Parental investment in the Columbian ground squirrel: empirical tests of sex allocation models

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Abstract. Parental allocation of resources into male or female offspring and differences in the balance of offspring sexes in natural populations are central research topics in evolutionary ecology. Fisher (Fisher, R. A. 1930. The genetical theory of natural selection, Clarendon Press, Oxford, UK) identified frequency-dependent selection as the mechanism responsible for an equal investment in the sexes of offspring at the end of parental care. Three main theories have been proposed for explaining departures from Fisherian sex ratios in light of variation in environmental (social) and individual (maternal condition) characteristics. The Trivers–Willard model (Trivers, R., and D. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92) of male-biased sex allocation by mothers in the best body condition is based on the competitive ability of male offspring for future access to mates and thus superior reproduction. The local resource competition model is based on competitive interactions in matrilines, as occur in many mammal species, where producing sons reduces future intrasexual competition with daughters. A final model invokes advantages of maintaining matrilines for philopatric females, despite any increased competition among females. We used 29 yr of pedigree and demographic data to evaluate these hypotheses in the Colombian ground squirrel (*Urocitellus columbianus*), a semisocial species characterized by strong female philopatry. Overall, male offspring were heavier than female offspring at birth and at weaning, suggesting a higher production cost. With more local kin present, mothers in the best condition biased their offspring sex ratio in favor of males, and mothers in poor condition biased offspring sex ratio in favor of females. Without co-breeding close kin, the pattern was reversed, with mothers in the best condition producing more daughters, and mothers in poor condition producing more sons. Our results do not provide strong support for any of the single-factor models of allocation to the sexes of offspring, but rather suggest combined influences of relative maternal condition and matriline dominance on offspring sex ratio.

Key words: Kin selection; local resource competition; matrilines; sex-ratio allocation; Trivers–Willard hypothesis.

Introduction

Life histories are a central focus of both ecology and evolution (Stearns 1992, Roff 2001). The success of different life history strategies can be assessed through individual variations in fitness (characteristics of reproduction and survival), and the expression of traits contributing to higher reproductive and survival rates (e.g., Endler 1986, Kruuk and Hill 2008). The fitness differences of individuals that carry different trait forms, in turn, depend on the interactions of those traits with the ecological and social environments (e.g., Lande and Arnold 1983). Thus, our

understanding of evolution rests on a foundation of ecological interactions that produce fitness differences (Hutchinson 1965). An aspect of reproduction that might result in fitness differences among individuals is the differential allocations of resources that parents make to male and female offspring. Such allocation differences might lead to variations in offspring sex ratio, if the fitness returns of producing males or females differ, depending on the environment.

In many animal species, offspring sex ratios are close to even, a generality that Darwin (1871) puzzled over. Fisher (1930) pointed out that it is not the numbers of male and female offspring that should be roughly equal in a population, but the amount of parental allocation of resources. Fitness returns of allocating resources to a male or female offspring should be equal in bisexual species, because every individual has a mother and father

and in turn will potentially become a mother or father. In other words, the fitness returns of male and female offspring are equal. When the ratio of male to female offspring allocation varies from even, frequency-dependent selection should bring it back into balance. If both sexes are equally costly to produce, then an even sex ratio of offspring should occur (Fisher 1930, Charnov 1979).

Nonetheless, extremely biased offspring sex ratios have been found in nature (e.g., Hamilton 1967) and hypotheses for explaining adaptive deviations from so-called "Fisherian sex ratios" have been subsumed into a theory of how resources are allocated between the sexes of offspring (Charnov 1982, Frank 1990, West 2009). In an early attempt at predicting biases from even sex allocations, Trivers and Willard (1973) suggested that mothers should vary in their body condition and ability to invest in offspring. If the future reproductive success of one sex is more variable than that of the other and can be influenced by augmented early investment, then mothers in better body condition should invest more in that sex. For instance, suppose that male future reproductive success is more variable than female future reproductive success, and is augmented by enhanced development early in life as in most polygynous and polygynandrous mammal species (Dobson 1982, Dobson et al. 2010). Then, mothers in relatively good body condition should produce more males, and mothers in relatively poor condition should produce more females. This hypothesis assumes that the relative cost of producing male and female offspring differs, that there is a positive association of maternal body condition and the production of males, that early investment in males should persist into adulthood, and that such males should have greater fitness as adults. Despite considerable empirical and theoretical study of offspring sex ratio in mammals (Clutton-Brock and Iason 1986, Festa-Bianchet 1996, Kojola 1998, Hewison and Gaillard 1999, Brown 2001, Cameron 2004, Cameron et al. 2008, Schindler et al. 2015, Toni et al. 2021), support for the prediction of a positive association of maternal condition and offspring sex ratio remains equivocal.

Clark (1978) developed the idea of local competition among relatives as an influence on offspring sex ratios that deviate from 50:50 to explain offspring sex ratios that typically vary between 60% and 75% male in species such as galagos (*Galago* sp.) and African wild dogs (*Lycaon pictus*). She noted that females are often limited in reproduction by competition over local resources, such as food, refuges from predation, or territories (reviewed by Emlen and Oring 1977). This competition should favor production of the dispersing sex. In polygynous and polygynandrous mammals, females are often highly philopatric and matrilineal, and the dispersing sex among juveniles and subadults is usually males (Greenwood 1980, Dobson 1982). When population density is already high, females should thus produce more males to prevent future local competition for

resources. Several studies have provided empirical support for the local resource competition model, including primates (Clark 1978), marsupials (Cockburn et al. 1985, Schwanz and Robert 2014), and rodents (Wells and Van Vuren 2017).

Silk (1983) expanded on this model by suggesting different maternal allocations to male and female offspring according to maternal dominance status. Dominant, high-condition, mothers able to tolerate increased local resource competition may benefit from producing female offspring in greater proportion to ensure matriline dominance, especially in species where females exhibit cooperative breeding. In contrast, subordinate adult females should produce more dispersing sons to lower the costs of local competition. Support for this hypothesis has been found in social rodents (Armitage 1987a) and primates (Simpson and Simpson 1982, Silk 1983, Johnson 1988; reviewed by Cockburn et al. 1985).

