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Thibaut Barra, Vincent Viblanc, Claire Saraux, Jan Murie, F. Stephen
Dobson

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

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4 Thibaut Barra^{1*}, Vincent A. Viblanc^{1*}, Claire Saraux¹, Jan O. Murie² & F. Stephen Dobson^{1,3 ϕ}

5
6 * Equal contribution

7
8 ¹University of Strasbourg, CNRS, Institut Pluridisciplinaire Hubert Curien, UMR 7178, 67000
9 Strasbourg, France

10 ²Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9

11 ³Department of Biological Sciences, Auburn University, 311 Funchess Hall, Auburn, AL 36849

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21 ϕ Corresponding author: F Stephen Dobson, Department of Biological Sciences, University of
22 Alberta, Edmonton, AB T6G 2E9; fsdobson@msn.com

23

24 **Running head:** Sex allocation models in a wild mammal

25 **ABSTRACT**

26 Parental allocation of resources into male or female offspring and differences in the balance of
27 offspring sexes in natural populations are central research topics in evolutionary ecology. Fisher
28 (1930) identified frequency-dependent selection as the mechanism responsible for an equal
29 investment in the sexes of offspring at the end of parental care. Three main theories are
30 proposed for explaining departures from Fisherian sex ratios in light of variation in
31 environmental (social) and individual (maternal condition) characteristics. The Trivers-Willard
32 (1973) model of male-biased sex allocation by mothers in the best body condition is based on
33 the competitive ability of male offspring for future access to mates and thus superior
34 reproduction. The local resource competition model is based on competitive interactions in
35 matriline, as occur in many mammal species, where producing sons reduces future intrasexual
36 competition with daughters. A final model invokes advantages of maintaining matriline for
37 philopatric females, despite any increased competition among females. We used 29 years of
38 pedigree and demographic data to evaluate these hypotheses in the Colombian ground squirrel
39 (*Urocyon columbianus*), a semi-social species characterized by strong female philopatry.
40 Overall, male offspring were heavier than female offspring at birth and at weaning, suggesting
41 a higher production cost. With more local kin present, mothers in the best condition biased their
42 offspring sex ratio in favor of males, and mothers in poor condition biased offspring sex ratio
43 in favor of females. Without co-breeding close kin, the pattern was reversed, with mothers in
44 the best condition producing more daughters, and mothers in poor condition producing more
45 sons. Our results do not provide strong support for any of the single-factor models of allocation
46 to the sexes of offspring, but rather suggest combined influences of relative maternal condition
47 and matriline dominance on offspring sex ratio.

48 **Keywords:** Kin selection, local resource competition, matriline, sex ratio allocation,
49 Trivers-Willard hypothesis

50 INTRODUCTION

51 Life-histories are a central focus of both ecology and evolution (Stearns 1992; Roff 2001). The
52 success of different life history strategies can be assessed through individual variations in
53 fitness (characteristics of reproduction and survival), and the expression of traits contributing
54 to higher reproductive and survival rates (e.g., Endler 1986; Kruuk and Hill 2008). The fitness
55 differences of individuals that carry different trait forms, in turn, depend on the interactions of
56 those traits with the ecological and social environments (e.g., Lande and Arnold 1983). Thus,
57 our understanding of evolution rests on a foundation of ecological interactions that produce
58 fitness differences (Hutchinson 1965). An aspect of reproduction that might result in fitness
59 differences among individuals is the differential allocations of resources that parents make to
60 male and female offspring. Such allocation differences might lead to variations in offspring
61 sex ratio, if the fitness returns of producing males or females differ, depending on the
62 environment.

63 In many animal species, offspring sex ratios are close to even, a generality that Darwin
64 (1871) puzzled over. Fisher (1930) pointed out that it is not the numbers of male and female
65 offspring that should be roughly equal in a population, but the amount of parental allocation of
66 resources. Fitness returns of allocating resources to a male or female offspring should be equal
67 in bisexual species, since every individual has a mother and father and in turn will potentially
68 become a mother or father. In other words, the fitness returns of male and female offspring are
69 equal. When the ratio of male to female offspring allocation varies from even, frequency-
70 dependent selection should bring it back into balance. If both sexes are equally costly to
71 produce, then an even sex ratio of offspring should occur (Fisher 1930, Charnov 1979).

72 Nonetheless, extremely biased offspring sex ratios have been found in nature (e.g.,
73 Hamilton 1967) and hypotheses for explaining adaptive deviations from so-called “Fisherian
74 sex ratios” have been subsumed into a theory of how resources are allocated between the sexes

75 of offspring (Charnov 1982, Frank 1990, West 2009). In an early attempt at predicting biases
76 from even sex allocations, Trivers and Willard (1973) suggested that mothers should vary in
77 their body condition and ability to invest in offspring. If the future reproductive success of one
78 sex is more variable than that of the other and can be influenced by augmented early
79 investment, then mothers in better body condition should invest more in that sex. For instance,
80 suppose that male future reproductive success is more variable than female future reproductive
81 success, and is augmented by enhanced development early in life as in most polygynous and
82 polygynandrous mammal species (Dobson 1982, Dobson et al. 2010). Then, mothers in
83 relatively good body condition should produce more males, and mothers in relatively poor
84 condition should produce more females. This hypothesis assumes that the relative cost of
85 producing male and female offspring differs, that there is a positive association of maternal
86 body condition and the production of males, that early investment in males should persist into
87 adulthood, and that such males should have greater fitness as adults. Despite considerable
88 empirical and theoretical study of offspring sex ratio in mammals (Clutton-Brock and Iason
89 1986; Festa-Bianchet 1996; Kojola 1998; Hewison and Gaillard 1999, Brown 2001; Cameron
90 2004; Cameron et al. 2008; Schindler et al. 2015; Toni et al. 2021), support for the prediction
91 of a positive association of maternal condition and offspring sex ratio remains equivocal.

92 Clark (1978) developed the idea of local competition among relatives as an influence
93 on offspring sex ratios that deviate from 50:50 to explain offspring sex ratios that typically
94 vary between 60-75% male in species such as galagos (*Galago sp.*) and African wild dogs
95 (*Lycaon pictus*). She noted that females are often limited in reproduction by competition over
96 local resources, such as food, refuges from predation, or territories (reviewed by Emlen and
97 Oring 1977). This competition should favor production of the dispersing sex. In polygynous
98 and polygynandrous mammals, females are often highly philopatric and matrilineal, and the
99 dispersing sex among juvenile and subadults is usually males (Greenwood 1980, Dobson

100 1982). When population density is already high, females should thus produce more males to
101 prevent future local competition for resources. Several studies have provided empirical support
102 for the local resource competition model, including primates (Clark 1978), marsupials
103 (Cockburn et al. 1985; Schwanz and Robert 2014), and rodents (Wells and Van Vuren 2017).

