

Offspring sex in mountain goat varies with adult sex ratio but only for mothers in good condition

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Received: 26 June 2015 / Revised: 22 October 2015 / Accepted: 26 October 2015 / Published online: 4 November 2015
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Abstract Studies of mammals have often produced results inconsistent with theories predicting adaptive sex-ratio manipulation. Some apparently strong trends weaken or disappear over time, suggesting that multiple variables affect sex ratio and that their relative importance may change over time. Mountain goats are sexually dimorphic ungulates that satisfy all the assumptions of the Trivers-Willard hypothesis. Therefore, females able to provide high levels of maternal care are expected to produce an excess of sons. An earlier study found that older females, that are larger and dominant, produced more sons than did younger females, which are smaller and subordinate. Here, we show that, as sample size tripled, that trend disappeared. A large-scale climate index, reproductive status at conception, and population density had no consistent effects on offspring sex ratio. A composite measure of female condition at conception revealed that offspring sex ratio varied with adult sex ratio, as predicted by the homeostatic hypothesis, but only for mothers in good condition at conception. These females were dominant, heavier, and older. Their probability of producing a son decreased from about 80 to 20 % as the adult sex ratio became more male-biased. For mothers with a low condition index, however, adult sex ratio had no effect on offspring sex ratio. Our research suggests that

offspring sex ratio is affected by complex interactions between individual condition and other variables, whose importance may vary over time and can only be elucidated by long-term studies.

Keywords Trivers-Willard hypothesis · Homeostatic hypothesis · *Oreamnos americanus* · Offspring sex ratio · Adult sex ratio · Female condition

Introduction

Fisher (1930) pointed out that because each sexually reproducing organism has one father and one mother, the average reproductive success of males and females should be equal. He predicted that natural selection should favor individuals that provide equal parental investment in each sex. In sexually dimorphic species, however, weaning a son typically requires more energy and often has greater fitness costs than weaning a daughter (Bérubé et al. 1996; Hewison and Gaillard 1999), presumably because sons grow faster during lactation. Later, Trivers and Willard (1973) proposed that females may adjust offspring sex ratio in response to their condition. For sexually dimorphic species, this hypothesis implies that females able to provide a large amount of maternal care should produce sons, which may develop into large and reproductively successful dominant adult males and provide high fitness returns in terms of grandchildren. That is because the main factor limiting male reproductive success in these species is intrasexual competition for access to mates (Clutton-Brock et al. 1988; Hogg and Forbes 1997). Females that can only provide limited maternal care may be better off having daughters, as their sons may never reproduce because they will be outcompeted by larger males. A low level of maternal care may have a greater negative impact on the survival of sons than of

Communicated by K. E. Ruckstuhl

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daughters (Clutton-Brock et al. 1985) so that sex ratios measured some time after birth may appear to vary according to maternal ability to care because of differential postnatal mortality.

Despite the logic and elegance of the Trivers-Willard hypothesis, studies of adaptive offspring sex ratio manipulation in mammals have produced inconsistent results, especially when maternal condition was not measured near the time of conception (Cameron 2004). Assuming that adaptive sex ratio manipulations do occur, at least under certain circumstances, two main reasons likely explain this inconsistency. First, a publication bias, because results supporting a hypothesis are more likely to be published than studies that fail to find significant effects (Festa-Bianchet 1996; Møller and Jennions 2001). Second, offspring sex ratios may be affected by diverse variables, including not only maternal state, but also population and environmental characteristics (Kruuk et al. 1999; Weladji et al. 2003; Baeta et al. 2012), and possibly, also paternal influences (Gomendio et al. 2006; Røed et al. 2007; Edwards and Cameron 2014). If the relative importance of factors affecting sex ratio manipulation varies over time, trends evident under one set of environmental or population variables may disappear when these variables change, especially if they interact with the female condition. For example, a strong relationship between maternal dominance and offspring sex ratio in red deer (*Cervus elaphus*) disappeared as density increased, apparently because of increased prenatal mortality of sons (Kruuk et al. 1999). Alternatively, the homeostatic hypothesis posits that juvenile sex ratio should depend on adult sex ratio (Werren and Charnov 1978; Williams 1979). Under this hypothesis, parents should produce the rarer sex because males should be advantaged in a population with many females and vice versa.

The Trivers-Willard hypothesis rests on three assumptions: (i) parental condition is related to offspring condition, (ii) differences in offspring condition persist into adulthood, and (iii) condition affects the reproductive success of one sex more importantly than the other. We have shown that mountain goats (*Oreamnos americanus*) satisfy the first and last assumptions: maternal mass correlates with offspring mass (Côté and Festa-Bianchet 2001c; Théoret-Gosselin et al. 2015), and in this sexually dimorphic species, adult mass is a stronger determinant of male than female reproductive success (Mainguy et al. 2009; Hamel et al. 2009b). Here, we first assessed whether mountain goats satisfy the second assumption of the Trivers-Willard hypothesis, by evaluating the relationship between mass at weaning and adult mass. We then evaluated whether females adaptively manipulated sex ratio in response to their condition. Strong individual differences in female reproductive potential (Côté and Festa-Bianchet 2001b; Hamel et al. 2009b) suggest that mountain goats may adaptively vary offspring sex ratio based on maternal ability to provide care. Maternal age, which is strongly correlated with

mass and social rank, had a large effect on offspring sex ratio in 1989–1997: the youngest mothers produced about 70 % daughters while the oldest ones produced about 70 % sons (Côté and Festa-Bianchet 2001a). Monitoring of this population has continued over 25 years, sample size has more than tripled, and many parameters such as population size have varied widely during the study (Fig. 1). We were therefore interested in testing whether the effect of maternal age on offspring sex ratio persisted under different environmental conditions. With a much larger sample size and information on several individual- and population-level variables, we examined the effects of maternal age, social rank, and condition near conception, as well as their interaction with population size, adult sex ratio, and climatic conditions on offspring sex ratio of individually marked females. We included maternal condition at conception because it provides a more direct test of the Trivers-Willard hypothesis than simply age or social rank (Cameron 2004). We considered the effects of population size because it was the variable most closely associated with the disappearance of a maternal social rank effect on offspring sex ratio in red deer (Kruuk et al. 1999). Adult sex ratio was also included to test the homeostatic hypothesis.