Biases in offspring sex ratios under the above hypotheses are expected to result primarily from differences in the fitness payoffs of producing or allocating resources to male or female offspring. The allocation of resources by parents might be best measured at the termination of parental care (Fisher 1930, Trivers and Willard 1973). However, in matrilineal species like social mammals, maternal investment can be extended throughout the lifespan, making estimation of maternal allocation of resources difficult. In addition, differential survival of offspring during the period of parental investment may cause a skew in allocation to the sexes (Austad 2015). Finally, the ecological and social influences on both allocation of resources to offspring and on offspring sex ratios are not mutually exclusive, so that more than one hypothesis might be supported in any particular species (e.g., Kruuk et al. 1999, Cockburn et al. 2002, Delean et al. 2009, Yeo and Hare 2021).

Columbian ground squirrels (*Urocitellus columbianus*) are a good system for the study of offspring energy allocation and sex ratio. They are semisocial, hibernating sciurid rodents that inhabit subalpine meadows in the Rocky Mountains of southwestern Canada (Boag and Murie 1981, Dobson et al. 1992). Within colonies, philopatric females overlap temporally and spatially with close kin, creating local matrilines (King and Murie 1985, King 1989a, b). Females with higher numbers of kin acquire direct and indirect fitness benefits from philopatry (Viblanc et al. 2010, Arnaud et al. 2012, Dobson et al. 2012). Males, on the other hand, contribute little or nothing to the production of offspring beyond sperm, during a short mating season (Manno and Dobson 2008, Raveh et al. 2010, 2011), and exhibit high variance in reproductive success (Raveh et al. 2010). Mothers are variable in size and body condition (Dobson 1992, Dobson et al. 1999, Rubach et al. 2016), and thus provide suitable variables for testing hypotheses about allocation of resources to offspring and variation in offspring sex ratios. The amount and quality of food resources are a major influence on allocations to

offspring by mothers (Dobson and Kjelgaard 1985, Dobson and Muri 1987, Dobson 1988). Finally, year-to-year environmental variations are extreme (Lane et al. 2012, Dobson et al. 2016), thus providing ample variation in annual availability of resources.

Our study had five purposes. First, we tested the repeatability of offspring sex ratio over the lifetimes of adult females, to examine trait flexibility. Second, we evaluated the costs to mothers of producing male and female offspring. We examined the costs of sons and daughters in terms of their mass at weaning, a value that should reflect the energetic costs of producing offspring. We also examined the fitness costs of producing sons and daughters for mothers, by testing for differences in maternal reproduction, survival, and mass gain during the active season. Third, we tested the Trivers and Willard (1973) prediction that mothers in good condition should produce costlier sons. For this, we focused on female mass at the start of the breeding season, known to strongly influence subsequent reproductive success (Dobson et al. 1999, Broussard et al. 2005, Rubach et al. 2016). We tested if females in good condition biased maternal investment towards males. Fourth, we tested Clark's predictions from the local resource competition hypothesis of male-biased offspring production when local density and competition for resources are high within matrilines (Clark 1978). Fifth, we examined Silk's (1983) prediction that females in the best body condition and in large matrilines should produce sex ratios biased towards daughters, because they can best bear costs associated with local resource competition and reap the benefits of augmented matrilines (Armitage 1987a, b).

We used a 29-yr long-term data set of known female reproductive allocations including litter size and offspring mass at birth and weaning, maternal mass at the start of the reproductive season, and matriline genealogies that reveal close kin relationships between Columbian ground squirrels, to empirically test models of resource allocation to the sexes of offspring. The data set on offspring sex ratio from parturition to offspring weaning, uniquely allowed distinguishing between offspring sex ratio at birth and at about the time that the major period of maternal care ended, and testing for differential maternal allocation to (and survival of) the sexes over the period of parental care.

MATERIALS AND METHODS

Study site and long-term monitoring

Data were collected from 1992 to 2020 at a 2.6-ha subalpine meadow in the Sheep River Wildlife Provincial Park, Alberta, Canada (50°38′10″ N, 114°39′56″ W, 1,550 m above sea level). Columbian ground squirrels were monitored yearly throughout the breeding season from emergence from hibernation (˜mid-April) to weaning of the offspring (˜early July). In each year of the study, all animals were trapped when first emerging from hibernation, using live traps (Tomahawk Live Trap Co., Hazelhurst, Wisconsin, USA; 13 × 13 × 40 cm) baited with a small amount of peanut butter. Ground squirrels were weighed to the nearest 5 g using a Pesola® spring-slide scale, given a unique ear tag number (No. 1-Monel metal; National Band and Tag Company, Newport, Kentucky, USA), and painted with a unique dorsal mark on the pelage for visual identification at a distance, using black human hair dye (Clairol, Stanford, Connecticut, USA).

Females typically estrous cycle within 3–5 d after emergence from hibernation, and are sexually receptive for a few hours on a single day (Murie and Harris 1982, Murie 1995, Raveh et al. 2010). We determined mating date for each female from behavioral observations, inspection of their genitalia, and the presence of copulatory plug material in or around the vulva (Murie and Harris 1982). Mated females were caught 22 d after mating, 2–3 d before expected parturition, and transported to a 1.5-km-distant field laboratory where they gave birth. Females were housed in polycarbonate microvent cages (47 × 27 × 20 cm; Allentown Caging Equipment Company, Allentown, New Jersey, USA), and provided wood chip bedding and shredded newspaper for nesting material. Food, including grains (a molasses-enriched horse feed), fresh apples, and fresh lettuce, and water were provided ad libitum twice a day. At birth, mothers (nearest 5 g) and pups (nearest 0.01 g) were weighed. Pups were sexed and marked with a small tissue biopsy used for establishing paternities (Hare and Murie 1992). The biopsy created a partial claw loss on a rear foot, and thus pups could be identified at birth and later at weaning. Newborns and their mothers were released approximately 1 d after birth into their nest burrow, known from behavioral observations of females stocking them with dry grass prior to capture and marked with colored flags.