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

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

123 Columbian ground squirrels (*Urocitellus columbianus*) are a good system for the study
124 of offspring energy allocation and sex ratio. They are semi-social, hibernating sciurid rodents

125 that inhabit subalpine meadows in the Rocky Mountains of southwestern Canada (Boag and
126 Murie 1981; Dobson et al. 1992). Within colonies, philopatric females overlap temporally and
127 spatially with close kin, creating local matriline (King and Murie 1985; King 1989a, 1989b).
128 Females with higher numbers of kin acquire direct and indirect fitness benefits from philopatry
129 (Viblanco et al. 2010; Arnaud et al. 2012; Dobson et al. 2012). Males, on the other hand,
130 contribute little or nothing to the production of offspring beyond sperm, during a short mating
131 season (Manno and Dobson 2008; Raveh et al. 2010, 2011), and exhibit high variance in
132 reproductive success (Raveh et al. 2010). Mothers are variable in size and body condition
133 (Dobson 1992; Dobson et al. 1999; Rubach et al. 2016), and thus provide suitable variables for
134 testing hypotheses about allocation of resources to offspring and variation in offspring sex
135 ratios. The amount and quality of food resources are a major influence on allocations to
136 offspring by mothers (Dobson and Kjelgaard 1985; Dobson and Muri 1987; Dobson 1988).
137 Finally, year-to-year environmental variations are extreme (Lane et al. 2012, Dobson et al.
138 2016), thus providing ample variation in annual availability of resources.

139 The purpose of our study was five-fold. First, we tested the repeatability of offspring
140 sex ratio over the lifetimes of adult females, to examine trait flexibility. Second, we evaluated
141 the costs to mothers of producing male and female offspring. We examined the estimated costs
142 of sons and daughters in terms of their mass at weaning, a value that should reflect the energetic
143 costs of producing offspring. We also examined the fitness costs of producing sons and
144 daughters for mothers, by testing for differences in maternal reproduction, survival and mass
145 gain during the active season. Third, we tested the Trivers and Willard (1973) prediction that
146 mothers in good condition should produce costlier sons. For this, we focused on female mass
147 at the start of the breeding season, known to strongly influence subsequent reproductive success
148 (Dobson et al. 1999; Broussard et al. 2005; Rubach et al. 2016). We tested if females in good
149 condition biased maternal investment towards males. Fourth, we tested Clark's predictions

150 from the local resource competition hypothesis of male-biased offspring production when local
151 density and competition for resources are high within matriline (Clark 1978). Fifth, we
152 examined Silk's (1983) prediction that females in the best body condition and in large
153 matriline should produce sex ratios biased towards daughters, since they can best bear costs
154 associated with local resource competition and reap the benefits of augmented matriline
155 (Armitage 1987a,b).

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

164

165 **MATERIALS AND METHODS**

166 **STUDY SITE AND LONG-TERM MONITORING**

167 Data were collected from 1992 to 2020 at a 2.6 ha subalpine meadow in the Sheep River
168 Wildlife Provincial Park, Alberta, Canada (50°38'10"N, 114°39'56"W, 1550m asl).
169 Columbian ground squirrels were monitored yearly throughout the breeding season from
170 emergence from hibernation (~ mid-April) to weaning of the offspring (~ early July). In each
171 year of the study, all animals were trapped when first emerging from hibernation, using live
172 traps (Tomahawk Live Trap Co., Hazelhurst, WI; 13 × 13 × 40 cm) baited with a small amount
173 of peanut butter. Ground squirrels were weighed to the nearest 5 g using a Pesola® spring-slide
174 scale, given a unique ear tag number (#1-Monel metal; National Band and Tag Company,

175 Newport, KY), and painted with a unique dorsal mark on the pelage for visual identification at
176 a distance, using black human hair dye (Clairol, Stamford, CT).

177 Females typically estrous cycle within 3-5 days after emergence from hibernation, and
178 are sexually receptive for a few hours on a single day (Murie and Harris 1982, Murie 1995,
179 Raveh et al. 2010). We determined mating date for each female from behavioral observations,
180 inspection of their genitalia, and the presence of copulatory plug material in or around the vulva
181 (Murie and Harris 1982). Mated females were caught 22 days after mating, 2-3 days before
182 expected parturition, and transported to a 1.5 km-distant field laboratory where they gave birth.
183 Females were housed in polycarbonate microvent cages (47 x 27 x 20 cm; Allentown Caging
184 Equipment Company, Allentown, NJ), and provided wood chip bedding and shredded
185 newspaper for nesting material. Food, including grains (a molasses-enriched horse feed), fresh
186 apples, fresh lettuce and water were provided *ad libitum* twice a day. At birth, mothers (nearest
187 5 g) and pups (nearest 0.01 g) were weighed. Pups were sexed and marked with a small tissue
188 biopsy used for establishing paternities (Hare and Murie 1992). The biopsy created a partial
189 claw loss on a rear foot, and thus pups could be identified at birth and later at weaning.
190 Newborns and their mothers were released approximately one day after birth into their nest
191 burrow, known from behavioral observations of females stocking them with dry grass prior to
192 capture and marked with colored flags.

193 Entire litters and mothers were caught 27-28 days after birth, when young first emerged
194 from nest burrows near the time of weaning. Young were then ear tagged for permanent
195 identification and weighed to the nearest 1 g. Mothers were weighed again to the nearest 5 g.
196 Since 1992, several generations of matrilineal genealogies are known from mother-offspring
197 associations. Complete life histories (including age and pedigree relationships) are known for
198 the vast majority of animals that lived on the study site. For each year of the study, we used the
199 long-term data to determine: (1) offspring sex ratio and individual mass at birth and at weaning,

200 and sex ratio variation among adult females, (2) female condition and energy allocation to
201 offspring in grams of body mass, and (3) the density of closely related kin.

202

203 OFFSPRING SEX RATIO

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

211

212 DATA ANALYSES

213 All analyses were conducted in the R statistical computing environment v. 4.0.2 (R Core Team
214 2020). Results are presented as means \pm 1 S.E., unless otherwise noted. Independent variables
215 were standardized prior to analyses, so that coefficients were directly comparable as effect
216 sizes. Where appropriate, we examined model residuals for normality by visual inspection of
217 density distributions, Q–Q plots, cumulative distribution functions and P–P plots using the
218 “fitdistrplus” package in R (Delignette-Muller & Dutang 2015). We also insured that no
219 substantial collinearity occurred between independent variables (all variance inflation factors
220 < 3 ; suggested cut-off, see Zuur, Ieno & Elphick 2010). The goodness-of-fit of each model was
221 evaluated by comparing the deviance of the model to the deviance of the null model (with the
222 intercept only) and expressed as explained deviance $ED = \frac{deviance_{null} - deviance_{model}}{deviance_{null}}$,
223 characterizing the percent-deviance explained by the model.

224

225 **Repeatability of offspring sex ratio**

226 For females that bred in multiple years, we estimated offspring sex ratio repeatability using the
227 "rptR" package in R (Stoffel et al. 2017). Repeatability was calculated as $R = \frac{V_G}{V_P} = \frac{V_G}{V_G + V_R}$,
228 where V_G is the among-group variance, V_R is the residual variance, and $V_P = V_G + V_R$ is the
229 total phenotypic variance in offspring sex ratio. V_G was either the among-individual variance
230 or the among-year variance, depending on whether repeatability within females or within years
231 was considered. Variance in offspring sex ratio was decomposed using separate generalized
232 linear mixed-effects models (GLMM, 'lme4' package in R; Bates et al. 2015), with offspring
233 sex ratio specified as a proportion of successes and failures for each mother as the dependent
234 variable (count data; matrix of "success" and "failures" with male = "success", female =
235 "failure"), and mother identity or year as a random factor. Confidence intervals around
236 repeatability estimates were calculated by parametric bootstrapping (N = 1000 random data
237 sets were generated from the distribution defined by the estimated parameters). As the amount
238 of variance in offspring sex ratio explained by mother ID or year was virtually zero, we
239 disregarded these factors as random variables in subsequent models on sex ratio.

