction between breeding female density (spatial clustering) and male density. Clustered females should be economically defendable by a single male only when competition from other males is low (Emlen and Oring 1977): hence, we predicted that rates of multiple paternity in female clusters should be

low when male density is low, and high when male density is high.

Female choice

We modeled multiple paternity as a function of maternal age and maternal condition. Maternal age was defined as a factor, where 0 represented yearling females, and 1 represented females 2 years and older. We used body mass as an estimate of maternal peri-oestrus condition (Wells 2016), which was measured for a subset of females ($n = 17$ females) and was defined as mass as measured within 1 week before or after estimated date of estrous.

Data were analyzed using R version 3.0.2 (R Core Team 2013). We used the packages lme4 (Bates et al. 2014) and rethinking (McElreath 2014) to fit mixed-effect models. Parameter estimates β (\pm SE) are reported in the logit form for binomial models.

Results

We genotyped a total of 476 offspring from 108 litters, and we were able to assign paternity with 80% or higher confidence to 270 (56.7%) mother–father–offspring trios. Our final dataset included 244 trios (of $\geq 80\%$ confidence) from 66 litters. Mean polymorphic information content (PIC) was 0.72 (range 0.63–0.75), and combined non-exclusion probability for a second parent was 0.011 (range 0.003–0.039; Table 2).

Mating patterns

In every year of the study, at least one male mated with multiple females or at least one female mated with multiple males; hence, this population meets the definition of polygamy (McEachern et al. 2009) or polygynandry (Munroe and Koprowski 2011). However, not all females mated multiply, and both monogamous and polygamous patterns were observed (Fig. 1). Across all years, rates of monogamy and polygamy were 37 and 63%, respectively, for females, compared to 49 and 51% for males. One case of polygyny extended across years, in which the same male mated with both an adult female and her adult daughter in 2009, and again in 2010. We detected one case of close incest out of approximately 100 matings, where a yearling female mated with her father.

Maximum annual reproductive success was higher for males than for females. Litter size for females did not exceed seven pups, whereas a single male sired 20 pups (with five females) in 1 year. Opportunity for sexual selection was substantially lower for females ($I_s = 0.06$) than for males ($I_s = 0.60$), with a difference in relative fitness (ΔI) of 0.54. Bateman's gradient was strongly positive for males ($y = 3.88 \times -1.41$, $r^2 = 0.78$, $p < 0.001$), but not different

from zero for females ($y = 0.46 \times +4.45$, $r^2 = 0.05$, $p = 0.252$; Fig. 2).

Male reproductive success

Yearling males rarely bred successfully (only 2 out of 29 known-aged yearling males), and age had a significantly positive effect on likelihood of reproduction ($\beta = 1.22 \pm 0.58$, $z = 2.09$, $p = 0.037$). Immigrant males rarely bred in their first year of residence in the population. Only 3 of 28 (11%) successfully reproduced in their first season, compared to 8 of 12 (67%) in their second season, and 3 of 3 (100%) in their third season. Further, those three new immigrant males produced only one or two offspring each, compared to an overall average of 5.6 offspring per male per year. Average male breeding tenure was 1.36 seasons ($n = 152$ males, range = 1–5 seasons). Male breeding tenure strongly affected reproductive success. For each additional breeding season present, males were more likely to reproduce that season ($\beta = 1.96 \pm 0.51$, $z = 3.83$, $p < 0.001$), gained a higher number of mates ($\beta = 0.91 \pm 0.20$, $z = 4.56$, $p < 0.001$), and produced more offspring ($\beta = 0.82 \pm 0.14$, $z = 5.74$, $p < 0.001$). After controlling for breeding tenure, neither male mass ($\beta = -0.02 \pm 0.10$, $z = -0.23$, $p = 0.821$) nor anogenital distance ($\beta = 0.07 \pm 0.52$, $z = 0.13$, $p = 0.895$) had an effect on likelihood of reproduction.

Multiple paternity

Over the course of this study, 62% of litters were multiply sired, but the proportion varied from year to year. Multiple paternity was the lowest in 2009 (25% of litters), and the highest in 1998, 2004, 2005, and 2014 (100% of litters). Multiple paternity did not affect litter size ($\beta = 0.07 \pm 0.35$, $t = 0.19$, $p = 0.851$). In the following models, the random effect estimates associated with each year were very small in magnitude compared to the random effect estimates associated with individual females, and compared to the fixed effects. This indicates that more of the variation in multiple paternity was explained by female identity and annual covariates (e.g., local density of related breeding females, and its interaction with total male density), rather than unobserved differences among years.

Encounter rate

Male density did not significantly affect the likelihood of multiple paternity ($\beta = 0.08 \pm 0.08$, $z = 0.93$, $p = 0.350$), and neither did density of males 2 years and older ($\beta = 0.23 \pm 0.15$, $z = 1.62$, $p = 0.106$). Operational sex ratio also did not affect multiple paternity ($\beta = -0.08 \pm 0.66$, $z = 0.13$, $p = 0.895$). Amount of precipitation on the estimated date of conception had a negative effect on likelihood of multiple paternity that approached statistical significance ($\beta = -0.13 \pm 0.07$, $z = -1.75$, $p = 0.081$).