Entire litters and mothers were caught 27–28 d after birth, when young first emerged from nest burrows near the time of weaning. Young were ear tagged for permanent identification and weighed to the nearest 1 g. Mothers were weighed again to the nearest 5 g. Since 1992, several generations of matrilineal genealogies are known from mother–offspring associations. Complete life histories (including age and pedigree relationships) are known for the vast majority of animals that lived on the study site. For each year of the study, we used the long-term data to determine (1) offspring sex ratio and individual mass at birth and at weaning, and offspring sex ratio variation among adult females; (2) female condition and energy allocation to offspring in grams of body mass; and (3) the density of closely related kin.

Offspring sex ratio

We calculated offspring sex ratio at birth and at weaning as the proportion of males produced in a litter: SR =

males/(males + females). Because some females did not give birth in the lab (especially in earlier years of the study, and after 2017), sample sizes differ between sex ratio at birth and at weaning. To characterize partial litter loss over the course of lactation, we further calculated the difference between sex ratio at weaning and sex ratio at birth for females having lost at least one offspring between birth and weaning: $\Delta SR = SR_{wean} - SR_{birth}$. ΔSR varied between -0.67 and 0.75 (mean $\pm$ SD = 0.00 ± 0.26, $n = 102$ litters).

Data analyses

All analyses were conducted in the R statistical computing environment v. 4.0.2 (R Development Core Team 2020). Results are presented as means $\pm$ 1 SE, unless otherwise noted. Independent variables were standardized prior to analyses, so that coefficients were directly comparable as effect sizes. Where appropriate, we examined model residuals for normality by visual inspection of density distributions, Q–Q plots, cumulative distribution functions and P–P plots using the "fitdistrplus" package in R (Delignette-Muller and Dutang 2015). We also ensured that no substantial collinearity occurred between independent variables (all variance inflation factors (VIF) <3; suggested cutoff, see Zuur et al. 2010). The goodness of fit of each model was evaluated by comparing the deviance of the model to the deviance of the null model (with the intercept only) and expressed as explained deviance $ED = (deviance_{null} - deviance_{model})/deviance_{null}$, characterizing the percent-deviance explained by the model.

Repeatability of offspring sex ratio.—For females that bred in multiple years, we estimated offspring sex ratio repeatability using the "rptR" package in R (Stoffel et al. 2017). Repeatability was calculated as

$$R = \frac{V_G}{V_P} = \frac{V_G}{V_G + V_R}$$

where V_G is the among-group variance, V_R is the residual variance, and $V_P = V_G + V_R$ is the total phenotypic variance in offspring sex ratio. V_G was either the among-individual variance or the among-year variance, depending on whether repeatability within females or within years was considered. Variance in offspring sex ratio was decomposed using separate generalized linear mixed-effects models (GLMM, "lme4" package in R; Bates et al. 2015), with offspring sex ratio specified as a proportion of successes and failures for each mother as the dependent variable (count data; matrix of "successes" and "failures" with male = "success," female = "failure"), and mother identity or year as a random factor. Confidence intervals around repeatability estimates were calculated by parametric bootstrapping ($N = 1,000$ random data sets were generated from the distribution defined by the estimated parameters). As the amount of

variance in offspring sex ratio explained by mother ID or year was virtually zero, we disregarded these factors as random variables in subsequent models on sex ratio.

Cost differences in male and female offspring.—1. *Differences in the energy invested in the production of male and female offspring.*—First, we tested for differential energy costs in the production of male/female offspring by comparing male and female mass at birth and at weaning. Offspring mass at birth and at weaning were specified as dependent variables in separate linear mixed models (LMMs), and offspring sex was included as an independent factor. We controlled for litter size at birth (mean $\pm$ SD = 3.22 ± 0.87, min = 1, max = 7) as a covariate in all models because of the known trade-off between number and mass of offspring in our species (e.g., Dobson et al. 1999, Skibiel et al. 2009). Mother ID and litter ID were included as random variables in the models to account for repeated measures over the years, and the non-independence of offspring born from the same mother and raised within the same litter. We also tested if female and male offspring differed in their survival from birth to weaning using a binomial GLMM. Offspring survival was included as the dependent variable (binary; survived = 1, died = 0) and offspring sex as the independent variable of interest. We further accounted for litter size and offspring mass at birth in the model as known influences on survival. As above, mother ID and litter ID were originally included as random variables in the models to account for repeated measures over the years, and the non-independence of offspring born from the same mother and raised within the same litter. However, mother ID explained virtually no variance in pup survival, and was removed from the final model.

2. *Fitness costs to mothers.*—Second, we tested if maternal fitness costs could be detected for mothers that invested into male or female-biased litters. We considered the effects of litter sex ratio at birth, or at weaning, on 3 proxies of maternal fitness: (1) reproductive output over the season (litter size at weaning; count data, mean $\pm$ SD = 2.54 ± 1.28 offspring, min = 0, max = 7; Poisson GLMM), (2) maternal mass gain (or loss) over the breeding season (continuous data, mean $\pm$ SD = 108.7 ± 46.8 g, min = -50 g, max = 280 g; LMM), and (3) mother survival (binary, 0/1; binomial GLMM) to the next year. We initially included mother ID, age and year as random factors in the models to account for variance in fitness parameters, but removed these when the variance explained was virtually null.

Testing the Trivers and Willard model of sex allocation.—3. *Maternal condition effects on litter sex ratio.*—We used a three-step analysis to test for maternal condition effects on sex ratio.

First, to test whether mothers that raised a litter, on average, biased the offspring sex towards males in

particularly favorable years, we calculated the average mass of breeding females at emergence from hibernation (mean ± SD = 419.72 g ± 20.70 g,   min = 376.6 g, max = 460.55 g), and the average sex ratio (see Fig. 1) at weaning for the population, for 28 yr of the 29 yr-study (no data on maternal mass in 2020 due to COVID-19). We then regressed mean offspring sex ratio at weaning on mean maternal mass at emergence (LM; $N = 28$).