240

241 **Cost differences in male and female offspring**

242 *Differences in the energy invested in the production of male and female offspring*

243 First, we tested for differential energy costs in the production of male/female offspring
244 production by comparing male and female mass at birth and at weaning. Offspring mass at
245 birth and at weaning were specified as dependent variables in separate linear mixed models
246 (LMMs), and offspring sex was included as an independent factor. We controlled for litter size
247 at birth (mean \pm s.d. = 3.22 ± 0.87 , min = 1, max = 7) as a covariate in all models because of
248 the known trade-off between number and mass of offspring in our species (e.g., Dobson et al.
249 1999; Skibieli et al. 2009). Mother ID and litter ID were included as random variables in the

250 models to account for repeated measures over the years, and the non-independence of offspring
251 born from the same mother and raised within the same litter. We also tested if female and male
252 offspring differed in their survival from birth to weaning using a binomial GLMM. Offspring
253 survival was included as the dependent variable (binary; survived = 1, died = 0) and offspring
254 sex as the independent variable of interest. We further accounted for litter size and offspring
255 mass at birth in the model as known influences on survival. As above, mother ID and litter ID
256 were originally included as random variables in the models to account for repeated measures
257 over the years, and the non-independence of offspring born from the same mother and raised
258 within the same litter. However, mother ID explained virtually no variance in pup survival, and
259 was removed from the final model.

260

261 *Fitness costs to mothers*

262 Second, we tested if maternal fitness costs could be detected for mothers that invested more
263 into male or female-biased litters. We considered the effects of litter sex ratio at birth, or at
264 weaning, on 3 proxies of maternal fitness: (1) reproductive output over the season (litter size
265 at weaning; count data, mean \pm s.d. = 2.54 ± 1.28 offspring, min = 0, max = 7; Poisson GLMM),
266 (2) maternal mass gain (or loss) over the breeding season (continuous data, mean \pm s.d. = 108.7
267 ± 46.8 g, min = -50 g, max = 280 g; LMM), and (3) mother survival (binary, 0/1; binomial
268 GLMM) to the next year. We initially included mother ID, age and year as random factors in
269 the models to account for variance in fitness parameters, but removed these when the variance
270 explained was virtually null.

271

272 **Testing Trivers and Willard's model of sex allocation**

273 *Maternal condition effects on litter sex ratio*

274 We used a 3-step analysis to test for maternal condition effects on sex ratio.

275 First, to test whether mothers that raised a litter, on average, biased the offspring sex
276 towards males in particularly favorable years, we calculated the average mass of breeding
277 females at emergence from hibernation (mean \pm s.d. = 419.72 g \pm 20.70 g, min = 376.6 g, max
278 = 460.55 g), and the average sex ratio (see Fig 1) at weaning for the population, for 28 years
279 of the 29 year-study (no data on maternal mass in 2020 due to COVID-19). We then regressed
280 mean offspring sex ratio at weaning on mean maternal mass at emergence (LM; N = 28).

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

291 Third, to test whether mothers biased the sex ratio of their litters towards males in years
292 where they were in particularly good condition compared to their lifetime average, we
293 calculated relative maternal mass at emergence within a year, i.e. female mass compared to her
294 mean mass over the years she weaned a litter. This annual relative condition index (mean \pm s.d.
295 = 0.00 g \pm 30.60, min = -133.00 g, max = 106.43 g) was calculated as:

$$296 \quad \text{annual relative condition}_{i,y} = \text{mass}_{i,y} - \mu_i,$$

297 where i is mother ID and y is year. A mother with a condition index > 0 (or < 0) in a given
298 year, thus was in better (or worse) condition than her lifetime average. We then used a GLM

299 specifying offspring sex ratio as a proportion of males and females for each mother and as the
300 dependent variable, and annual relative condition as the independent variable.

301

302 *Maternal condition effects on male and female offspring mass gain*

303 We tested whether the gain in offspring mass over the course of lactation for males
304 (mean \pm s.d. = 97.34 g \pm 22.14, min = 45.04 g, max = 198.06 g) and females (92.12 g \pm 19.57,
305 min = 35.82 g, max = 169.61 g) was differently affected by maternal condition at the start of
306 the breeding season. We used a linear model (LM) with offspring mass gain specified as the
307 dependent variable, and maternal mass at emergence from hibernation, offspring sex and the
308 interaction between offspring sex and maternal mass at emergence specified as independent
309 variables. In addition, we controlled for litter size at birth, offspring mass at birth, and lactation
310 duration (mean \pm s.d. = 26.27 days \pm 1.12, min = 23 days, max = 31 days) as covariates in the
311 model, because they were possible influences on offspring mass gain.

312

313 **Testing local resource competition models of sex allocation**

314 *Clark's model of local resource competition*

315 To test Clark's (1978) prediction that mothers should bias offspring sex ratio towards the
316 dispersing (male) sex when local kin competition for resources is high, we performed a two-
317 step analysis. First, we tested if offspring sex ratio was biased towards males (the dispersing
318 sex) in years of high population density. For this, we calculated the average sex ratio (see Fig
319 1) at weaning for the population, and regressed it on overall population density (mean \pm s.d. =
320 62.69 individuals \pm 22.87, min = 32 days, max = 120 days; N = 29 years). Second, we used the
321 long-term matrilineal genealogies to determine the total number of kin females (mothers,
322 daughters, and littermate sisters) in each year of the study (mean \pm s.d. = 0.89 \pm 0.72, min = 0,
323 max = 4). We restricted our analyses to reproductive females only, defined as females that

324 mated and were potentially able to hold a territory at some point during the breeding season
325 (Festa-Bianchet and Boag 1982, Murie and Harris 1988). We subsequently examined litter sex
326 ratio at weaning and changes in offspring sex ratio from birth to weaning (LM; Δ SR) in relation
327 to the numbers of kin present in the population (independent variables). We also tested if the
328 proportion of offspring (dependent variable, binomial proportion GLM) lost during lactation
329 by individual mothers, controlling for litter size at birth in the model, depended on the numbers
330 of kin present in the population.