Methods

Study area and captures

We studied mountain goats at Caw Ridge (54° N, 119° W), Alberta, Canada. Goats used approximately 28 km² of alpine tundra and open subalpine forest at 1750- to 2170-m elevation. The landscape includes gently rolling hills and steep grassy slopes, as well as rockslides and a few cliff faces that are crucial escape terrain. The climate is subarctic-arctic, with short, cool summers followed by long, harsh winters. The main predators are wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and cougars (*Puma concolor*). Black bears (*Ursus americanus*), coyotes (*Canis latrans*), wolverines (*Gulo gulo*), and golden eagles (*Aquila chrysaetos*) may also prey on mountain goats (Festa-Bianchet and Côté 2008).

We used longitudinal data from marked individuals monitored between 1989 and 2014. We captured goats in traps baited with salt. We immobilized adult goats (≥ 3 years) with xylazine hydrochloride and reversed its effects with idazoxan (Haviernick et al. 1998). We marked individuals with plastic ear tags and collars and collected ear biopsies for DNA analyses to confirm maternity (Mainguy 2008). Since 1993, 98 % of goats aged 1 year and older have been marked. We aged adult goats not marked as juveniles by counting their horn annuli, a technique reliable up to 7 years of age (Stevens and Houston 1989). We measured the length of the hind foot with a measuring tape (± 1 mm). We weighed captured goats with a spring scale (± 0.5 kg; see Côté et al. 1998). We also recorded

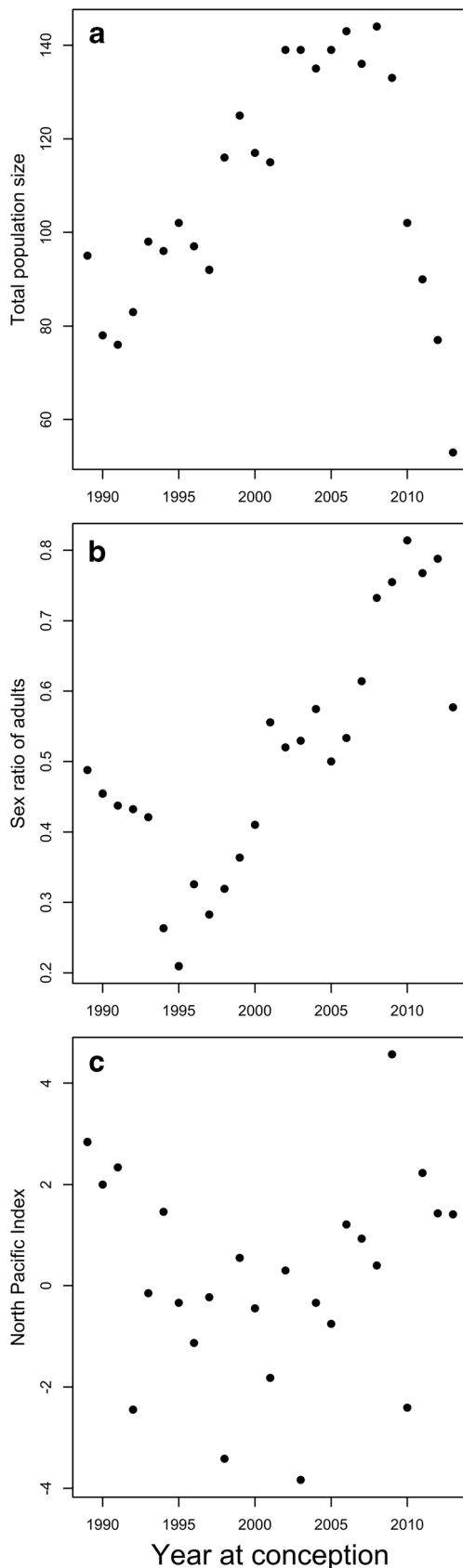


Fig. 1 Annual variation in the three environmental variables considered in this study. **a** Total population size in September. **b** Sex ratio (males/females) of adults (≥ 3 years) in September. **c** North Pacific Index, i.e., representing the climatic conditions during conception

mass (± 0.5 kg) using remotely controlled electronic platform scales baited with salt (Bassano et al. 2003). We adjusted mass to September 1 using the predictions of summer mass gain for each age-sex class, accounting for reproductive status in females. Kids rarely suckled in September, and therefore mass on September 1 approximates weaning mass. For each class, we ran a linear mixed model (LMM—“lmer” function from the R package “lme4”; Bates et al. 2014) using individual identity and year as random intercepts, and chose the best polynomial regression to fit the relationship with Julian day (Hamel et al. 2010). When mass was measured more than once in a year for an individual, we averaged all adjusted masses for that individual-year. For >90 % of individual-years with more than one mass, the average mass differed by less than ~ 2 kg from individual mass adjustments.

Behavioral observations

From mid-May to mid-September 1989–2014, we recorded daily behavioral observations using spotting scopes (15–45X). Goats at Caw Ridge give birth to a single offspring in late May/early June. We evaluated the annual reproductive status of each female from observations of nursing behavior from mid-May to mid-September (weaning). We determined the sex of kids by their urination posture and by observations of the vulvar patch in females (Festa-Bianchet and Côté 2008). For most kids, sex was also confirmed from DNA analyses from microsatellite markers (Mainguy 2008). These classifications always matched the sex assigned from behavioral observations.

We determined the social rank of each mother annually based on ad libitum observations of agonistic interactions recorded among adult females. For each dyad, we scored an individual as dominant if it won more than 50 % of the interactions with the other individual (Côté 2000). Because relationships were highly linear every year, we applied the method of de Vries (1998) using Matman 1.0 for Windows (Noldus Information 1998) to order adult females in an annual hierarchy (Côté 2000). Since the number of adult females varied annually, we transformed social ranks according to the formula $1 - \text{rank}/N_i$, where N_i was the number of adult females during year i (Côté 2000). Hence, social rank varied from 0 to 1 from subordinate to dominant.