Table 2 Summary statistics for population allele frequencies and paternity assignment, by year, as calculated in Cervus 3.0.7

Year	No. of individuals genotyped	No. of loci	Mean alleles per locus	Mean prop. loci typed	Mean exp. Hz	Mean PIC	Combined non-exclusion probability (second parent)
1996	56	6	7.8	0.88	0.77	0.73	0.004
1997	65	6	8.3	0.94	0.78	0.75	0.003
1998	27	6	8.3	0.98	0.78	0.74	0.004
1999	24	6	6.8	0.99	0.73	0.68	0.011
2000	22	6	6.5	0.99	0.73	0.67	0.014
2001	29	6	5.5	0.94	0.69	0.63	0.026
2002	33	5	7.4	0.91	0.74	0.70	0.016
2003	62	5	7.0	0.91	0.76	0.72	0.018
2004	123	5	8.2	0.94	0.75	0.71	0.020
2005	132	4	8.8	0.91	0.75	0.72	0.039
2008	53	6	8.8	0.94	0.78	0.75	0.005
2009	65	6	10.2	0.98	0.78	0.75	0.004
2010	73	6	9.5	0.98	0.76	0.73	0.004
2011	53	6	8.7	0.98	0.78	0.74	0.004
2012	72	6	10.2	0.99	0.74	0.71	0.006
2013	49	6	9.8	1	0.78	0.74	0.003
2014	47	6	9.0	1	0.78	0.74	0.004
2015	33	6	7.8	0.99	0.75	0.71	0.006
Average			8.3	0.96	0.76	0.72	0.011

Hz heterozygosity, PIC polymorphic information content

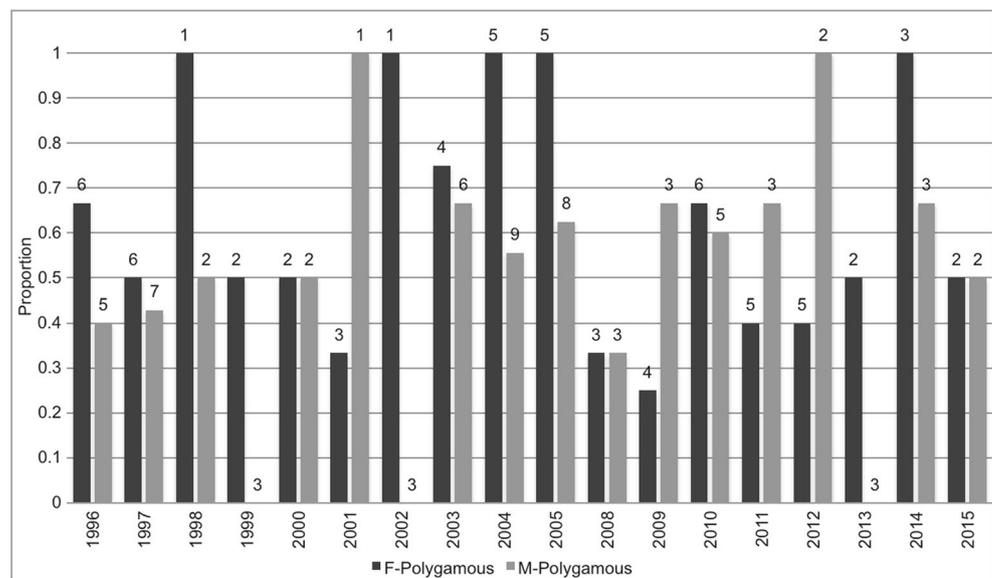
Snow depth on the estimated date of conception had no effect on multiple paternity ($\beta = 0.00 \pm 0.00, z = 0.33, p = 0.740$).

Male monopolization

Average breeding asynchrony (an estimate of temporal clustering) was 3.4 days (range = 0–29); breeding asynchrony had no effect on multiple paternity ($\beta = -0.04 \pm 0.05, z = -0.76,$

$p = 0.450$). Local density of breeding females did not affect the likelihood of multiple paternity ($\beta = 0.03 \pm 0.19, z = 0.18, p = 0.859$). However, when related versus unrelated females were distinguished, local density of related breeding females had a negative effect on multiple paternity ($\beta = -5.00 \pm 2.47, z = -2.03, p = 0.043$), while local density of unrelated breeding females had no effect on multiple paternity ($\beta = 0.24 \pm 1.24, z = 0.20, p = 0.846$). Further, there was a significant interaction

Fig. 1 Frequency of polygamous mating by year by sex. Females are represented with black bars, males by gray; labels above bars indicate total number of individuals of each sex that produced at least one offspring that year. Individuals that did not produce at least one offspring are not included in the frequencies above. Frequency of monogamy for each sex is equal to 1–proportion of polygamy