331

332 *Silk's model of matriline dominance*

333 To test Silk's (1983) prediction that dominant females in relatively good body condition (i.e.,
334 who can best incur the costs of local resource competition with kin) should produce sex ratios
335 biased towards daughters, we further examined the interaction between maternal condition
336 relative to other females and kin numbers. Here, we calculated relative condition as the
337 differential between the mass of a mother and the mean mass of all females in the population
338 at the start of the breeding season in a given year. Lactating females are socially dominant over
339 other ground squirrels (Murie and Harris 1988), females in better body condition produce larger
340 and heavier litters (Dobson et al. 1999), and mothers with the greatest reproductive investments
341 are socially dominant (Viblanco et al. 2016). Condition relative to other females (mean \pm s.d. =
342 0.00 g \pm 49.51, range = -191.25 g to 174.23 g) was calculated as:

343
$$relative\ condition_{i,y} = mass_{i,y} - \mu_y ,$$

344 where i is mother ID and y is year. A relative condition > 0 (or < 0) would indicate that a female
345 was in relatively better (or worse) condition than other females of the population in a given
346 year. Relative condition increased in a quadratic fashion with age, so that, on average, it was $<$
347 0 for females until 4 years, increased up until 6-7 years old, before decreasing afterwards (see
348 Appendix S1), consistent with previous quadratic relations found for dominance-related

349 aggression and age in this species (Viblanco et al. 2016). We subsequently examined litter sex
350 ratio at weaning (GLM, binomial) and changes in offspring sex ratio from birth to weaning
351 (LM; Δ SR) in relation to a female's relative condition, the number of kin present in the
352 population, and the interaction between both variables (independent variables).

353

354 **RESULTS**

355 REPEATABILITY OF OFFSPRING SEX RATIO

356 At termination of parental care (weaning), offspring sex ratio in our population was on average
357 51.3 % male ($n = 1581$ offspring, $N = 195$ mothers), ranging from 36.2% in 2020 to 74.2% in
358 2009 (Fig. 1). The estimated repeatability of offspring sex ratio was virtually nil both when
359 considering inter-individual variation (binomial GLMM; $R = 0.000 \pm 0.006$, $CI_{95} = [0.000 -$
360 $0.022]$, $n = 622$ litters, $N = 203$ mothers), and when considering inter-annual variation ($R =$
361 0.007 ± 0.006 , $CI_{95} = [0.000 - 0.021]$, $n = 622$ litters, $N = 29$ years).

362

363 COST DIFFERENCES BETWEEN MALE AND FEMALE OFFSPRING

364 **Differences in the energy invested in the production of male and female offspring**

365 At birth, controlling for litter size, male offspring were 4.15% heavier than female offspring
366 (Fig 2A; Appendix S2: Table S1A). Similarly, at weaning and when controlling for litter size,
367 male offspring were 3.61 % heavier than female offspring (Fig 2B; Appendix S2: Table S2B).
368 Controlling for litter size and offspring mass at birth, male and female offspring did not differ
369 significantly in their survival rates (75% for males, 76.8% for females; Appendix S2: Table
370 S2) from birth to weaning. Offspring survival was positively associated with offspring mass at
371 birth (z -mass odds ratio = $+1.86 \pm 0.16$, Appendix S2: Table S2), but not significantly with
372 litter size at birth (z -litter size odds ratio = $+1.20 \pm 0.25$, Appendix S2: Table S2).

373

374 **Fitness costs to mothers**

375 When testing for costs to mothers, maternal reproduction (litter size weaned) was not
376 significantly related to litter sex ratio at birth (GLMM, with Poisson error term; odds ratio =
377 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}
378 $= [0.81 - 1.10]$, $t = -0.76$, $P = 0.45$, $n = 559$). Maternal survival to the next year was neither
379 significantly influenced by litter sex ratio at birth (GLMM, with binomial error term; odds ratio
380 $= 0.98 \pm 0.39$, $CI_{95} = [0.45 - 2.13]$, $z = -0.05$, $P = 0.96$, $n = 415$) or at weaning (odds ratio =
381 1.08 ± 0.35 , $CI_{95} = [0.57 - 2.05]$, $z = 0.24$, $P = 0.81$, $n = 536$). Maternal mass gain over the
382 season was positively, but not significantly, related to litter sex ratio at birth (LMM; $8.44 \pm$
383 7.83 , $CI_{95} = [-6.90 - 23.78]$, $t = 1.08$, $P = 0.28$, $n = 350$), and tended to be positively associated
384 with litter sex ratio at weaning (9.81 ± 5.39 , $CI_{95} = [-0.75 - 20.37]$, $t = 1.82$, $P = 0.07$, $n = 508$).
385 Thus, for a 1%-point increase in litter sex ratio at weaning (e.g. from 50 to 51% male), maternal
386 mass gain over the course of reproduction increased by 0.098 grams, on average.

387

388 **TESTING TRIVERS AND WILLARD'S MODEL OF SEX ALLOCATION**

389 **Maternal condition effects on sex ratio**

390 Over 28 years, the mean sex ratio at weaning of offspring in the population (Fig 1) was not
391 significantly associated with mean maternal mass at the start of the breeding season (LM; z -
392 mean female mass $= -0.01 \pm 0.02$, $t = -0.41$, $CI_{95} = [-0.04, 0.03]$, $P = 0.69$, $N = 28$ years).

393 Maternal body mass at the start of the breeding season did not significantly affect
394 offspring sex ratio at weaning (GLM; binomial; z -mass odds ratio $= 0.88 \pm 0.09$, $CI_{95} = [0.74,$
395 $1.04]$, $z = -1.46$; $P = 0.15$, $n = 1499$, $ED = 0.29\%$). Similarly, for females that lost at least one
396 offspring over lactation, maternal body mass did not significantly affect changes in offspring
397 sex ratio from birth to weaning (LM; z -mass $= +0.03 \pm 0.03$, $CI_{95} = [-0.02, 0.08]$, $t = 1.11$, $P =$
398 0.27 , $n = 102$, $ED = 1.22\%$). Overall, controlling for litter size at birth (all VIFs < 1.2), the

399 proportion of offspring lost during lactation was not significantly related to maternal mass at
400 emergence (GLM binomial; odds ratio: z -emergence mass = 0.96 ± 0.07 , $CI_{95} = [0.84 - 1.10]$,
401 $P = 0.57$, $n = 1336$, $ED = 0.03\%$).

402 When considering maternal yearly condition index (maternal yearly mass relative to
403 her lifetime average), mothers did not seem to bias litter sex ratio differently in years when
404 they were in relatively better or worse condition compared to their lifetime average (GLM; z -
405 yearly condition odds ratio = 0.96 ± 0.05 , $CI_{95} = [0.86, 1.06]$, $z = -0.84$, $P = 0.40$, $n = 1499$, ED
406 = 0.1%). Maternal yearly condition also did not seem to significantly affect changes in
407 offspring sex ratio from birth to weaning, for those mothers that lost young during lactation
408 (LM; z -yearly condition = 0.01 ± 0.03 , $CI_{95} = [-0.04, 0.07]$, $t = 0.54$, $P = 0.590$, $n = 102$, ED
409 = 0.29%).