Female condition at conception

Social rank, mass, and age are the main individual traits influencing reproduction in female mountain goats (Côté

and Festa-Bianchet 2001b; Hamel et al. 2009a, 2010). These traits are strongly positively correlated (r 's ranging from 0.65 to 0.88). We therefore performed a principal component analysis (PCA) to combine them. Because mass and rank sometimes had missing values, we performed an imputed PCA using the function “imputePCA” from the R package “missMDA” (Husson and Josse 2014) to predict the PCA scores for the missing values. The first axis of the PCA explained 88 % of the variance and was the only influential axis as determined by the rapid decrease in consecutive eigenvalues (Cattell 1966; Fig. 2). Positive scores represented females that were dominant, heavier, and older at conception (Fig. 2). These scores therefore represented an index of female condition at conception (hereafter referred to as PC1). We used mass as an index of body condition rather than mass corrected for size because we only measured size during captures, and mothers were not captured after 1996 to avoid kid abandonment (Côté et al. 1998). Therefore, both the size and the mass of a mother were measured in fewer than 10 % of mother-years, and these are limited to the first few years of the study. On the other hand, mass was measured almost every year with platform scales. Mass has been shown to be the best metric to describe individual variation in body condition in ungulates, integrating several body condition components such as fat and protein that are essential for reproduction (Hewison et al. 1976; Taillon et al. 2011). Furthermore, we are confident that the results based on mass are robust because mass is highly correlated with hind foot length in mountain goats (r [95 % confidence interval (CI)]=0.84 [0.81–0.86]), thereby suggesting that there is limited variability in mass for a given size and that mass is a good correlate of body condition in this species.

Reproductive status and offspring sex can also influence female condition and subsequent reproduction in mountain goats (Hamel et al. 2010). We therefore considered reproductive status in the year of conception as another indicator of female condition at conception (three categories: no offspring, produced a daughter, produced a son).

Environmental conditions at conception

We considered three variables to describe environmental conditions at conception that could influence the probability of producing a son: (i) total population size in September, (ii) adult sex ratio in September, and (iii) climatic conditions during the rut (early November to early December; Mainguy 2008). Total population size in September varied between 53 and 144 (Fig. 1a), and adult sex ratio (males/females) ranged from 0.21 to 0.81 (Fig. 1b). These two variables were measured in September instead of at conception in November because it was the latest month of data collection. Nevertheless, population size and adult sex ratio in September are highly correlated to those at conception in November because these variables vary more among than within years (e.g., correlation of population size in September in consecutive years: r [95 % CI]=0.88 [0.71–0.95], and correlation of population size in August and September of the same year: r [95 % CI]=0.99 [0.98–1.00]). To characterize climatic conditions during the breeding season, we used the November to March anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994; Fig. 1c). For our study site, high NPI values are associated with snowier and colder weather compared with low NPI values (Hamel et al. 2009b). These three environmental

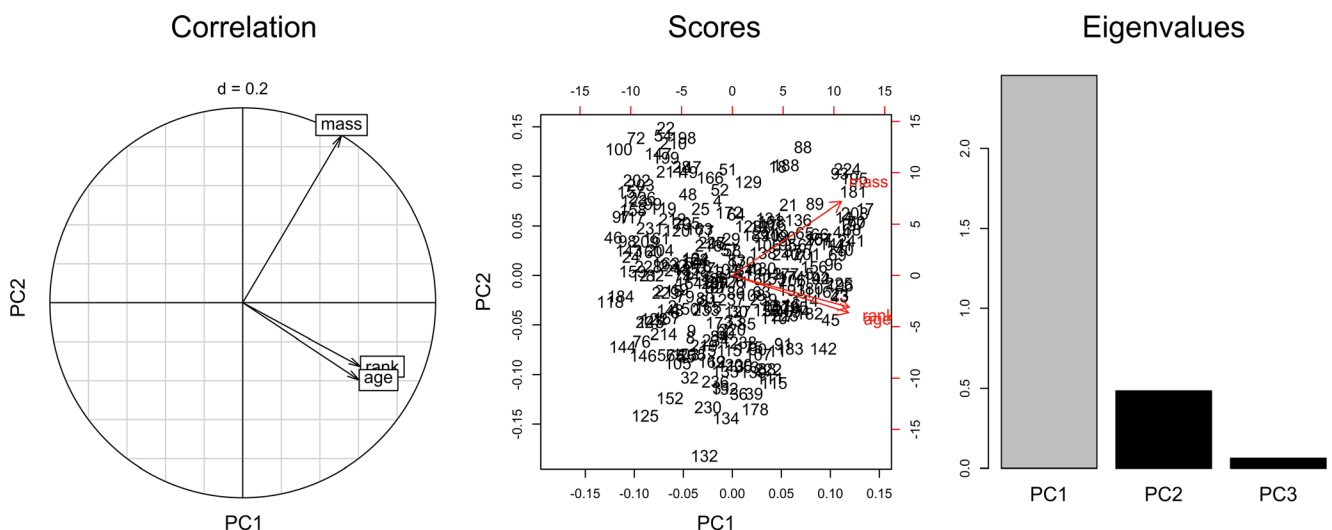


Fig. 2 Principal component analysis on adult female mass, social rank, and age. The *left panel* shows the correlation among the variables according to the first two axes (PC1 and PC2). The *middle panel* shows

the distribution of the scores according to the first two axes. The *right panel* shows the eigenvalues of the components

variables were not significantly correlated (all paired r values $<|0.24|$ and p values >0.3).