Second, we used the entire data set to test for individual effects of maternal body mass at emergence of hibernation on offspring sex ratio at weaning. For this, we used a generalized linear model (GLM) specifying offspring sex ratio as a proportion of successes and failures for each mother as the dependent variable, and maternal mass at the start of the season as the independent variable. Further, considering only females having lost at least one offspring during lactation, we tested the effects of maternal body mass at emergence from hibernation on the change in offspring sex ratio from birth to weaning (ΔSR) by regressing ΔSR on maternal mass at emergence. We also tested if the proportion of offspring (dependent variable, binomial proportion GLM) lost during lactation for individual mothers, controlling for litter size at birth, depended on maternal body mass at emergence.
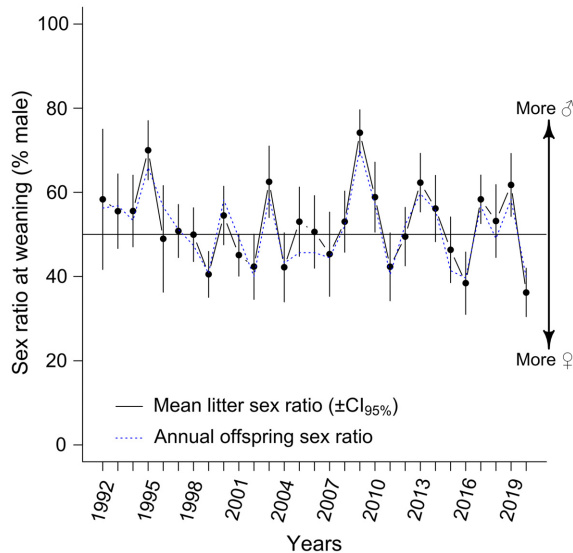

FIG. 1. Annual offspring sex ratio (% males) at weaning in the Columbian ground squirrel (*Urocitellus columbianus*) from 1992 to 2020. The black line represents the mean litter sex ratio for mothers (mean of individual mother values = 51.3%) in the population each year with associated 95% CI obtained by bootstrap (1,000 simulations, 50% of the litters resampled each time). The blue dotted line represents the sex ratio of all offspring at weaning in the entire population (total number of weaned males/([total number of weaned males + total number of weaned females]). A sex ratio above 50% (solid black horizontal line) is biased towards males, and below, towards females.

Third, to test whether mothers biased the sex ratio of their litters towards males in years when they were in particularly good condition compared to their lifetime average, we calculated relative maternal mass at emergence within a year, that is, female mass compared to her mean mass over the years she weaned a litter. This annual relative condition index (mean ± SD = 0.00 g ± 30.60, min = −133.00 g, max = 106.43 g) was calculated as

$$\text{annual relative condition}_{i,y} = \text{mass}_{i,y} - \mu_i,$$

where i is mother ID and y is year. A mother with an annual relative condition index >0 (or <0) in a given year, thus was in better (or worse) condition than her lifetime average. We then used a GLM specifying offspring sex ratio as a proportion of males and females for each mother and as the dependent variable, and annual relative condition as the independent variable.

4. Maternal condition effects on male and female offspring mass gain.—We tested whether the gain in offspring mass over the course of lactation for males (mean ± SD = 97.34 g ± 22.14, min = 45.04 g, max = 198.06 g) and females (92.12 g ± 19.57, min = 35.82 g, max = 169.61 g) was differently affected by maternal condition at the start of the breeding season. We used a linear model (LM) with offspring mass gain specified as the dependent variable, and maternal mass at emergence from hibernation, offspring sex, and the interaction between offspring sex and maternal mass at emergence specified as independent variables. In addition, we controlled for litter size at birth, offspring mass at birth, and lactation duration (mean ± SD = 26.27 d ± 1.12, min = 23 d, max = 31 d) as covariates in the model, because they were possible influences on offspring mass gain.

Testing local resource competition models of sex allocation.—*5. Clark's model of local resource competition.*—To test Clark's (1978) prediction that mothers should bias offspring sex ratio towards the dispersing (male) sex when local kin competition for resources is high, we performed a two-step analysis. First, we tested if offspring sex ratio was biased towards males (the dispersing sex) in years of high population density. For this, we calculated the average sex ratio (see Fig. 1) at weaning for the population, and regressed it on overall population density (mean ± SD = 62.69 individuals ± 22.87, min = 32, max = 120; $N = 29$ yr). Second, we used the long-term matrilineal genealogies to determine the total number of kin females (mothers, daughters, and littermate sisters) in each year of the study (mean ± SD = 0.89 ± 0.72, min = 0, max = 4). We restricted our analyses to reproductive females only, defined as females that mated and were potentially able to hold a territory at some point during the breeding season (Festa-Bianchet

and Boag 1982, Murie and Harris 1988). We subsequently examined litter sex ratio at weaning and changes in offspring sex ratio from birth to weaning (LM; ΔSR) in relation to the numbers of kin present in the population (independent variables). We also tested if the proportion of offspring (dependent variable, binomial proportion GLM) lost during lactation by individual mothers, controlling for litter size at birth in the model, depended on the number of kin present in the population.

6. Silk's model of matriline dominance.—To test Silk's (1983) prediction that dominant females in relatively good body condition (i.e., who can best incur the costs of local resource competition with kin) should produce sex ratios biased towards daughters, we further examined the interaction between maternal condition relative to other females and kin numbers. Here, we calculated relative condition as the differential between the mass of a mother and the mean mass of all females in the population at the start of the breeding season in a given year. Lactating females are socially dominant over other ground squirrels (Murie and Harris 1988), females in better body condition produce larger and heavier litters (Dobson et al. 1999), and mothers with the greatest reproductive investments are socially dominant (Viblanc et al. 2016). Condition relative to other females (mean ± SD = 0.00 g ± 49.51, range = −191.25 g to 174.23 g) was calculated as

$$\text{relative condition}_{i,y} = \text{mass}_{i,y} - \mu_y,$$

where i is mother ID and y is year. A relative condition >0 (or <0) would indicate that a female was in relatively better (or worse) condition than other females of the population in a given year. Relative condition increased in a quadratic fashion with age, so that, on average, it was <0 for females until 4 yr, increased up until 6–7 yr old, before decreasing afterwards (see Appendix S1), consistent with previous quadratic relations found for dominance-related aggression and age in this species (Viblanc et al. 2016). We subsequently examined litter sex ratio at weaning (GLM, binomial) and changes in offspring sex ratio from birth to weaning (LM; ΔSR) in relation to a female's relative condition, the number of kin present in the population, and the interaction between both variables (independent variables).