410

411 **Maternal condition effects on mass gain of male and female offspring**

412 Regardless of sex (non-significant interaction, Appendix S2: Table S3A), offspring mass gain
413 over lactation was positively related to maternal mass at the start of the breeding season (z -
414 maternal mass = $+3.42 \pm 1.28$), to offspring mass at birth (z -offspring mass birth = $+4.40 \pm$
415 0.44), to lactation duration (z -lactation duration = $+4.48 \pm 0.66$), and negatively related to litter
416 size at birth (z -litter size birth = -7.58 ± 1.08) (Fig 3; Appendix S2: Table S3B). Controlling
417 for these effects in the model (Appendix S2: Table S3B) male offspring gained 1.68 % more
418 mass than females over lactation (Fig. 3A). The absence of an interaction between maternal
419 body mass and offspring sex suggests no differential allocation to males and females according
420 to maternal condition. Taken together, the results do not provide strong support for Trivers and
421 Willard's model of sex allocation in Columbian ground squirrels.

422

423 LOCAL RESOURCE COMPETITION MODELS OF SEX ALLOCATION

424 **Clark's model of local resource competition**

425 Offspring sex ratio at weaning was not significantly associated with population size over the
426 course of our study (LM; z -population density = -0.02 ± 0.02 , $t = -1.16$, $CI_{95} = [-0.05, 0.02]$, P
427 = 0.25, $N = 29$ years) (Appendix S2: Figure S1). Offspring sex ratio at weaning was positively
428 and significantly, though weakly, associated with a female's kin numbers in a given year
429 (GLM; z -kin odds ratio = $+1.10 \pm 0.05$, $CI_{95} = [1.00, 1.21]$, $z = 2.05$, $P = 0.040$, $n = 1371$, ED
430 = 0.6%). This effect appeared to be mediated through differential mortality of male and female
431 offspring during lactation, since offspring sex ratio at birth was not significantly related to a
432 female's kin numbers in a given year (GLM; z -kin odds ratio = $+1.02 \pm 0.05$, $CI_{95} = [0.92,$
433 $1.11]$, $z = 0.30$, $P = 0.764$, $n = 1243$, $ED = 0.02\%$). Indeed, for females that lost at least one
434 offspring over lactation, kin numbers were positively, though weakly, associated with changes
435 in offspring sex ratio from birth to weaning (LM; z -kin = $+0.05 \pm 0.03$, $CI_{95} = [-0.00, 0.10]$, t
436 = 1.87, $P = 0.065$, $n = 97$, $ED = 3.5\%$). Controlling for litter size at birth (all VIFs < 1.01), the
437 overall proportion of offspring lost during lactation was not significantly related to kin numbers
438 (GLM binomial; odds ratio: z -kin = 1.08 ± 0.07 , $CI_{95} = [0.95 - 1.23]$, $P = 0.22$, $n = 1246$, ED
439 = 0.18%). Taken together, these results appear to provide some support for local resource
440 competition as an influence on sex ratio in Columbian ground squirrels.

441

442 **Silk's model of matriline dominance**

443 Adding maternal body mass relative to female conspecifics in a given year and its interaction
444 with kin numbers to the above models revealed a significant interaction between maternal
445 relative condition and kin numbers affecting sex ratio at weaning (Fig 4; z -maternal relative
446 condition x z -kin odds ratio = $+1.18 \pm 0.06$, $CI_{95} = [1.06, 1.33]$, $t = 2.88$, $P = 0.004$, $n = 466$;
447 see Appendix S2: Table S4A; $ED = 2.1\%$). The proportion of males in weaned litters increased
448 with maternal condition relative to other females within a year, but only when kin numbers

449 were high (with 2 or more co-breeding female kin). It was only when kin were absent that
450 mothers in relatively good condition produced more daughters (Fig 4). Changes in offspring
451 sex ratio from birth to weaning, in contrast, did not seem to be significantly affected by the
452 interaction between maternal relative condition and kin (Appendix S2: Table S4B). Removing
453 the interaction did not reveal any effect of maternal relative condition (z -maternal relative
454 condition = $+0.00 \pm 0.00$, $CI_{95} = [-0.00, 0.00]$, $t = 1.26$, $P = 0.21$, $n = 97$), but indicated a subtle
455 effect of kin numbers (z -kin = $+0.04 \pm 0.02$, $CI_{95} = [-0.00, 0.08]$, $t = 1.93$, $P = 0.056$, $n = 97$,
456 $ED = 5.1\%$) on changes in sex ratio from birth to weaning (ΔSR). These results do not seem to
457 support Silk's model of matriline dominance in Columbian ground squirrels.

458

459 **DISCUSSION**

460 As predicted by Fisher (1930), and over 29 years of study, offspring sex ratio at the end
461 of parental care in Columbian ground squirrels was roughly even at 51.3 % male. However,
462 sex ratio varied markedly, from 36.2% to 74.2% male (repeatability was virtually null) among
463 years, suggesting scope for trait responses to variations in maternal, social, and ecological
464 conditions. We tested three hypotheses proposed to explain deviations from Fisherian sex ratios
465 in the animal realm from an adaptive perspective: the Trivers and Willard (1973), Clark (1978),
466 and Silk (1983) models of maternal allocation to male and female offspring. These hypotheses
467 are not mutually exclusive, but make different predictions about parental allocations to male
468 and female offspring that can influence offspring sex ratio. Trivers and Willard (1973) focused
469 on female energy allocation. For Columbian ground squirrels, where increased maternal
470 condition is related to increased reproductive output (Dobson and Kjelgaard 1985; Dobson and
471 Murie 1987; Dobson 1988; Risch et al. 1995; Dobson et al. 1999; Skibieli et al. 2009), they
472 predict a positive association between maternal body condition and male offspring production.
473 In contrast, Clark (1978) focused on local resource competition, predicting an increased

474 production of the dispersing sex (males) when local competition is high. Finally, Silk (1983)
475 made the opposite prediction of Trivers and Willard (1973), in that behaviorally dominant
476 females in good condition (in our case, indexed by higher body mass relative to other females)
477 should produce females to enhance the benefits of matriline.

478 The Trivers and Willard (1973) hypothesis was not well supported by our results for
479 Columbian ground squirrels (but see Schindler et al. 2015), although the conditions for this
480 hypothesis were generally met. Offspring sex ratio was close to Fisher's (1930) even
481 expectation at about 51%. Males seemed slightly more energetically expensive to produce,
482 because they were about 4% heavier than females. However, they incurred no detectable fitness
483 costs to mothers. Part of this mass difference was accounted for by differential growth during
484 lactation, when young are under ground and solely dependent on the mother for sustenance.
485 This condition likely persists into adulthood, since males are both larger and heavier than
486 females at every age (Dobson 1992). Heavier males obtain advantageous matings and produce
487 more offspring (Raveh et al. 2010; Balmer et al. 2019). Thus, we could examine the prediction
488 that more should be invested in males by mothers with the greatest breeding resources. Female
489 ground squirrels breed primarily from daily resource consumption, but their resources at the
490 start of the spring breeding season have a significant influence on reproduction (Dobson et al.
491 1999; Broussard et al. 2005; Rubach et al. 2016).