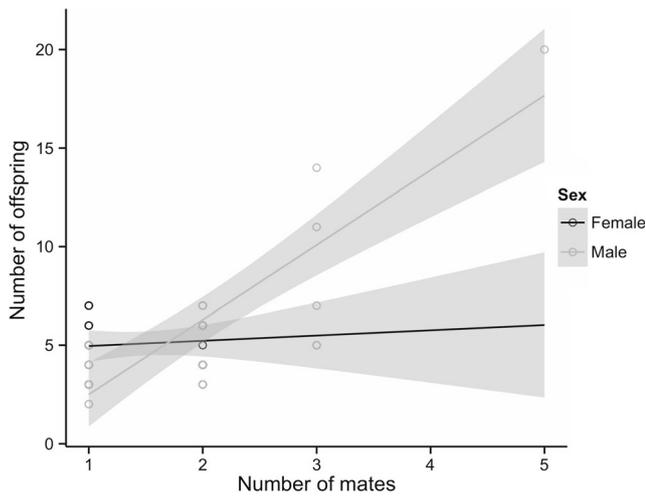


Fig. 2 Bateman's gradients for male (light gray) and female (black) golden-mantled ground squirrels in the East River Valley of Colorado (2008–2015). Shading represents 95% confidence intervals

between the local density of related breeding females and total male density ($\beta = 0.42 \pm 0.20$, $z = 2.06$, $p = 0.039$; Fig. 3). High female density decreased the likelihood of multiple paternity when males were relatively scarce (five total males), but increased the likelihood of multiple paternity when males were abundant (15 total males).

Female choice

The effect of maternal age on multiple paternity was nearly statistically significant, with females 2 years or older possibly less likely than yearling females to produce multiply-sired litters ($\beta = -1.67 \pm 0.87$, $z = -1.91$, $p = 0.056$). Though sample size was small ($n = 17$ females), the effect of maternal peri-oestrous mass was slightly but reliably negative, and approached statistical significance ($\beta = -0.05 \pm 0.03$, $z = -1.75$, $p = 0.080$; Fig. 4).

Discussion

The mating system of golden-mantled ground squirrels is consistent with that of other small-bodied ground squirrels, in which mating patterns are typically polygynandrous (Raveh et al. 2010). Further, the species exhibits high rates of multiple paternity, with nearly two-thirds of litters multiply sired, which is within the range reported for other squirrels with a low level of sociality (e.g., 54% for 13-lined ground squirrels, *ICTIDOMYS TRIDECIMLINEATUS*, Schwagmeyer and Foltz 1990; 55% for round-tailed ground squirrels, *XEROSPERMOPHILUS TERETICAUDUS*, Munroe and Koprowski 2011; 78% for Belding's ground squirrels, *UROCITELLUS BELDINGI*, Hanken and Sherman 1981; and 80% for Richardson's ground squirrels, *UROCITELLUS RICHARDSONII*, Hare et al. 2004). However, the population in this study exhibited substantial variation in the rate of multiple paternity across years, and we evaluated the ability of three hypotheses—based on encounter rates between females and potential mates, the ability of males to monopolize fertile females, and/or age- or condition-dependent female choice—to explain this variation. Our results best supported the male monopolization model with tentative, though not statistically significant, support for both the encounter rate and female choice models; we will discuss each of the findings in turn.

Despite multiple mating by both sexes, the opportunity for sexual selection was lower in females than in males, and the difference in opportunity for sexual selection between males and females was lower than for other ground squirrels (Munroe and Koprowski 2011); this minimal difference in opportunity for sexual selection may contribute to the minimal sexual dimorphism observed in this species (Matějů and Kratochvíl 2013). Additionally, female variance in reproductive success was low and did not depend on number of mates. This finding is in contrast to other small-bodied squirrels, where female reproductive success did increase with number of mates (yellow-pine chipmunks, *TAMIAS AMOENUS*, Schulte-Hostedde et al. 2004; round-tailed ground squirrels, Munroe