<center>RESULTS</center>

Repeatability of offspring sex ratio

At termination of parental care (weaning), offspring sex ratio in our population was on average 51.3% male ($n = 1,581$ offspring, $N = 195$ mothers), ranging from 36.2% in 2020 to 74.2% in 2009 (Fig. 1). The estimated repeatability of offspring sex ratio was virtually nil both when considering interindividual variation (binomial GLMM; $R = 0.000 \pm 0.006$, $CI_{95} = [0.000-0.022]$, $n = 622$ litters, $N = 203$ mothers), and when considering interannual variation ($R = 0.007 \pm 0.006$, $CI_{95} = [0.000-0.021]$, $n = 622$ litters, $N = 29$ yr).

Cost differences between male and female offspring

Differences in the energy invested in the production of male and female offspring.—At birth, controlling for litter size, male offspring were 4.15% heavier than female offspring (Fig. 2A; Appendix S2: Table S1A). Similarly, at weaning and when controlling for litter size, male offspring were 3.61% heavier than female offspring (Fig. 2B; Appendix S2: Table S2B). Controlling for litter size and offspring mass at birth, male and female offspring did not differ significantly in their survival rates (75.0% for males, 76.8% for females; Appendix S2: Table S2) from birth to weaning. Offspring survival was positively associated with offspring mass at birth (*z*-mass odds ratio = +1.86 ± 0.16, Appendix S2: Table S2), but not significantly with litter size at birth (*z*-litter size odds ratio = +1.20 ± 0.25, Appendix S2: Table S2).

Fitness costs to mothers.—When testing for costs to mothers, maternal reproduction (litter size weaned) was not significantly related to litter sex ratio at birth (GLMM, with Poisson error term; odds ratio = 0.87 ± 0.09, $CI_{95} = [0.71, 1.07]$, $z = -1.34$, $P = 0.18$, $n = 415$) or at weaning (0.94 ± 0.07, $CI_{95} = [0.81-1.10]$, $t = -0.76$, $P = 0.45$, $n = 559$). Maternal survival to the
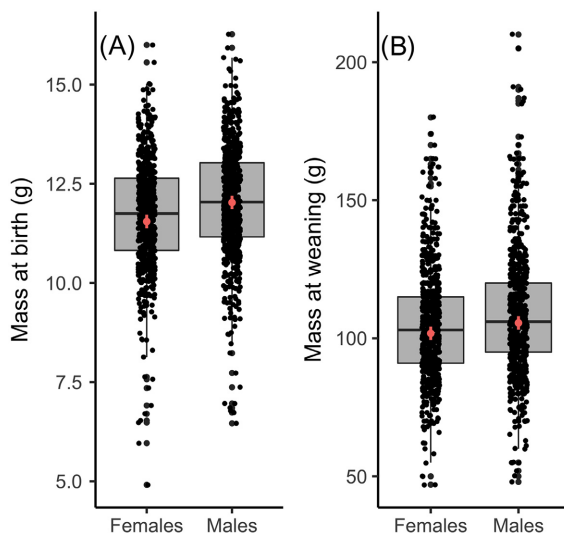
FIG. 2. Offspring mass (g) at (A) birth and (B) weaning according to sex in the Columbian ground squirrel. Boxplots present the median, 25th and 75th percentiles of the distribution. Red dots and lines present the marginal estimated means and 95% CI for female and male offspring mass, accounting for litter size at birth and weaning, respectively (see Models in text).

next year was neither significantly influenced by litter sex ratio at birth (GLMM, with binomial error term; odds ratio = 0.98 ± 0.39, $CI_{95} = [0.45–2.13]$, $z = -0.05$, $P = 0.96$, $n = 415$) or at weaning (odds ratio = 1.08 ± 0.35, $CI_{95} = [0.57–2.05]$, $z = 0.24$, $P = 0.81$, $n = 536$). Maternal mass gain over the season was positively, but not significantly, related to litter sex ratio at birth (LMM; 8.44 ± 7.83, $CI_{95} = [-6.90$ to $23.78]$, $t = 1.08$, $P = 0.28$, $n = 350$), and tended to be positively associated with litter sex ratio at weaning (9.81 ± 5.39, $CI_{95} = [-0.75$ to $20.37]$, $t = 1.82$, $P = 0.07$, $n = 508$). Thus, for a 1%-point increase in litter sex ratio at weaning (e.g. from 50% to 51% male), maternal mass gain over the course of reproduction increased by 0.098 g, on average.

Testing the Trivers and Willard model of sex allocation

Maternal condition effects on sex ratio.—Over 28 yr, the mean sex ratio at weaning of offspring in the population (Fig. 1) was not significantly associated with mean maternal mass at the start of the breeding season (LM; z-mean female mass = -0.01 ± 0.02, $t = -0.41$, $CI_{95} = [-0.04, 0.03]$, $P = 0.69$, $N = 28$ yr).

Maternal body mass at the start of the breeding season did not significantly affect offspring sex ratio at weaning (GLM; binomial; z-mass odds ratio = 0.88 ± 0.09, $CI_{95} = [0.74, 1.04]$, $z = -1.46$; $P = 0.15$, $n = 1,499$, ED = 0.29%). Similarly, for females that lost at least one offspring over lactation, maternal body mass did not significantly affect changes in offspring sex ratio from birth to weaning (LM; z-mass = $+0.03 \pm 0.03$, $CI_{95} = [-0.02, 0.08]$, $t = 1.11$, $P = 0.27$, $n = 102$, ED = 1.22%). Overall, controlling for litter size at birth (all VIFs < 1.2), the proportion of offspring lost during lactation was not significantly related to maternal mass at emergence (GLM binomial; odds ratio: z-emergence mass = 0.96 ± 0.07, $CI_{95} = [0.84–1.10]$, $P = 0.57$, $n = 1,336$, ED = 0.03%).