492 Adult female condition at near the time of conception is most likely to influence
493 offspring sex ratio (Cameron et al. 1999; Cameron 2004; Sheldon and West 2004; Cameron
494 and Linklater 2007). However, we found no significant pattern for male-biased litters in years
495 where the mean condition of females in the population was higher at the beginning of the spring
496 breeding season. Also, there was no significant association between individual maternal body
497 mass at the beginning of the spring breeding season and either sex ratio of young at weaning,
498 or change in sex ratio of young between birth and weaning for mothers that lost young during

499 lactation. Finally, individual mothers did not produce male-biased litters in years when they
500 were in better condition compared to their lifetime average, as the Trivers-Willard (1973)
501 hypothesis would predict. The Trivers-Willard hypothesis appears well supported in some taxa
502 and weakly or not supported in others (Cameron 2004; Robert and Schwanz 2011; Schindler
503 et al. 2015; Douhard et al. 2016; Hamel et al. 2016; Douhard 2017). Identification of the
504 underlying reasons for such variation (e.g., phylogeny, social structure, food availability,
505 environmental constraints) might be evident in a meta-analysis of published results on sex ratio
506 and the Trivers-Willard hypothesis.

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

524 Silk (1983) expanded on Clark's original model by considering the importance of kin
525 neighbors on offspring sex ratio, but argued that mothers in good condition should produce
526 more daughters to maintain and promote advantages associated with the matriline of closely
527 related kin, while mothers in poor condition should produce more males to avoid additional
528 competition. Silk's (1983) hypothesis was that dominance matters in primate species, such
529 that dominant females produced more daughters and subordinate females produced more sons
530 that dispersed from their natal groups. In Columbian ground squirrels, adult females are
531 individually territorial, but show both material and fitness benefits to living close to co-
532 breeding relatives, despite the possibility of reproductive competition. Material benefits
533 include lowered aggression, and closer proximity of more easily-defendable territories (Harris
534 and Murie 1984; King and Murie 1985; King 1989a, 1989b; Arnaud et al. 2012). Fitness
535 benefits of proximity to close relatives include improved individual reproductive success
536 (Viblanco et al. 2010) and augmented inclusive fitness via a substantial indirect fitness
537 component (about 40%; Dobson et al. 2012). Thus, it is reasonable to predict that adult females
538 in the best condition and social circumstances (viz., surrounded by close kin) should produce
539 daughters.

540 When considering maternal body mass relative to other females in a given year, we
541 found that the presence of female kin was associated with offspring sex ratio bias. Mothers in
542 better body condition produced slightly more sons, but only when more co-breeding close kin
543 were present. The opposite pattern occurred for mothers that started the season in relatively
544 poor condition. This would seem to contradict Silk's (1983) ideas about promotion of the
545 matriline through the birth of daughters to adult females in good condition, but support Clark's
546 (1978) idea that mothers in matrilineal groups that suffer from resource competition should produce
547 more of the dispersing sex among their offspring. Further support for Clark's (1978) hypothesis
548 of the influence of local resource competition was somewhat present in adult females that

549 suffered a partial litter loss. These females tended to produce more males as the number of co-
550 breeding female close kin increased (with an associated trend towards greater juvenile male
551 survival from birth to weaning), as might be expected if they invested more in males to avoid
552 future resource competition. Silk (1983) suggested that competitive mothers reduce daughter
553 production of subordinate females via harassment. In Columbian ground squirrels, lactating
554 mothers in better body condition produce larger and heavier litters (Dobson et al. 1999), and
555 are known to be socially dominant (Murie and Harris 1988; Viblanc et al. 2016). On the other
556 hand, harassment as a result of aggression and infanticide is biased towards non-kin in this
557 species (King 1989a, Stevens 1998, Viblanc et al. 2016), and whether the selective mortality
558 of daughters we observed with increasing kin numbers during lactation resulted from increased
559 female harassment towards subordinate kin remains unclear.

560 Examining offspring sex ratios at weaning, Wells and Van Vuren (2018) found that
561 golden mantled ground squirrels (*Callospermophilus lateralis*) had increasing male-bias at
562 weaning with increased numbers of nearby close kin, though older females surrounded by
563 many kin had offspring sex-ratios biased towards females. Armitage (1987a), working with
564 yellow-bellied marmots (*Marmota flaviventris*), found that young breeding females in
565 matriline produced more daughters, and females without kin nearby produced more males.
566 Michener (1980) found that female Richardson's ground squirrels (*Urocitellus richardsonii*)
567 that produced more females maintained matriline over generations, whereas those producing
568 fewer females did not. More recently, Yao & Hare (2021) suggested that litter sex ratio in this
569 species varied with litter size and female experience (first-time, second or third litters
570 produced) (but see Gedir & Michener 2014), indicating possible complex adjustments related
571 to resource competition and matriline maintenance. In alpine marmots (*Marmota marmota*),
572 females without kin helpers produce significantly more of that sex (male) in their litters
573 (Allaine et al. 2000; Allaine 2004). The presence or absence of close kin clearly has an

574 influence on the sex ratio of offspring in this group of rodents (viz., marmotines), but the
575 influences and effects appear to vary from species to species.

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

591

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609

610 **AUTHOR CONTRIBUTION**

611 TB analyzed the data, collected data in the field, and co-wrote the manuscript; VAV co-
612 designed the study, analyzed the data, collected data in the field, and co-wrote the manuscript;
613 CS co-designed the study, analyzed the data, collected data in the field, and commented on the
614 manuscript; JOM originated the long-term study, collected data in the field and commented on
615 the manuscript; FSD co-designed the study, collected data in the field and co-wrote the
616 manuscript.

617

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829 **Figure captions**

830

831 **Fig 1.** Annual offspring sex ratio (% males) at weaning in the Columbian ground squirrel
832 (*Uroditellus columbianus*) from 1992 to 2020. The black line represents the mean litter sex
833 ratio for mothers (mean of individual mother values = 51.3%) in the population each year with
834 associated 95%CI obtained by bootstrap (1000 simulations, 50% of the litters resampled each
835 time). The blue dotted line represents the sex ratio of all offspring at weaning in the entire
836 population (total number of weaned males / (total number of weaned males + total number of
837 weaned females)). A sex ratio above 50% (solid black horizontal line) is biased towards males,
838 and below, towards females.

839

840 **Fig 2.** Offspring mass (in grams) at **(A)** birth and **(B)** weaning according to sex in the
841 Columbian ground squirrel. Boxplots present the median, 25 and 75 percentiles of the
842 distribution. Red dots and lines present the marginal estimated means and 95% CI for female
843 and male offspring mass, accounting for litter size at birth and weaning, respectively (see
844 Models in text).