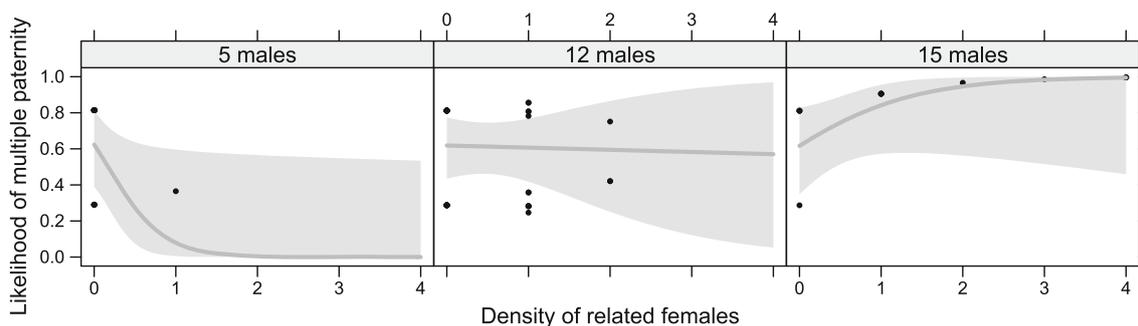
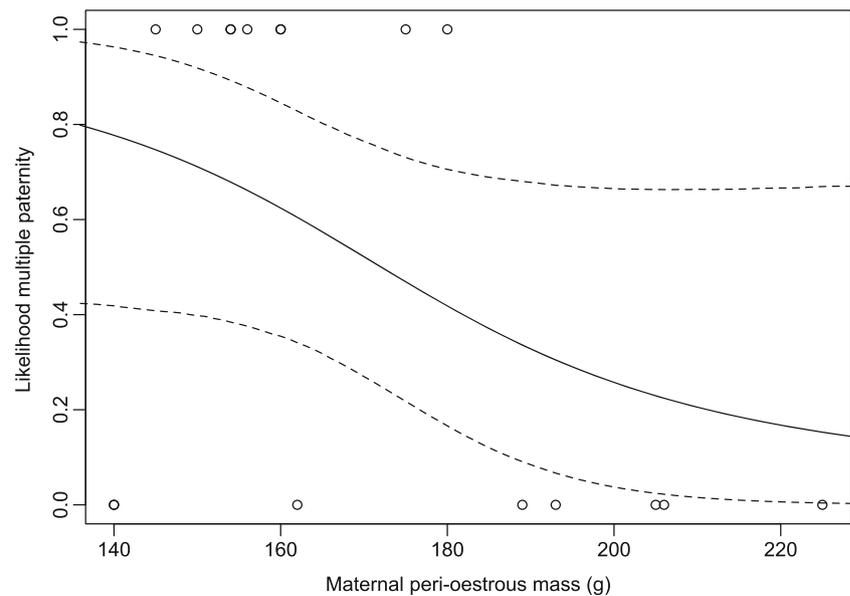


Fig. 3 Likelihood of a litter being multiply sired, modeled as an interaction between local density of breeding female kin and total males. The left-hand panel represents the lowest male density, and the

right-hand panel represents the highest male density. Lines are modeled relationships, with shaded 95% confidence intervals; points are partial residuals from the model

Fig. 4 Likelihood of producing a multiply-sired litter (0 = no multiple paternity, 1 = multiple paternity), by maternal mass near estimated date of conception. *Open circles* represent observed data. *Solid line* represents predictions from the model + 95% confidence interval (*dashed lines*)



and Koprowski 2011; and eastern chipmunks, *Tamias striatus*, Bergeron et al. 2012). In a highly-seasonal environment, such as that inhabited by our high-elevation population of golden-mantled ground squirrels, litter sizes may be constrained by resource availability, not by sperm-limitation. Regardless, though this does not rule out indirect (genetic) benefits of multiple paternity, it appears that female golden-mantled ground squirrels do not realize a direct fertility benefit from additional mates.

In contrast to females, males were able to substantially increase their annual reproductive success through additional mates. In polygynandrous ground squirrels, scramble competition for fertile females is thought to involve several components: overt male–male conflict, sperm competition, and skill in locating mates (Schwagmeyer and Wootner 1986; Raveh et al. 2010). Male mass may confer an advantage in overt conflict, but as has been found in the Rio Grande ground squirrel (*Ictidomys parvidens*, Schwanz et al. 2016), body mass did not affect reproductive success. Neither did reproductive investment (testes size), which may confer advantages in sperm competition. However, longer male tenure, which may influence conflict ability and skill in locating mates, had a strong positive effect on reproductive success. Specifically, both young and new immigrant males appeared to be at a reproductive disadvantage in our population, rarely acquiring mates and siring offspring. However, it is important to note that we did not directly observe copulations, and hence are reporting number of effective matings (i.e., those resulting in paternity) instead of the number of matings. Females who produced singly-sired litters may have actually mated with multiple males, including yearlings and immigrant males, but only accepted sperm from older or longer-resident males. Therefore, low reproductive success of yearling males may

result from low rates of reproductive maturity for males at this elevation after their first hibernation (Bronson 1979; CPW, unpublished data), the greater competitive ability of older males or their sperm, or female preference for older males. Low reproductive success of immigrant males could have resulted from their difficulty in locating females in a new area, female preference for familiar males, or the greater competitive ability of resident males. Taken together, our results suggest that male experience (perhaps associated with dominance) is important for access to female mates and siring of more offspring.