Statistical analyses

Mass at weaning vs. adult mass

We compared mass at weaning with mass at a later age (“older mass”). We had various sample sizes at each age because individuals were not weighed each year. We therefore performed a LMM with older mass as the dependent variable and “mass at weaning” as the predictor, including age, sex, and their interactions as covariates, and individual identity ID and year as random intercepts. This model allowed us to analyze together all “weaning vs. older mass” pairs while accounting for differences in older mass among age and sex classes. Because mass increased nonlinearly with age, we fitted a spline regression (with $df=3$, selected with likelihood ratio tests). The data set included 448 mass comparisons (196 males, 292 females) from 110 individuals (51 males, 59 females) with a median [range] comparisons/individual of 3 [1–9] for males and 4 [1–11] for females, and a median [range] number of observations per year of 18 [2–40] for males and 27 [1–68] for females over 25 years.

Probability of producing a son

We used generalized linear mixed models (GLMMs—“glmer” function from the R package “lme4”, with a logit link and mother ID as a random intercept; Bates et al. 2014) to assess whether the probability to produce a son was influenced by maternal condition at conception (condition index PC1 and reproductive status), environmental conditions at conception (population size, adult sex ratio, and NPI), and relevant interactions between maternal and environmental conditions (Table 1).

We determined whether a variable was an influential predictor of the probability of producing a son using a model selection approach based on Akaike’s information criterion (AIC; Burnham and Anderson 2002). We defined a set of models a priori (Table 1) and computed ΔAIC and AIC weights to select the most parsimonious model. When models were equivalent ($\Delta AIC \leq 2$), we considered the model with fewest parameters as the most parsimonious, and selected it. We determined whether each variable included in the selected model had an effect by examining its estimate and 95 % confidence interval (CI) based on profile likelihood (Bates et al. 2014). We reported these results as odd ratios, a measure of effect size in logistic regression. An odd ratio is the ratio of the odds of an event occurring in one group to the odds of it occurring in another group, i.e., $[p/(1-p)]/[q/(1-q)]$, where p and q represent the probabilities of each event (Littell et al. 2002). An odd ratio of 1 indicates

that the event is equally probable in both groups. As the odd ratio moves towards 0, the event is less likely to occur in the first group, whereas when it moves towards infinity, the event is more likely to occur in the first group. For continuous variables, odd ratios represent the odds of an event occurring with an increase of one unit of the variable (e.g., the ratio of the odds of an event occurring as mass increases from 30 to 31 kg).

Models with missing values are not comparable. Female reproductive status at conception included some missing values because the sex of kids that died in the first few days after birth was unknown. We thus used a reduced dataset without missing values, reran the selected model (model 1; Table 1) and evaluated whether AIC was improved by adding reproductive status at conception. The complete data set included 523 mother-years from 125 mothers (median [range]=4 [1–10] observations/mother), while the reduced data set included 448 mother-years from 117 mothers (3 [1–9] observations/mother). The median [range] number of reproducing females each year was 21 [4–35] over 25 years. We standardized all continuous variables to compare the relative influence of each predictor with the others (Schielzeth 2010). Because the models included categorical predictors, we standardized continuous variables by dividing them by two standard deviations (Gelman 2008). We also centered independent variables to remove the collinearity between main effects and interactions, thereby allowing us to interpret main effects independently of interactions (Schielzeth 2010). All analyses were performed in R version 3.1.3 (R Core Team 2015). It was not possible to record data blind because our study involved focal animals in the field.

Results

Mass at weaning vs. adult mass

Mass at weaning was positively related to mass at an older age (estimate [95 % CI]=0.64 [0.34–0.94], t value=4.16; Fig. 3). A difference of 10 kg at weaning led to a difference of about 5 kg (females) to 8 kg (males) at age 7, when goats reach asymptotic mass. Although mass at weaning seemed to have a stronger influence on adult mass for males than for females (Fig. 3), the confidence interval of the interaction between mass at weaning and sex included zero (estimate [95 % CI]=0.33 [–0.28–0.94], t value=1.04). These mass differences are important as they represent approximately 20 % of the variation in adult mass in both sexes (mass range was 60 to 87 kg in adult females and 80 to 119 kg in adult males). In addition, mass gain improves reproductive success: an increase of 5 kg increases the chance of producing an offspring by 10 % in females (Hamel et al. 2009b), and an increase of

Table 1 Model selection for the influence of maternal and environmental conditions at conception on the probability of producing a son in the spring in adult female mountain goats, at Caw Ridge, Alberta (1989–2014). The selected model is in italics

Models	<i>K</i>	AIC	Δ AIC	<i>Wt</i>
[1] <i>PC1+AdultSR+PC1×AdultSR+(1 id)</i>	5	723.4	0	0.41
[2] PC1+NPI+AdultSR+PC1×NPI+PC1×AdultSR+(1 id)	7	725.1	1.7	0.17
[3] PC1+PopSize+AdultSR+PC1×PopSize+PC1×AdultSR+(1 id)	7	726.2	2.8	0.10
[4] AdultSR+(1 id)	3	726.2	2.8	0.10
[5] PC1+AdultSR+(1 id)	4	727.4	4.0	0.06
[6] PC1+PopSize+AdultSR+NPI+PC1×PopSize+PC1×AdultSR+PC1×NPI+(1 id)	9	728.1	4.8	0.04
[7] 1+(1 id)	2	728.3	4.9	0.03
[8] NPI+(1 id)	3	728.9	5.6	0.02
[9] PC1+(1 id)	3	729.5	6.2	0.02
[10] PopSize+(1 id)	3	729.7	6.4	0.02
[11] PC1+NPI+(1 id)	4	730.3	6.9	0.01
[12] PC1+PopSize+(1 id)	4	731.0	7.7	0.01
[13] PC1+NPI+PC1×NPI+(1 id)	5	731.2	7.9	0.01
[14] PC1+PopSize+PC1×PopSize+(1 id)	5	732.7	9.3	0
[15] PC1+PopSize+NPI+PC1×PopSize+PC1×NPI+(1 id)	7	734.9	11.5	0

K number of parameters; *Wt* AIC weights; *PC1* mother condition at conception (scores of first axis of a principal component analysis on mass, social rank, and age); *PopSize* total population size in September; *AdultSR* sex ratio (males/females) of adults (≥ 3 years) in September; *NPI* North Pacific Index, representing climatic conditions during conception; *(1|id)* random intercept of mother identity

8 kg doubles time spent in courtship and reproductive success in males (Mainguy and Côté 2008; Mainguy et al. 2009).