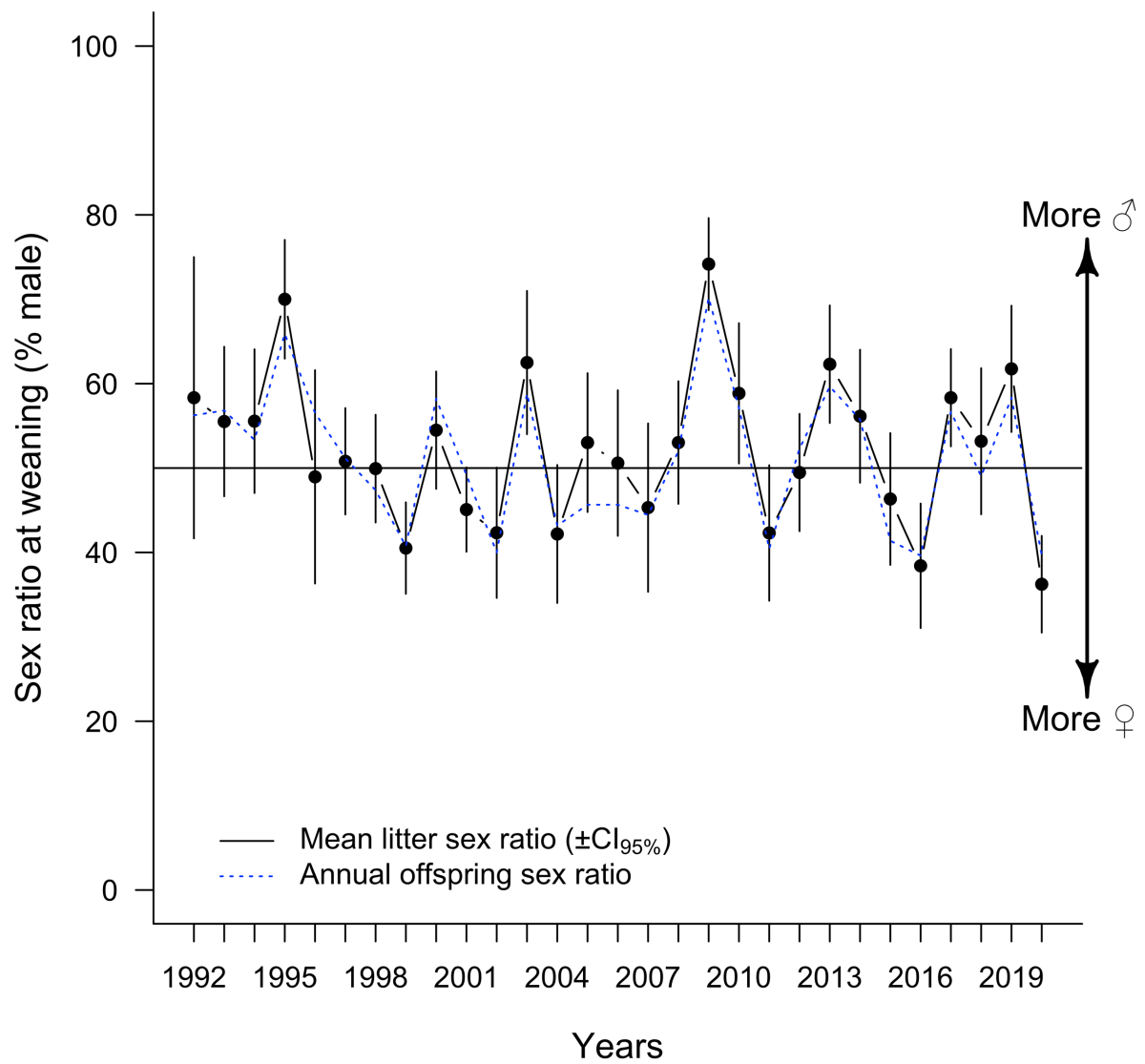
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846 **Fig 3.** Offspring mass gain (g) over the lactation period as a function of (A) offspring sex, (B)
847 offspring mass at birth (standardized), (C) maternal mass at the start of the breeding season
848 (standardized), (D) litter size at birth (standardized), and (E) lactation duration (in days,
849 standardized) in Columbian ground squirrels. Boxplots present the median, 25 and 75
850 percentiles of the distribution. Red dots and lines present the marginal estimated means and
851 95% CI for female and male offspring mass, accounting for all other effects in the model.
852 Linear relationships show the raw data points and the predicted effect with 95% confidence
853 intervals, also accounting for the other effects in the model (see text).

854

855 **Fig 4.** Interaction plot representing the effects of maternal relative condition within years
856 (standardized, see Methods) on litter sex ratio at weaning as a function of number of kin
857 present. The line and 95% confidence intervals were computed from a Generalized Linear
858 Model that examined litter sex ratio at weaning as a matrix of count data, i.e. matrix of
859 “success” and “failures” with male = “success”, female = “failure.”