We expected that precipitation would affect multiple paternity by reducing male mobility. We found a negative effect of precipitation on multiple paternity that approached statistical significance, perhaps because wet conditions reduce above-ground activity in this species (Kneip et al. 2011). We did not find an effect of snow depth, in contrast to a study of yellow-bellied marmots (*Marmota flaviventris*) conducted in the same area, which found that snow depth during the breeding season had larger effects on limiting multiple paternity than did social or individual variables (Martin et al. 2014). However, yellow-bellied marmots are polygynous, and females often live in discrete habitat patches defended by a single territorial male (Armitage 2014); hence, single paternity is much more common than multiple paternity (82 vs. 18% of litters, Martin et al. 2014), and deep snow may impede the movements between distant patches that are required for a female to encounter multiple males. Because male golden-mantled ground squirrels are not territorial (CPW, unpublished data), females may have ready access to multiple males regardless of snow depth.

An increase of multiple paternity with increasing density has been documented in several rodent species (Dean et al.

2006; Bryja et al. 2008; Streatfield et al. 2011; but see Sommaro et al. 2015), including squirrels: a scarcity of reproductive males was thought to underlie a seasonal decline in multiple paternity in eastern chipmunks (Bergeron et al. 2011), Columbian ground squirrels exhibited higher rates of multiple paternity in years with more breeding males (Jones et al. 2012), and the number of potential male mates predicted a higher rate of multiple male mating in red squirrels (*Tamiasciurus hudsonicus*, McFarlane et al. 2011). Yet, male density alone did not increase the rate of multiple paternity of golden-mantled ground squirrels.

Male-bias in operational sex ratio is also expected to increase multiple paternity by increasing the rate at which females encounter male mates (Kokko et al. 2006), and in socially-monogamous vertebrates, increases in male-biased sex ratios are associated with increases in extra-pair paternity (Gowaty and Bridges 1991; Kokko et al. 2006). However, the relationship between OSR and multiple paternity in species with polygynandrous mating systems is less clear. Male-biased OSR was associated with increased multiple mating by female 13-lined ground squirrels (Schwagmeyer and Brown 1983), but somewhat reduced multiple mating by female Columbian ground squirrels (*Urocitellus columbianus*, Murie 1995). In both Richardson's ground squirrels (*Urocitellus richardsonii*, Michener and McLean 1996) and Cape ground squirrels (*Xerus inaurus*, Waterman 1998), female rate of multiple mating was independent of changes in OSR: females mated with multiple males when the OSR was strongly male-biased and when it was less so. OSR did not affect rates of multiple paternity in golden-mantled ground squirrels, though through post-copulatory female choice (Eberhard 1996), it is possible for OSR to have increased the rate of multiple mating without affecting the rate of multiple paternity (e.g., Murie 1995). Taken together, these findings suggest that, with the exception of a possible effect of precipitation on male availability, the encounter rate model is not sufficient to explain variation in the rate of multiple paternity in our system; instead of being a passive response to mate availability, variation in multiple paternity likely results from the interaction between encounter rates and the active strategies of males or females.

The ability of males to monopolize paternity is thought to vary with the spatial and temporal availability of fertile females (Emlen and Oring 1977; Shuster and Wade 2003). Spatial clustering of females did reduce the rate of multiple paternity in golden-mantled ground squirrels, but the effect was limited to female kin, perhaps because female kin are more clustered than nonkin (Wells 2016). Competitive males, which maximize their reproductive success by maximizing their number of mates, should be attracted to clusters of females and motivated to defend them. However, the effect of female clustering was reversed at high male density, presumably when male–male competition is higher. Male–male

competition increases the chance of mating interference (Kokko and Rankin 2006), including disrupted copulations (Klemme et al. 2007), leading to higher rates of multiple paternity. Apparently, individual males were able to monopolize females only when competition from other males was low. Unlike spatial clustering, temporal clustering of breeding females did not affect multiple paternity. In theory, a single dominant male should be able to take advantage of asynchronously fertile females by sequentially monopolizing each one (Emlen and Oring 1977), but in golden-mantled ground squirrels, this advantage is either not present (perhaps because of intense male–male competition) or may be outweighed by female choice.

Contrary to expectations, we found that young females and those that were lighter in weight, hence presumably in poorer condition, tended to be more likely than older and heavier females to produce multiply sired litters, not less likely. Much of the work on age-specific changes in mating preferences has used invertebrate models, where reproductive value is highest for young females and declines with age (Gray 1999; Wilgers and Hebets 2012; Atwell and Wagner 2014), but maximal reproductive value might occur at a somewhat older age in some ground squirrels (Dobson et al. 1999). Further, similar results for both age and condition suggest the possibility of a common explanation. We suggest that females that are young or in poor condition have lower fertility than other females, and that, as in Gunnison's prairie dogs (*Cynomys gunnisoni*, Hoogland 1998), multiple mating may increase the likelihood of conception. For yearling females, there is some evidence that the number of mates is positively associated with litter size (CPW, unpublished data). Alternatively, multiple mating may be a way for yearling females to avoid inbreeding with their father (Stockley et al. 1993; Schradin et al. 2012); given the high turnover of adult males in this population, and nearly complete dispersal of male offspring, older females are unlikely to encounter male relatives as potential mates.