Probability of producing a son

Two equivalent models presented support to the data (Table 1). The most parsimonious (model 1) had an AIC weight of 0.41, or about three times more support than model 2, indicating strong support for model 1 (Table 1). Model 1 included female condition index (PC1), sex ratio of adults in September, and their interaction (Table 1). Considering the estimates of these variables and their confidence intervals, the only significant effect (odd ratio CI excluding 1 in a logistic regression) was the interaction between female condition index and adult sex ratio (Table 2). Offspring sex varied with adult sex ratio only for mothers with a high condition index, i.e., dominant, heavier, and older (Fig. 4). These females produced more sons when adult sex ratio was female-biased (red in Fig. 4) and more daughters when it was male-biased (blue in Fig. 4). The odds of producing a son for these females were about 2.5 times lower when the adult sex ratio was male-biased (Table 2), and the probability of producing a son then decreased from about 80 to 20 % (Fig. 4). On the other hand, mothers that had a low condition index at conception, i.e., subordinate, lighter and younger females, had a similar probability of producing a son irrespective of adult sex ratio (the blue and the red zones overlap in Fig. 4).

Based on the reduced data set, the probability of producing a son did not vary with maternal reproductive status at

conception: adding this variable to model 1 (Table 1) led to an increase of AIC by 1.9, and the odds of producing a son did not vary according to reproductive status (odd ratio [95 % CI]: no offspring vs. daughter produced=1.00 [0.61–1.63], *z* value=−0.004; son vs. daughter produced=1.39 [0.82–2.29], *z* value=1.3; *F* value for main effect of reproductive status=0.85).

Discussion

Our analyses of 25 years of data suggest that offspring sex ratio in mountain goats is affected by an interaction of maternal body condition at conception and adult sex ratio, but only for females in good condition. Several reviews of the Trivers-Willard hypothesis have been published (Cameron 2004), including two specifically on ungulates (Hewison and Gaillard 1999; Sheldon and West 2004). Those reviews found that support for the hypothesis was mixed, but it generally increased when studies measured female condition near conception. Recent studies have pointed to a potential mechanism for adaptive sex ratio manipulation, suggesting that blood glucose content should be related to a female's ability to mobilize energy and therefore correlate with the production of sons, which require greater maternal care than daughters (Cameron et al. 2008; Schwanz and Robert 2014). While female condition near the time of conception, possibly affecting her blood glucose content, may at times be related to adaptive sex ratio manipulation, we suggest that the inconsistent results reported

Fig. 3 Relationship between mass at weaning (September 1) and adult mass in male and female mountain goats, at Caw Ridge, Alberta (1989–2014). The *black lines* and the *grey zones* represent the model predictions and 95 % confidence intervals for each sex at age 7, i.e., the age at which goats reach asymptotic mass. The *dots* show the partial residuals, i.e., accounting for the effects of the other variables in the model