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863 **Fig 1.**

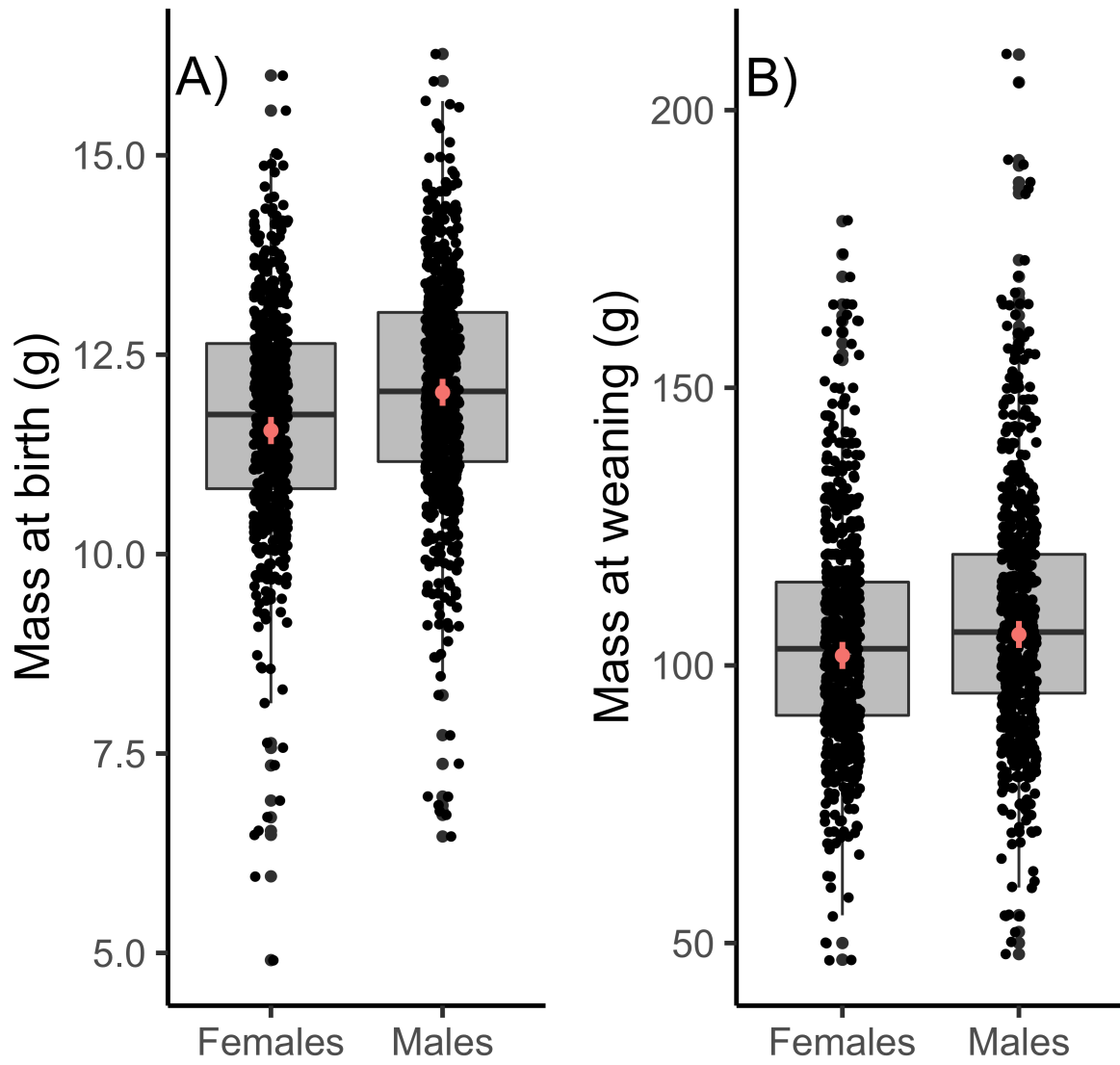
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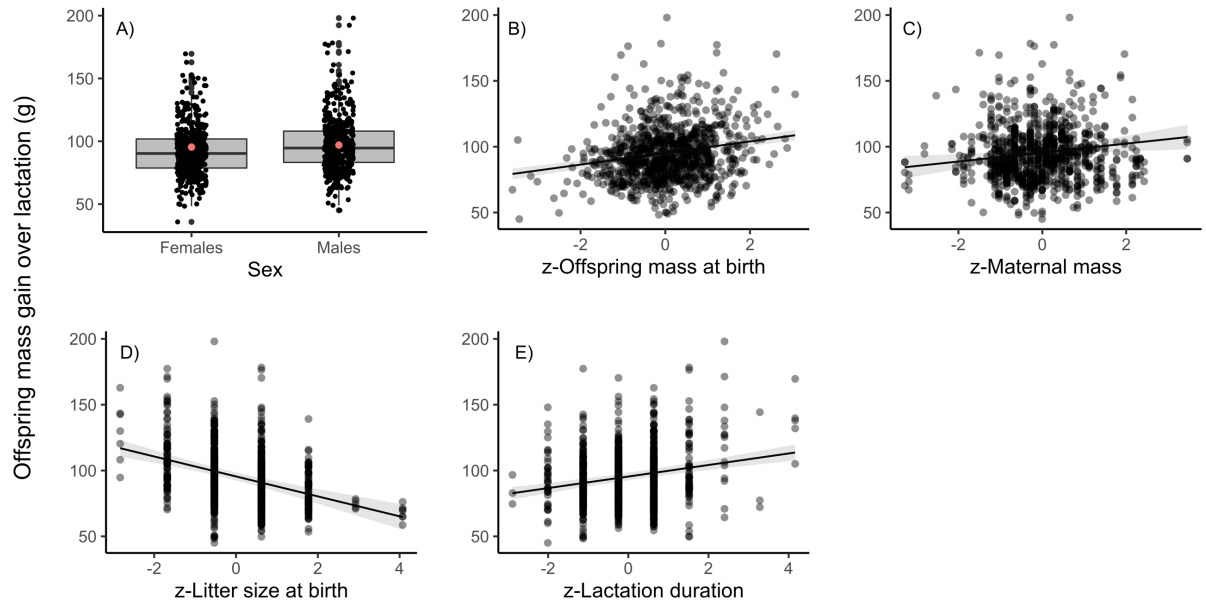


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870 **Fig 2.**

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875 **Fig 3.**

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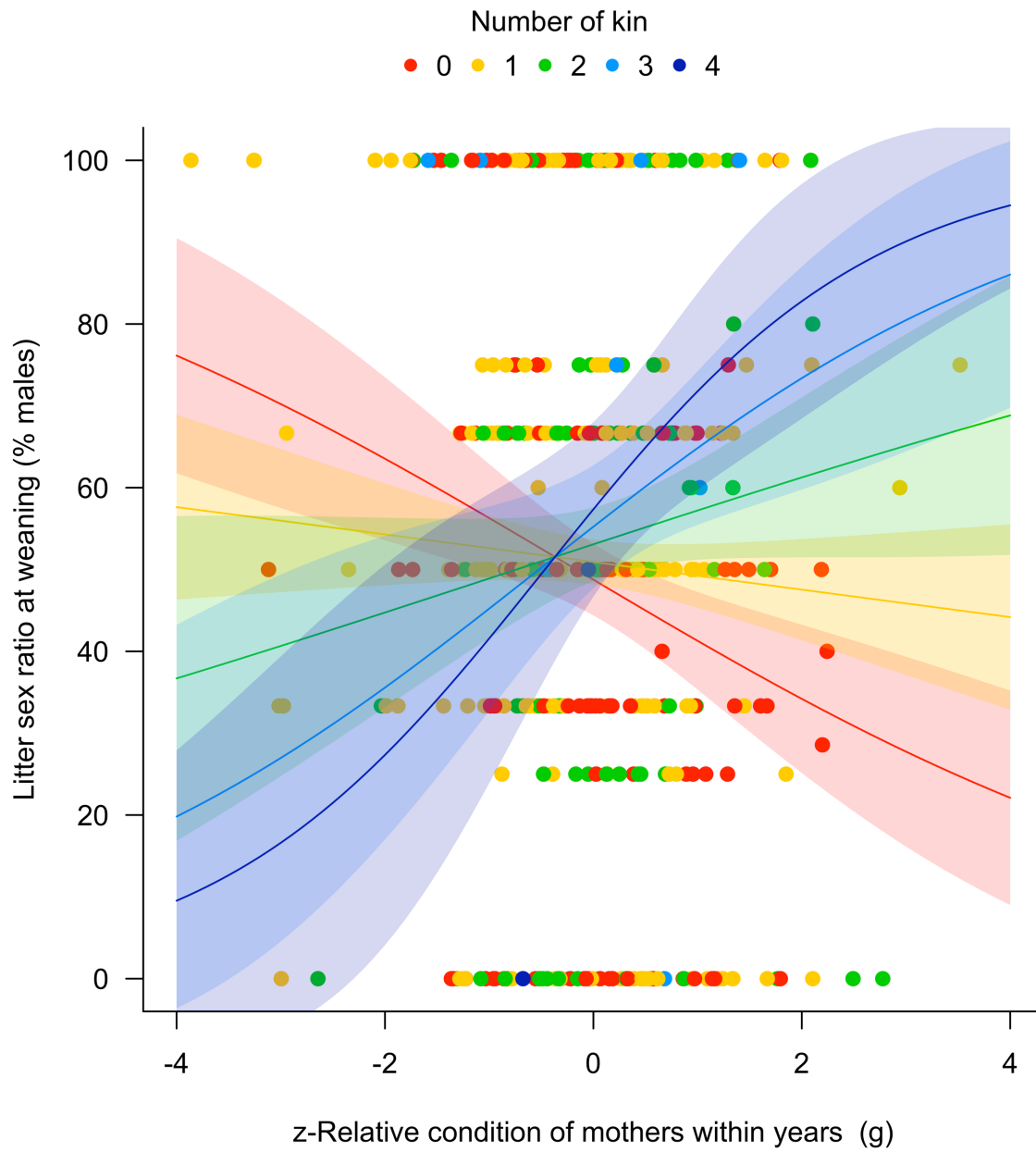
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892 **Fig 4.**

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