Age or condition of the female may have additional effects on mating, since more socially or physically dominant females may be able to choose their mate or mates. In gray mouse lemurs (*Microcebus murinus*, Huchard et al. 2012), yellow-bellied marmots (Martin et al. 2014), and Gunnison's prairie dogs (Hoogland 1998), heavier females were more able than their lighter-weight counterparts to evade social mates and engage in additional copulations. By contrast, heavier golden-mantled ground squirrel females were less likely to produce multiply sired litters. This difference likely reflects species-specific differences in female mating preferences, shaped by the fitness benefit of multiple paternity ("Bateman gradient"). Female Gunnison's prairie dogs gain fitness with additional mates (Hoogland 1998), as may female gray mouse lemurs and yellow-bellied marmots, but female golden-mantled ground squirrels do not. In free-living populations,

female and male preferences for mating may come into conflict. Differences in the slope of male and female Bateman gradients in our study suggest a conflict over multiple mating (Arnqvist and Rowe 2005): while females do not gain a direct fitness benefit from more than one mate, males do. Yet, multiple paternity was observed in the majority of litters produced in our population. Though the effect of female peri-oestrous mass did not quite reach statistical significance, it is revealing that no female over 200 g produced a multiply-sired litter; females of this size are larger than the average male during the breeding season, and hence may have been able to evade mating attempts from non-preferred males. If lighter-weight females are less able to resist mating attempts, multiple paternity in their litters may be characterized as “convenience polyandry,” wherein females mate multiply because it is less costly than continuing to evade males (Arnqvist and Rowe 2005). In support for the female choice model, older and heavier females were apparently able to exert their preference for single sires. Combined, our results suggest that variation in environmental, social, and individual conditions can contribute to variation in the rate of multiple paternity in the same population over time.

Acknowledgments We thank the Rocky Mountain Biological Lab for logistical support, B. Barr for weather data from Gothic, and the many research assistants, including G. Aldridge, K. Jenderseck, C. Wickham, T. Anderson, and C. Mueller, who have participated in data collection. We thank M. Finger, A. Goodbla, A. Schrier, and other members of the Genomic Variation Lab at the University of California, Davis, for advice on microsatellite methods and parentage analysis. J.M. Eadie, A.K. Townsend, and two anonymous reviewers provided valuable comments on an earlier draft of this manuscript. We thank the California Agricultural Experiment Station; the Graduate Group in Ecology, University of California, Davis; Henry A. Jastro Research Fellowship, University of California, Davis; the American Society of Mammalogists; and the American Museum of Natural History Theodore Roosevelt Memorial Grant for funding this work.

Compliance with ethical standards

Funding This work was funded by the California Agricultural Experiment Station (DHV); the Graduate Group in Ecology, University of California, Davis (CPW); Henry A. Jastro Research Fellowship, University of California, Davis (CPW); an American Society of Mammalogists Grant-in-Aid of Research (CPW); and an American Museum of Natural History Theodore Roosevelt Memorial Grant (CPW).

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Our trapping protocol was approved by Animal Care and Use Committees of the University of California, Davis, and the Rocky Mountain Biological Laboratory and adhered to guidelines approved by the American Society of Mammalogists (Sikes and Gannon 2011).

Informed consent This study did not involve human subjects, so no informed consent was obtained.