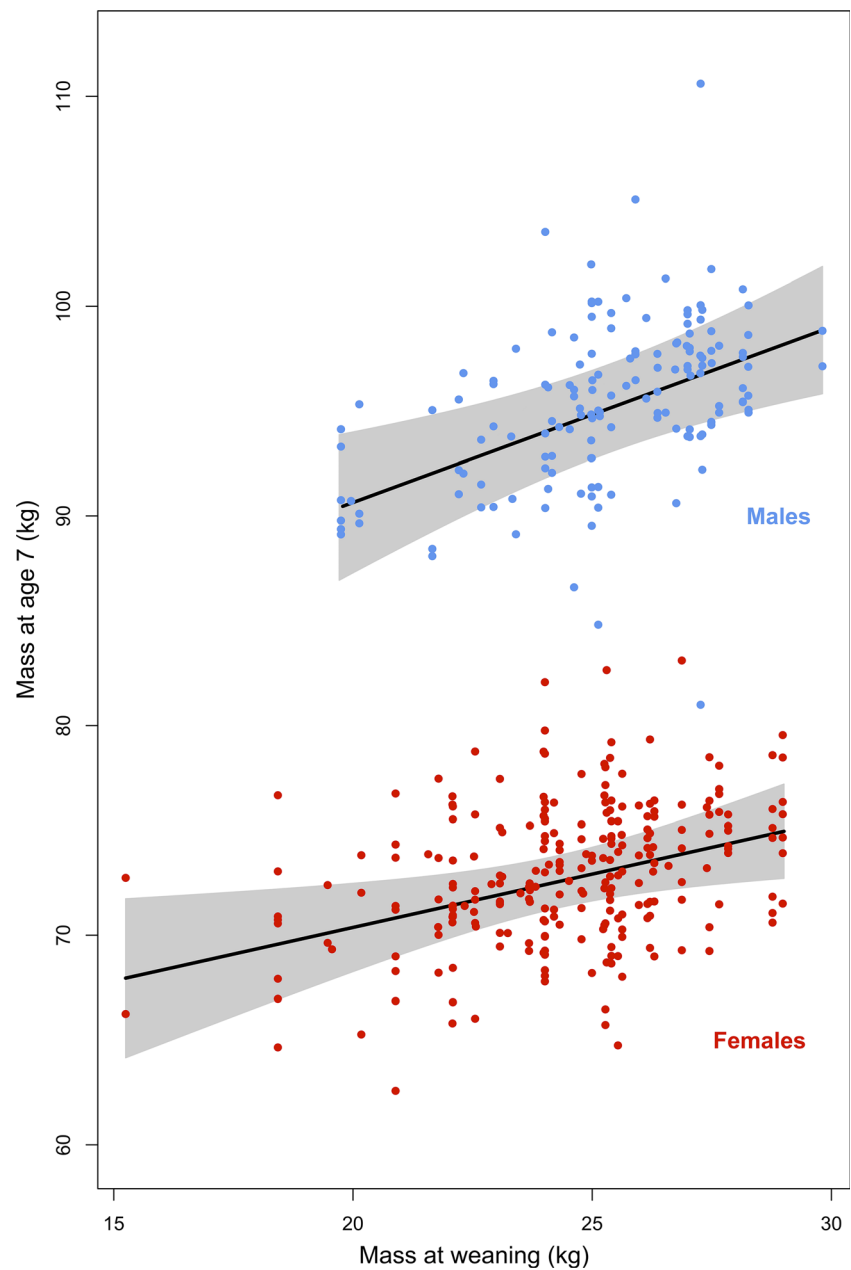


Table 2 Odd ratios (OR) and 95 % confidence intervals (CI) of variables included in the selected model (in italics in Table 1), showing the influence of maternal and environmental conditions at conception on the probability of producing a son in the spring in female mountain goats, at Caw Ridge, Alberta (1989–2014)

Fixed effect	OR [95 % CI]*	z value
Intercept	0.93 [0.77–1.12]	−0.74
PC1	1.24 [0.87–1.79]	1.17
Adult sex ratio	0.71 [0.49–1.03]	−1.77
<i>PC1 × Adult sex ratio</i>	<i>0.38 [0.18–0.78]</i>	<i>−2.60</i>
Variance of random intercept “mother identity”	0.08	

*An odd ratio of 1 means no effect (see “Statistical analyses” for how to interpret odd ratios). Significant odd ratios are highlighted in italics (i.e., 95 % CI excluding 1)

PC1 mother condition at conception (scores of the first axis of a principal component analysis on mass, social rank, and age)

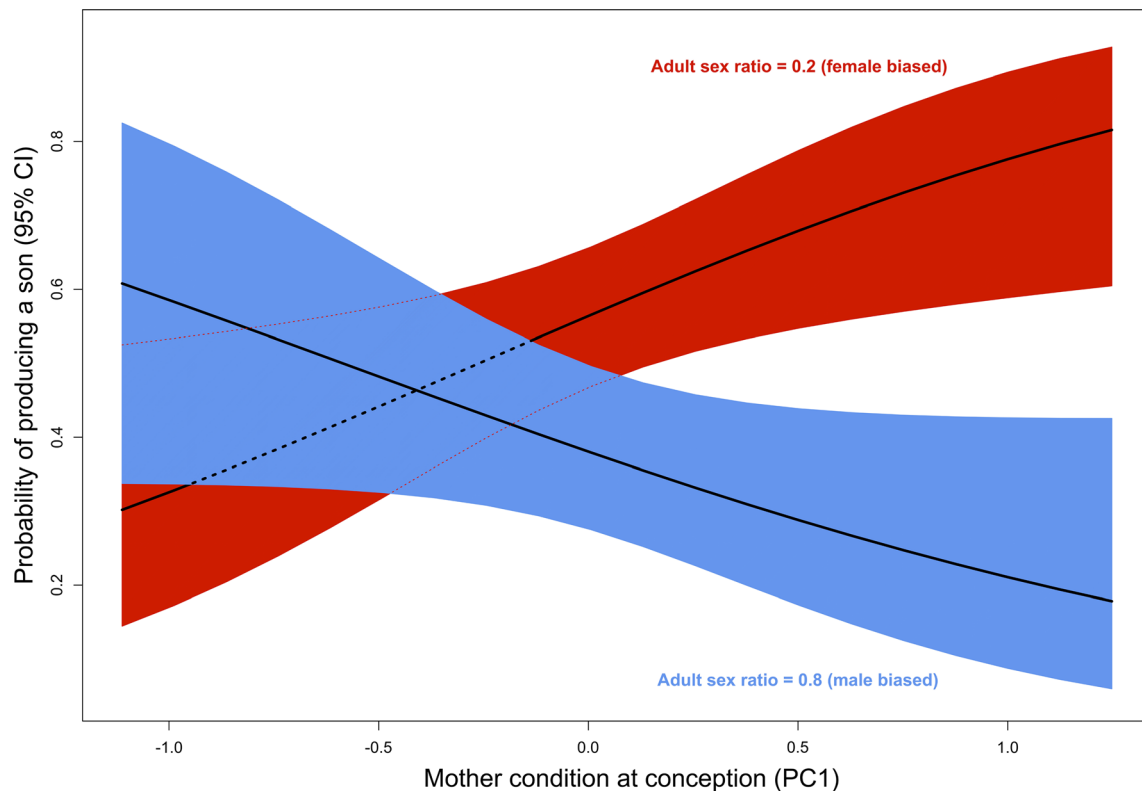


Fig. 4 Changes in the probability of producing a son in the spring according to mother condition at conception (i.e., scores of the first axis of a principal component analysis on mother mass [lowest and highest PC1 score equalled 65.3 and 99.4 kg, respectively], social rank [0 and 1]

and age [2 and 16 years]) in interaction with the sex ratio of adults in the population at conception, in female mountain goats at Caw Ridge, Alberta (1989–2014). The *black lines* represent the model predictions and the *red* and the *blue zones* the 95 % confidence interval

by several studies in mammals may also be attributed to temporal changes in the factors that affect offspring sex ratio, or to interactions among factors. The disappearance of a social rank effect on offspring sex ratio of red deer hinds (Clutton-Brock et al. 1984) with increasing population density was attributed to greater prenatal mortality of male embryos (Kruuk et al. 1999). Therefore, post-conception mechanisms may affect sex ratio, leading to deviations from the Trivers-Willard hypothesis without necessarily negating the possibility that a Trivers-Willard trend may exist at conception. As ecological circumstances vary over time, however, different factors may prevail in affecting sex ratio (Kruuk et al. 1999; Bradshaw et al. 2003; Cunningham et al. 2009). In addition, our study and that of Martin and Festa-Bianchet (2011) suggest that only some categories of females may show apparently adaptive sex ratio manipulations. Short-term studies may be unable to reveal this complexity because they typically monitor only a narrow range of ecological and environmental variability (Clutton-Brock and Sheldon 2010), or confuse unusual events with global patterns, as suggested by Gedir and Michener (2014).