When considering maternal yearly condition index (maternal yearly mass relative to her lifetime average), mothers did not seem to bias litter sex ratio differently in years when they were in relatively better or worse condition compared to their lifetime average (GLM; z-yearly condition odds ratio = 0.96 ± 0.05, $CI_{95} = [0.86, 1.06]$, $z = -0.84$, $P = 0.40$, $n = 1,499$, ED = 0.1%). Maternal yearly condition also did not seem to significantly affect changes in offspring sex ratio from birth to weaning, for those mothers that lost young during lactation (LM; z-yearly condition = 0.01 ± 0.03, $CI_{95} = [-0.04, 0.07]$, $t = 0.54$, $P = 0.590$, $n = 102$, ED = 0.29%).

Maternal condition effects on mass gain of male and female offspring.—Regardless of sex (non-significant interaction, Appendix S2: Table S3A), offspring mass gain over lactation was positively related to maternal mass at the start of the breeding season (z-maternal mass = $+3.42 \pm 1.28$), to offspring mass at birth (z-offspring mass birth = $+4.40 \pm 0.44$), to lactation duration (z-lactation duration = $+4.48 \pm 0.66$), and negatively related to litter size at birth (z-litter size birth = -7.58 ± 1.08; Fig. 3; Appendix S2: Table S3B). Controlling for these effects in the model (Appendix S2: Table S3B) male offspring gained 1.68% more mass than females over lactation (Fig. 3A). The absence of an interaction between maternal body mass and offspring sex suggests no differential allocation to males and females according to maternal condition. Taken together, the results do not provide strong support for the Trivers and Willard model of sex allocation in Columbian ground squirrels.

Local resource competition models of sex allocation

Clark's model of local resource competition.—Offspring sex ratio at weaning was not significantly associated with population size over the course of our study (LM; z-population density = -0.02 ± 0.02, $t = -1.16$, $CI_{95} = [-0.05, 0.02]$, $P = 0.25$, $N = 29$ yr; Appendix S2: Fig. S1). Offspring sex ratio at weaning was positively and significantly, though weakly, associated with a female's kin numbers in a given year (GLM; z-kin odds ratio = $+1.10 \pm 0.05$, $CI_{95} = [1.00, 1.21]$, $z = 2.05$, $P = 0.040$, $n = 1,371$, ED = 0.6%). This effect appeared to be mediated through differential mortality of male and female offspring during lactation, because offspring sex ratio at birth was not significantly related to a female's kin numbers in a given year (GLM; z-kin odds ratio = $+1.02 \pm 0.05$, $CI_{95} = [0.92, 1.11]$, $z = 0.30$, $P = 0.764$, $n = 1,243$, ED = 0.02%). Indeed, for females that lost at least one offspring over lactation, kin numbers were positively, though weakly, associated with changes in offspring sex ratio from birth to weaning (LM; z-kin = $+0.05 \pm 0.03$, $CI_{95} = [-0.00, 0.10]$, $t = 1.87$, $P = 0.065$, $n = 97$, ED = 3.5%). Controlling for litter size at birth (all VIFs < 1.01), the overall proportion of offspring lost during lactation was not significantly related to kin numbers (GLM binomial; odds ratio: z-kin = 1.08 ± 0.07, $CI_{95} = [0.95–1.23]$, $P = 0.22$, $n = 1,246$, ED = 0.18%). Taken together, these results provide some support for local resource competition as an influence on sex ratio in Columbian ground squirrels.

Silk's model of matriline dominance.—Adding maternal body mass relative to female conspecifics in a given year and its interaction with kin numbers to the above models revealed a significant interaction between maternal relative condition and kin numbers affecting sex ratio at weaning (Fig. 4; z-maternal relative condition × z-kin odds ratio = $+1.18 \pm 0.06$, $CI_{95} = [1.06, 1.33]$, $t = 2.88$, $P = 0.004$, $n = 466$; see Appendix S2: Table S4A; ED = 2.1%). The proportion of males in weaned litters increased with maternal condition relative to other females within a year, but only when kin numbers were high (with two or more co-breeding female kin). It was
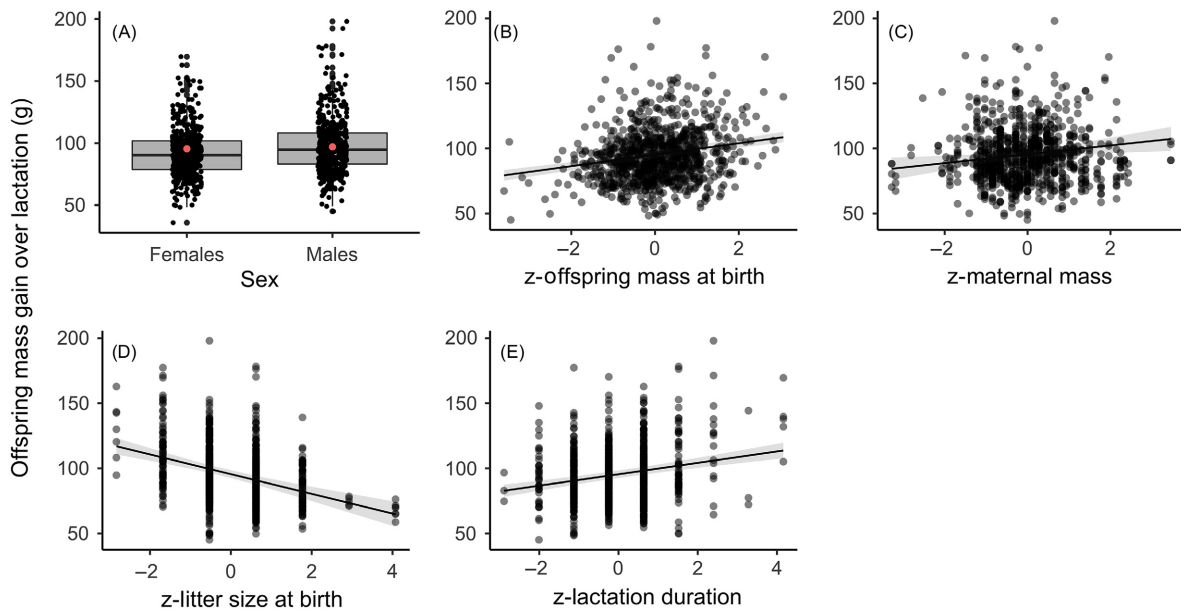
FIG. 3. Offspring mass gain (g) over the lactation period as a function of (A) offspring sex, (B) offspring mass at birth (standardized), (C) maternal mass at the start of the breeding season (standardized), (D) litter size at birth (standardized), and (E) lactation duration (in days, standardized) in Columbian ground squirrels. Boxplots present the median, 25th and 75th percentiles of the distribution. Red dots and lines present the marginal estimated means and 95% CI for female and male offspring mass, accounting for all other effects in the model. Linear relationships show the raw data points and the predicted effect with 95% confidence intervals, also accounting for the other effects in the model.