References

- Andersson M, Iwasa Y (1996) Sexual selection. *Trends Ecol Evol* 11:53–58
- Arct A, Drobniak SM, Cichon M (2015) Genetic similarity between mates predicts extrapair paternity—a meta-analysis of bird studies. *Behav Ecol* 26:959–968
- Armitage KB (2014) *Marmot biology: sociality, individual fitness, and population dynamics*. Cambridge University Press, Cambridge
- Arnqvist G, Rowe L (2005) *Sexual Conflict*. Princeton University Press, Princeton
- Atwell A, Wagner WE (2014) Female male choice plasticity is affected by the interaction between male density and female age in a field cricket. *Anim Behav* 98:177–183
- Bartels MA, Thompson DP (1993) *Spermophilus lateralis*. *Mamm Species* 440:1–8
- Bateman AJ (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–6, <http://CRAN.R-project.org/package=lme4>
- Bergeron P, Reale D, Humphries MM, Garant D (2011) Evidence of multiple paternity and mate selection for inbreeding avoidance in wild eastern chipmunks. *J Evol Biol* 24:1685–1694
- Bergeron P, Montiglio P-O, Reale D, Humphries MM, Garant D (2012) Bateman gradients in a promiscuous mating system. *Behav Ecol Sociobiol* 66:1125–1130
- Bronson MT (1979) Altitudinal variation in the life history of the golden-mantled ground squirrel (*Spermophilus lateralis*). *Ecology* 60:272–279
- Bryja J, Patezenhauerová H, Albrecht T, Mošanský L, Stanko M, Stopka P (2008) Varying levels of female promiscuity in four *Apodemus* mice species. *Behav Ecol Sociobiol* 63:251–260
- Cotton S, Small J, Pomiankowski A (2006) Sexual selection and condition-dependent mate preferences. *Curr Biol* 16:R755–R765
- Daly M (1978) The cost of mating. *Am Nat* 112:771–774
- Dean MD, Ardlie KG, Nachman MW (2006) The frequency of multiple paternity suggests that sperm competition is common in house mice (*Mus domesticus*). *Mol Ecol* 15:4141–4151
- Dobson FS, Risch TS, Murie JO (1999) Increasing returns in the life history of Columbian ground squirrels. *J Anim Ecol* 68:73–86
- Eberhard WG (1996) *Female control: sexual selection by cryptic female choice*. Princeton University Press, Princeton
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Ferron J (1985) Social behaviour of the golden-mantled ground squirrel (*Spermophilus lateralis*). *Can J Zool* 63:2529–2533
- Gowaty PA, Bridges WC (1991) Behavioral, demographic, and environmental correlates of extrapair fertilizations in eastern bluebirds, *Sialia sialis*. *Behav Ecol* 2:339–350
- Gray DA (1999) Intrinsic factors affecting female choice in house crickets: time cost, female age, nutritional condition, body size, and size-relative reproductive investment. *J Insect Behav* 12:691–700
- Hanken J, Sherman PW (1981) Multiple paternity in Belding’s ground squirrel litters. *Science* 212:351–353
- Hare JF, Todd G, Untereiner WA (2004) Multiple mating results in multiple paternity in Richardson’s ground squirrels, *Spermophilus richardsonii*. *Can Field Nat* 118:90–94
- Hoogland JL (1998) Why do female Gunnison’s prairie dogs copulate with more than one male? *Anim Behav* 55:351–359
- Hoogland JL (2013) Why do female prairie dogs copulate with more than one male?—insights from long-term research. *J Mamm* 94:731–744
- Huchard E, Canale CI, Le Gros C, Perret M, Henry PY, Kappeler PM (2012) Convenience polyandry or convenience polygyny? Costly