Population size varied substantially during our study but did not explain changes in offspring sex ratio. Instead, we found an interaction between female condition at conception

and adult sex ratio. Although the Trivers-Willard hypothesis predicts that females in good condition should consistently produce sons in a sexually dimorphic species like mountain goats, some females only produced a male-biased offspring sex ratio in years when there were many adult females in the population. In years when adult sex ratio was less skewed in favor of females, mothers in good condition switched to producing daughters. Mothers in average or poor condition, on the other hand, did not consistently deviate from a 50:50 sex ratio according to any of the variables that we examined. Therefore, the disappearance of the apparently adaptive pattern of sex ratio variation reported by Côté and Festa-Bianchet (2001a) does not seem attributable to changes in population density. Instead, we suggest that sex ratio may be affected by multiple variables that interact with each other, whose relative importance changes over time, and may not affect all females equally.

Compared to our earlier analysis (Côté and Festa-Bianchet 2001a), here, we performed a much more powerful test of the Trivers-Willard hypothesis, and found no support for it in mountain goats, a species that satisfies all of its assumptions. In particular, mass at weaning is correlated with adult mass, a major determinant of male reproductive success (Mainguy et al. 2009). It has been suggested that in species with male-

biased juvenile mortality, the Trivers-Willard hypothesis may not apply (Leimar 1996), and in mountain goats, fewer males than females recruit into the breeding population (Festa-Bianchet and Côté 2008). Some of the young males that do not breed in our study population, however, emigrate and their reproductive success is unknown. We specifically examined the effects of maternal body condition on sex ratio and found results inconsistent with the Trivers-Willard prediction, despite a strong effect of our measure of body condition on reproductive success, and therefore presumably on the ability to provide maternal care (Hamel et al. 2009a, b).

We found a strong trend suggesting that females in good condition produced more offspring of the rarer sex among adults in the year of conception (Fig. 4). Females with high PC1 scores produced about four times more sons when there were fewer adult males in the population. The homeostatic hypothesis has received little support from previous studies of wild mammals, but it is unclear whether many of these studies even tested it. It received weak but significant support from a study of Richardson's ground squirrels (*Urocitellus richardsoni*) based on a very large sample size (Gedir and Michener 2014). If the trend we found is adaptive, we should see differences in the relative reproductive success of sons and daughters born to females in good condition according to sex ratio in the adult population in the year of birth. The relative reproductive success of sons and daughters of females in average or poor condition should be independent of adult sex ratio. Despite 25 years of monitoring, however, we do not yet have the required data to answer this question, partly because of the slow life history of mountain goats, where very few individuals of either sex reproduce before 4 years of age (Festa-Bianchet and Côté 2008; Mainguy et al. 2009).

Our research emphasizes the importance of sample size for sex ratio studies, not just in terms of the number of individuals monitored, but also in terms of the numbers of years of monitoring, which usually increases the range of environmental and ecological conditions during the study (Clutton-Brock and Sheldon 2010). It also underlines the importance of publishing non-significant or inconsistent results when these are based on rigorous protocols and large sample sizes (Festa-Bianchet 1996; Brown and Silk 2002). Otherwise, researchers would obtain a biased impression of available results.

Acknowledgments Our long-term research is primarily financed by the Natural Sciences and Engineering Research Council of Canada. We also obtained support from the Alberta Fish and Wildlife Division, the Rocky Mountain Goat Foundation, the Alberta Conservation Association, the Alberta Sport, Recreation, Parks and Wildlife Foundation, the Alberta Wildlife Enhancement Fund, Université de Sherbrooke and Université Laval. We are indebted to the many people who helped with fieldwork at Caw Ridge over the years, and to K. G. Smith for his role in the

initiation of the study. We thank two anonymous reviewers for constructive comments on a previous version of this manuscript.

Compliance with ethical standards The authors declare that they have no competing interests.

Compliance with ethical standards All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

References

- Baeta R, Bélisle M, Garant D (2012) Importance of breeding season and maternal investment in studies of sex-ratio adjustment: a case study using tree swallows. *Biol Lett* 8:401–404
- Bassano B, von Hardenberg A, Pelletier F, Gobbi G (2003) A method to weigh free-ranging ungulates without handling. *Wildlife Soc B* 31: 1205–1209
- Bates D, Maechler M, Bolker BM (2014) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8, <http://CRAN.R-project.org/package=lme4>
- Bérubé CH, Festa-Bianchet M, Jorgenson JT (1996) Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behav Ecol* 7:60–68
- Bradshaw CJA, Harcourt RG, Davis LS (2003) Male-biased sex ratios in New Zealand fur seal pups relative to environmental variation. *Behav Ecol Sociobiol* 53:297–307
- Brown GR, Silk JB (2002) Reconsidering the null hypothesis: is maternal rank associated with birth sex ratios in primate groups? *Proc Natl Acad Sci U S A* 99:11252–11255
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Cameron EZ (2004) Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism. *Proc R Soc Lond B* 271:1723–1728
- Cameron EZ, Lemons PR, Bateman PW, Bennett NC (2008) Experimental alteration of litter sex ratios in a mammal. *Proc R Soc Lond B* 275:323–327
- Cattell RB (1966) The Scree test for the number of factors. *Multivar Behav Res* 1:245–276
- Clutton-Brock TH, Albon SD, Guinness FE (1984) Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308:358–360
- Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131–133
- Clutton-Brock TH, Green D, Hiraiwa-Hasegawa M, Albon SD (1988) Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behav Ecol Sociobiol* 23:281–296
- Clutton-Brock TH, Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol Evol* 25:562–573
- Core Team R (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Côté SD (2000) Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137:1541–1566
- Côté SD, Festa-Bianchet M (2001a) Offspring sex ratio in relation to maternal age and social rank in mountain goats. *Behav Ecol Sociobiol* 49:260–265