only when kin were absent that mothers in relatively good condition produced more daughters (Fig. 4). Changes in offspring sex ratio from birth to weaning, in contrast, did not seem to be significantly affected by the interaction between maternal relative condition and kin (Appendix S2: Table S4B). Removing the interaction did not reveal any effect of maternal relative condition (z-maternal relative condition = +0.00 ± 0.00, CI_{95} = [−0.00, 0.00], $t = 1.26$, $P = 0.21$, $n = 97$), but indicated a subtle effect of kin numbers (z-kin = +0.04 ± 0.02, CI_{95} = [−0.00, 0.08], $t = 1.93$, $P = 0.056$, $n = 97$, ED = 5.1%) on changes in sex ratio from birth to weaning (ΔSR). These results do not seem to support Silk's model of matriline dominance in Columbian ground squirrels.

DISCUSSION

As predicted by Fisher (1930), and over 29 yr of study, offspring sex ratio at the end of parental care in Columbian ground squirrels was roughly even at 51.3% male. However, sex ratio varied markedly, from 36.2% to 74.2% male (repeatability was virtually null) among years, suggesting scope for trait responses to variations in maternal, social, and ecological conditions. We tested three hypotheses proposed to explain deviations from Fisherian sex ratios in the animal realm from an adaptive perspective: the Trivers and Willard (1973), Clark (1978), and Silk (1983) models of maternal allocation to male and
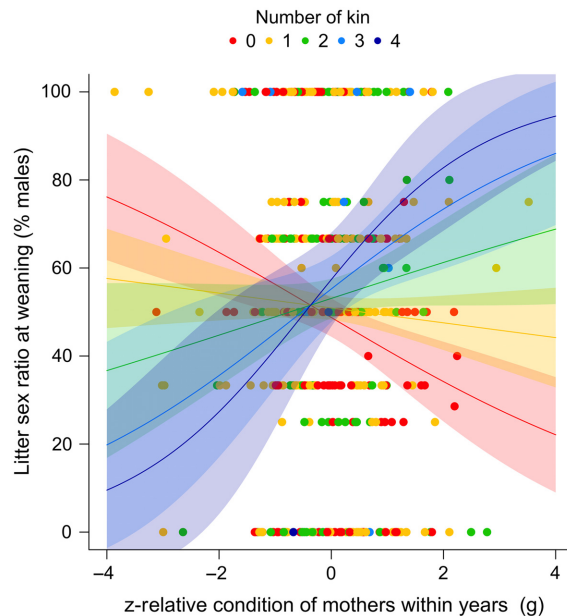

FIG. 4. Interaction plot representing the effects of maternal relative condition within years (standardized, see Methods) on litter sex ratio at weaning as a function of number of kin present. The line and 95% confidence intervals were computed from a generalized linear model that examined litter sex ratio at weaning as a matrix of count data, that is, matrix of "success" and "failures" with male = success, female = failure.

female offspring. These hypotheses are not mutually exclusive, but make different predictions about parental allocations to male and female offspring that can influence offspring sex ratio. Trivers and Willard (1973) focused on female energy allocation. For Columbian ground squirrels, where increased maternal condition is related to increased reproductive output (Dobson and Kjelgaard 1985, Dobson and Murie 1987, Dobson 1988, Risch et al. 1995, Dobson et al. 1999, Skibiel et al. 2009), they predict a positive association between maternal body condition and male offspring production. In contrast, Clark (1978) focused on local resource competition, predicting an increased production of the dispersing sex (males) when local competition is high. Finally, Silk (1983) made the opposite prediction of Trivers and Willard (1973), in that behaviorally dominant females in good condition (in our case, indexed by higher body mass relative to other females) should produce females to enhance the benefits of matrilines.

The Trivers and Willard (1973) hypothesis was not well supported by our results for Columbian ground squirrels (but see Schindler et al. 2015), although the conditions for this hypothesis were generally met. Offspring sex ratio was close to Fisher's (1930) even expectation at about 51%. Males seemed slightly more energetically expensive to produce, because they were about 4% heavier than females. However, they incurred no detectable fitness costs to mothers. Part of this mass difference was accounted for by differential growth during lactation, when young are under ground and solely dependent on the mother for sustenance. This condition likely persists into adulthood, because males are both larger and heavier than females at every age (Dobson 1992). Heavier males obtain advantageous matings and produce more offspring (Raveh et al. 2010, Balmer et al. 2019). Thus, we could examine the prediction that more should be invested in males by mothers with the greatest breeding resources. Female ground squirrels breed primarily from daily resource consumption, but their resources at the start of the spring breeding season have a significant influence on reproduction (Dobson et al. 1999, Broussard et al. 2005, Rubach et al. 2016).

Adult female condition near the time of conception is most likely to influence offspring sex ratio (Cameron et al. 1999, Cameron 2004, Sheldon and West 2004, Cameron and Linklater 2007). However, we found no significant pattern for male-biased litters in years where the mean condition of females in the population was higher at the beginning of the spring breeding season. Also, there was no significant association between individual maternal body mass at the beginning of the spring breeding season and either sex ratio of young at weaning, or change in sex ratio of young between birth and weaning for mothers that lost young during lactation. Finally, individual mothers did not produce male-biased litters in years when they were in better condition compared to their lifetime average, as the Trivers and Willard (1973) hypothesis would predict. The Trivers–Willard

hypothesis appears well supported in some taxa and weakly or not supported in others (Cameron 2004, Robert and Schwanz 2011, Schindler et al. 2015, Douhard et al. 2016, Hamel et al. 2016, Douhard 2017). Identification of the underlying reasons for such variation (e.g., phylogeny, social structure, food availability, environmental constraints) might be evident in a meta-analysis of published results on sex ratio and the Trivers-Willard hypothesis.