- sex under female control in a promiscuous primate. *Proc R Soc Lond B* 279:1371–1379
- Isvaran K, Clutton-Brock T (2007) Ecological correlates of extra-group paternity in mammals. *Proc R Soc Lond B* 274:219–224
- Jennions MD, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev* 75:21–64
- Jesmer BR, Van Vuren DH, Wilson JA, Kelt DA, Johnson ML (2011) Spatial organization in female golden-mantled ground squirrels. *Am Midl Nat* 165:162–168
- Jones AG, Arguello JR, Arnold SJ (2002) Validation of Bateman's principles: a genetic study of mating patterns and sexual selection in newts. *Proc R Soc Lond B* 269:2533–2539
- Jones PH, Van Zant JL, Dobson FS (2012) Variation in reproductive success of male and female Columbian ground squirrels (*Urocitellus columbianus*). *Can J Zool* 90:736–743
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106
- Klemme I, Ylönen H, Eccard JA (2007) Reproductive success of male bank voles (*Clethrionomys glareolus*): the effect of operational sex ratio and body size. *Behav Ecol Sociobiol* 61:1911–1918
- Kneip É, Van Vuren DH, Hostetler JA, Oli MK (2011) Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. *J Mamm* 92:367–377
- Kodric-Brown A, Nicoletto PF (2001) Age and experience affect female choice in the guppy (*Poecilia reticulata*). *Am Nat* 157:316–323
- Kokko H, Rankin DJ (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philos T Roy Soc B* 361:319–334
- Kokko H, Jennions MD, Brooks R (2006) Unifying and testing models of sexual selection. *Annu Rev Ecol Evol S* 37:43–66
- Magnhagen C (1991) Predation risk as a cost of reproduction. *Trends Ecol Evol* 6:183–186
- Martin JGA, Petelle MB, Blumstein DT (2014) Environmental, social, morphological, and behavioral constraints on opportunistic multiple paternity. *Behav Ecol Sociobiol* 68:1531–1538
- Matějů J, Kratochvíl L (2013) Sexual size dimorphism in ground squirrels (Rodentia: Sciuridae: marmotini) does not correlate with body size and sociality. *Front Zool* 10:27
- McEachern MB, McElreath RL, Van Vuren DH, Eadie JM (2009) Another genetically promiscuous 'polygynous' mammal: mating system variation in *Neotoma fuscipes*. *Anim Behav* 77:449–455
- McEachern MB, Van Vuren DH, Floyd CH, May B, Eadie JM (2011) Bottlenecks and rescue effects in a fluctuating population of golden-mantled ground squirrels (*Spermophilus lateralis*). *Conserv Genet* 12:285–296
- McElreath R (2014) rethinking: Statistical Rethinking book package. R package version 1.391, <https://github.com/rmcelreath/rethinking>
- McFarlane SE, Lane JE, Taylor RW, Gorrell JC, Coltman DW, Humphries MM, Boutin S, McAdam AG (2011) The heritability of multiple male mating in a promiscuous mammal. *Biol Lett* 7: 368–371
- McKeever S (1964) The biology of the golden-mantled ground squirrel, *Citellus lateralis*. *Ecol Monogr* 34:383–401
- Michener GR (1983) Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Eisenberg JF, Kleiman D (eds) *Advances in the study of mammalian behavior*. American Society of Mammalogists, Shippensburg, PA, pp 528–572
- Michener GR, McLean IG (1996) Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. *Anim Behav* 52:743–758
- Morton ML, Sherman PW (1978) Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. *Can J Zool* 56:2578–2590
- Munroe K, Koprowski J (2011) Sociality, Bateman's gradients, and the polygynandrous genetic mating system of round-tailed ground squirrels (*Xerospermophilus tereticaudus*). *Behav Ecol Sociobiol* 65:1811–1824
- Murie JO (1995) Mating behavior of Columbian ground squirrels. I. Multiple mating by females and multiple paternity. *Can J Zool* 73: 1819–1826
- Naim DM, Telfer S, Sanderson S, Kemp SJ, Watts PC (2011) Prevalence of multiple mating by female common dormice, *Muscardinus avellanarius*. *Conserv Genet* 12:971–979
- Phillips JA (1981) Growth and its relationship to the initial annual cycle of the golden-mantled ground squirrel, *Spermophilus lateralis*. *Can J Zool* 59:865–871
- Raveh S, Heg D, Dobson FS, Coltman DW, Gorrell JC, Balmer A, Neuhaus P (2010) Mating order and reproductive success in male Columbian ground squirrels (*Urocitellus columbianus*). *Behav Ecol* 21:537–547
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>
- Schradin C, Lindholm AK, Johannesen J, Schoepf I, Yuen C-H, König B, Pillay N (2012) Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Mol Ecol* 21:541–553
- Schulte-Hostedde AI, Millar JS (2004) Intraspecific variation of testis size and sperm length in the yellow-pine chipmunk (*Tamias amoenus*): implications for sperm competition and reproductive success. *Behav Ecol Sociobiol* 55:272–277
- Schulte-Hostedde AI, Millar JS, Gibbs HL (2004) Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. *Behav Ecol* 15:351–356
- Schwagmeyer PL, Brown CH (1983) Factors affecting male-male competition in thirteen-lined ground squirrels. *Behav Ecol Sociobiol* 13: 1–6
- Schwagmeyer PL, Foltz DW (1990) Factors affecting the outcome of sperm competition in thirteen-lined ground squirrels. *Anim Behav* 39:156–162
- Schwagmeyer PL, Wootner SJ (1986) Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behav Ecol Sociobiol* 19: 359–364
- Schwanz LE, Sherwin WB, Ognenovska K, Lacey EA (2016) Paternity and male mating strategies of a ground squirrel (*Ictidomys parvidens*) with an extended mating season. *J Mamm* 97:576–588
- Shuster SM, Wade MJ (2003) *Mating systems and strategies*. Princeton University Press, Princeton
- Sikes RS, Gannon WL (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mamm* 92:235–253
- Slatyer RA, Mautz BS, Backwell PRY, Jennions MD (2012) Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biol Rev* 87:1–33
- Solomon NG, Keane B (2007) Reproductive strategies in female rodents. In: Wolff JO, Sherman PW (eds) *Rodent societies: an ecological and evolutionary perspective*. University of Chicago Press, Chicago, pp 42–56
- Sommaro LV, Chiappero MB, Vera NS, Coda JA, Priotto JW, Steinmann AR (2015) Multiple paternity in a wild population of the corn mouse: its potential significance for females. *J Mamm* 96:908–917
- Stockley P, Searle JB, Macdonald DW, Jones CS (1993) Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. *Proc R Soc Lond B* 254:173–179
- Streatfield CA, Mabry KE, Keane B, Crist TO, Solmon NG (2011) Intraspecific variability in the social and genetic mating systems of prairie voles *Microtus ochrogaster*. *Anim Behav* 82: 1387–1398

- Thonhauser KE, Thoß M, Musolf K, Klaus T, Penn DJ (2014) Multiple paternity in wild house mice (*Mus musculus musculus*): effects on offspring genetic diversity and body mass. *Ecol Evol* 4:200–209
- Waterman JM (1998) Mating tactics of male cape ground squirrels, *Xerus inauris*: consequences of year-round breeding. *Anim Behav* 56: 459–466
- Wells CP (2016) Reproductive ecology of female golden-mantled ground squirrels. Dissertation. University of California, Davis
- Wilgers DJ, Hebets EA (2012) Age-related female mating decisions are condition dependent in wolf spiders. *Behav Ecol Sociobiol* 66:29–38
- Wolff JO, Macdonald DW (2004) Promiscuous females protect their offspring. *Trends Ecol Evol* 19:127–134
- Zeh JA, Zeh DW (1997) The evolution of polyandry II: post-copulatory defenses against genetic incompatibility. *Proc R Soc Lond B* 264: 69–75