- Côté SD, Festa-Bianchet M (2001b) Reproductive success in female mountain goats: the influence of maternal age and social rank. *Anim Behav* 62:173–181
- Côté SD, Festa-Bianchet M (2001c) Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* 127:230–238
- Côté SD, Festa-Bianchet M, Fournier F (1998) Life-history effects of chemical immobilization and radiocollars on mountain goats. *J Wildlife Manage* 62:745–752
- Cunningham JA, Hamlin KL, Lemke TO (2009) Fetal sex ratios in Southwestern Montana elk. *J Wildlife Manage* 75:639–646
- de Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Anim Behav* 55:827–843
- Edwards AM, Cameron EZ (2014) Forgotten fathers: paternal influences on mammalian sex allocation. *Trends Ecol Evol* 29:158–164
- Festa-Bianchet M (1996) Offspring sex ratio studies of mammals: does publication depend upon the quality of the data or the direction of the results? *Écoscience* 3:42–44
- Festa-Bianchet M, Côté SD (2008) Mountain goats: ecology, behavior and conservation of a mountain ungulate. Island Press, Washington
- Fisher RA (1930) The genetical theory of natural selection. Clarendon, Oxford
- Gedir JV, Michener GR (2014) Litter sex ratios in Richardson's ground squirrels: long-term data support random sex allocation and homeostasis. *Oecologia* 174:1225–1239
- Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. *Stat Med* 27:2865–2873
- Gomendio M, Malo AF, Soler AJ, Fernandez-Santos MR, Estes MC, Garcia AJ, Roldan ERS, Garde J (2006) Male fertility and sex ratio at birth in red deer. *Science* 314:1445–1447
- Hamel S, Côté SD, Festa-Bianchet M (2010) Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology* 91:2034–2043
- Hamel S, Côté SD, Gaillard J-M, Festa-Bianchet M (2009a) Individual variation in reproductive costs of reproduction: high-quality females always do better. *J Anim Ecol* 78:143–151
- Hamel S, Gaillard J-M, Festa-Bianchet M, Côté SD (2009b) Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* 90:1981–1995
- Haviernick M, Côté SD, Festa-Bianchet M (1998) Immobilization of mountain goats with xylazine and reversal with idazoxan. *J Wildlife Dis* 34:342–347
- Hewison AJM, Angibault JM, Boutin J, Bideau E, Vincent JP, Sempéré A (1976) Annual variation in body composition of roe deer (*Capreolus capreolus*) in moderate environmental conditions. *Can J Zool* 74:245–253
- Hewison AJM, Gaillard J-M (1999) Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends Ecol Evol* 14:229–234
- Hogg JT, Forbes SH (1997) Mating in bighorn sheep: frequent male reproduction via a high-risk "unconventional" tactic. *Behav Ecol Sociobiol* 41:33–48
- Husson F, Josse J (2014) missMDA: handling missing values with/in multivariate data analysis (principal component methods). R package version 1.7.3, <http://CRAN.R-project.org/package=missMDA>
- Kruuk LEB, Clutton-Brock TH, Albon SD, Pemberton JM, Guinness FE (1999) Population density affects sex ratio variation in red deer. *Nature* 399:459–461
- Leimar O (1996) Life-history analysis of the Trivers and Willard sex-ratio problem. *Behav Ecol* 7:316–325
- Littell RC, Stroup WW, Freund RJ (2002) SAS for linear models, 4th edn. SAS Institute Inc, North Carolina
- Mainguy J (2008) Variabilité génétique et reproduction des mâles chez la chèvre de montagne. Université Laval, Dissertation
- Mainguy J, Côté SD (2008) Age- and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. *Behav Ecol Sociobiol* 62:935–943
- Mainguy J, Côté SD, Festa-Bianchet M, Coltman DW (2009) Father-offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal. *Proc R Soc Lond B* 276:4067–4075
- Martin JGA, Festa-Bianchet M (2011) Sex ratio bias and reproductive strategies: what sex to produce when? *Ecology* 92:441–449
- Møller AP, Jennions MD (2001) Testing and adjusting for publication bias. *Trends Ecol Evol* 16:580–586
- Noldus Information Technology (1998) Matman, Reference Manual. Wageningen, The Netherlands, <http://www.noldus.com/knowledge-base/matman>
- Røed KH, Holand Ø, Mysterud A, Tverdal A, Kumpula J, Nieminen M (2007) Male phenotypic quality influences offspring sex ratio in a polygynous ungulate. *Proc R Soc Lond B* 274:727–733
- Schielezeth H (2010) Simple means to improve the interpretability of regression coefficients. *Method Ecol Evol* 1:103–113
- Schwanz LE, Robert KA (2014) Proximate and ultimate explanations of mammalian sex allocation in a marsupial model. *Behav Ecol Sociobiol* 68:1085–1096
- Sheldon BC, West SA (2004) Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *Am Nat* 163:40–54
- Stevens V, Houston DB (1989) Reliability of age determination of mountain goats. *Wildlife Soc B* 17:72–74
- Taillon J, Brodeur V, Festa-Bianchet M, Côté SD (2011) Variation in body condition of migratory caribou at calving and weaning: which measures should we use? *Écoscience* 18:295–303
- Théoret-Gosselin R, Hamel S, Côté SD (2015) The role of maternal behavior and offspring development in the survival of mountain goat kids. *Oecologia* 178:175–186
- Trenberth KE, Hurrell JW (1994) Decadal atmosphere-ocean variations in the Pacific. *Clim Dynam* 9:303–319
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92
- Weladji RB, Holand Ø, Steinheim G, Lenvik D (2003) Sex-specific pre-weaning maternal care in reindeer (*Rangifer tarandus t.*). *Behav Ecol Sociobiol* 53:308–314
- Werren JH, Charnov EL (1978) Facultative sex ratios and population dynamics. *Nature* 272:349–350
- Williams GC (1979) The question of adaptive sex ratio in outcrossed vertebrates. *Proc R Soc Lond B* 205:567–580