We found a weak, but significant, association between kin numbers and sex ratio at weaning. The proportion of males in a litter increased by a factor 1.15 (unstandardized odds ratio) for a 1-unit increase in kin numbers in the population. In other words, for one extra breeding kin in the population, sex ratio would increase by 15%, for instance from 50% male to 57.5% male. This observation is consistent with Clark's (1978) model of local kin competition. Clark's hypothesis was devised to explain a strong overall male bias in the offspring sex ratios of species such as galagos and African wild dogs. To avoid competition with close relatives, Clark (1978) suggested that breeding females in such systems might produce more sons, if males were the predominant dispersing sex. For species without a strong overall sex bias in numbers of offspring, however, the hypothesis still makes predictions about the preferential production of the sex of offspring by mothers with respect to kinship, when resources are in short supply. In Columbian ground squirrels, females with co-breeding close relatives, like mothers, daughters, and sisters, live in close proximity in matrilines (Arnaud et al. 2012, Dobson et al. 2012), whereas subadult males are predominant dispersers (Wiggett and Boag 1992, Neuhaus 2006). Closely related adult females have the potential for competition with respect to using environmental resources, but the presence of close co-breeding female kin clearly benefits reproduction and fitness (Viblanc et al. 2010, Dobson et al. 2012).

Silk (1983) expanded on Clark's original model by considering the importance of kin neighbors on offspring sex ratio, but argued that mothers in good condition should produce more daughters to maintain and promote advantages associated with the matriline of closely related kin, while mothers in poor condition should produce more males to avoid additional competition. Silk's (1983) hypothesis was that dominance matters in primate species, such that dominant females produced more daughters and subordinate females produced more sons that dispersed from their natal groups. In Columbian ground squirrels, adult females are individually territorial, but show both material and fitness benefits to living close to co-breeding relatives, despite the possibility of reproductive competition. Material benefits include lowered aggression, and closer proximity of more easily defendable territories (Harris and Murie 1984, King and Murie 1985, King 1989a, b, Arnaud et al. 2012). Fitness benefits of proximity to close relatives include improved individual reproductive success (Viblanc et al. 2010) and augmented inclusive fitness via a substantial indirect fitness

component (about 40%; Dobson et al. 2012). Thus, it is reasonable to predict that adult females in the best condition and social circumstances (viz., surrounded by close kin) should produce daughters.

When considering maternal body mass relative to other females in a given year, we found that the presence of female kin was associated with offspring sex-ratio bias. Mothers in better body condition produced slightly more sons, but only when more co-breeding close kin were present. The opposite pattern occurred for mothers that started the season in relatively poor condition. This would seem to contradict Silk's (1983) ideas about promotion of the matriline through the birth of daughters to adult females in good condition, but supports Clark's (1978) idea that mothers in matrilines that suffer from resource competition should produce more of the dispersing sex among their offspring. Further support for Clark's (1978) hypothesis of the influence of local resource competition was somewhat present in adult females that suffered a partial litter loss. These females tended to produce more males as the number of co-breeding female close kin increased (with an associated trend towards greater juvenile male survival from birth to weaning), as might be expected if they invested more in males to avoid future resource competition. Silk (1983) suggested that competitive mothers reduce daughter production of subordinate females via harassment. In Columbian ground squirrels, lactating mothers in better body condition produce larger and heavier litters (Dobson et al. 1999), and are known to be socially dominant (Murie and Harris 1988, Viblanc et al. 2016). On the other hand, harassment as a result of aggression and infanticide is biased towards non-kin in this species (King 1989a, Stevens 1998, Viblanc et al. 2016), and whether the selective mortality of daughters we observed with increasing kin numbers during lactation resulted from increased female harassment towards subordinate kin remains unclear.

Wells and Vuren (2017) examined offspring sex ratios at weaning, and found that golden mantled ground squirrels (*Callospermophilus lateralis*) had increasing male bias at weaning with increased numbers of nearby close kin, though older females surrounded by many kin had offspring sex ratios biased towards females. Armitage (1987a), working with yellow-bellied marmots (*Marmota flaviventris*), found that young breeding females in matrilines produced more daughters, and females without kin nearby produced more males. Michener (1980) found that female Richardson's ground squirrels (*Urocitellus richardsonii*) that produced more females maintained matrilines over generations, whereas those producing fewer females did not. More recently, Yao and Hare (2021) suggested that litter sex ratio in this species varied with litter size and female experience (first-time, second, or third litters produced; but see Gedir and Michener 2014), indicating possible complex adjustments related to resource competition and matriline maintenance. In alpine marmots (*Marmota marmota*), females without kin helpers produce significantly more of that sex (male) in their litters (Allaine et al. 2000, Allaine 2004). The presence or absence of close kin clearly has an influence on the sex ratio of offspring in this group of rodents (viz., marmotines), but the influences and effects appear to vary from species to species.

Given the variation among species in likely influences on sex ratios and allocation of resources to the sexes of offspring, multiple influences in Columbian ground squirrels should not be surprising. In addition, skewed sex ratios could also occur because of differential susceptibility of male and female fetuses to in utero environments and stress (Vandenbergh and Huggett 1994, Schacht et al. 2019, Firman 2020). In our study, two factors appeared most influential, the relative body condition of mothers when breeding commenced (a strong influence on reproductive success; Dobson et al. 1999, Broussard 2005), and how many co-breeding close kin these females shared (another major influence on reproduction and fitness; Viblanc et al. 2010, Dobson et al. 2012). Mothers in superior body condition in a strong matriline produced more sons. Mothers in good condition but with little or no matriline advantages produced more female offspring, perhaps favoring a stronger future matriline advantage. Mothers in relatively poor condition but with strong networks of close kin produced more daughters, and those with no or few co-breeding kin produced more sons. Thus, variation in sex ratios among offspring are perhaps best explained by a combination of factors with demonstrated influences on reproduction.

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