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Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*)

Abstract In polygynous mammals, high-quality females may increase their fitness by producing a high proportion of sons. During a 9-year study of marked mountain goats (*Oreamnos americanus*), we assessed the relative effects of maternal age, social rank and reproductive status on offspring sex ratio. The sex ratio of kids in the population did not differ from unity (75 males, 85 females). The proportion of female kids decreased markedly with maternal age. Young females (≤6 years old) produced approximately 70% daughters, while old females (≥10 years old) produced about 25% daughters. The proportion of females born did not vary with maternal social rank when accounting for mother's age. Weaning success one year did not affect the probability of producing a son or a daughter the following year. Kid sex was independent of the sex of the kid produced by the same female the previous year. Because the proportion of daughters produced decreased dramatically with age, and because males appear more costly to rear than females in sexually dimorphic ungulates, our data suggest that the ability to provide maternal care may increase with age in mountain goats. Accepting that older mothers are better mothers because of higher social rank and experience, our data support the predictions of the Trivers and Willard hypothesis.

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Introduction

The question of adaptive variation of offspring sex ratio has interested ecologists since Darwin (1871). In theory, females may increase their fitness by adjusting offspring sex ratio according to their quality, because the sex of the offspring with a higher probability of attaining high reproductive success may vary with the mothers' quality (Charnov 1982).

In a seminal paper on parental ability to alter offspring sex ratio, Trivers and Willard (1973) suggested that in sexually dimorphic species, where the reproductive success of males is more variable than that of females, high-quality females, such as those of high social dominance rank, should produce more sons than daughters. This hypothesis is based on the assumption that maternal investment is correlated with offspring reproductive success, so that sons of high-quality mothers should have higher reproductive success than sons of low-quality mothers (Clutton-Brock et al. 1986; Gomendio et al. 1990). On the other hand, low-quality females should produce more daughters than sons because sons have a greater fitness cost than daughters (Clutton-Brock et al. 1981; Gomendio et al. 1990; Hewison and Gaillard 1999).

Many field and laboratory studies support the Trivers and Willard (1973) hypothesis (reviews in Clutton-Brock and Iason 1986; Hiraiwa-Hasegawa 1993; Hewison and Gaillard 1999). Others, however, have found no effect of maternal quality on offspring sex ratio, or effects opposed to the predictions of the Trivers and Willard model (Verme 1983; Clutton-Brock and Iason 1986; Berman 1988; Festa-Bianchet 1991; Rhine 1994; Hewison and Gaillard 1999). Even within the same species, different authors have reported sex ratio trends in opposite directions [red deer (*Cervus elaphus*): Clutton-Brock et al. 1984, 1986; Post et al. 1999; roe deer (*Capreolus capreolus*): Wauters et al. 1995; Hewison and Gaillard 1996; Hewison et al. 1999].

An alternative hypothesis, based on local resource competition (LRC), has been proposed to explain biases

in production of the dispersing sex, usually males in mammals (Clark 1978). According to a modified version of this hypothesis (Silk 1983), high-quality females should produce more daughters than sons because females 'inherit' the social rank and home range of their mother while males generally disperse. In this situation, subordinate mothers that produced more males than females would reduce future competition with offspring within their home range. Several studies, especially of primates (Silk 1983, 1988; Gomendio 1990) but also of ungulates (Hewison and Gaillard 1996; Post et al. 1999), obtained results in the direction predicted by the LRC hypothesis, but others did not (review in Clutton-Brock and Iason 1986).

Because life history theory predicts that reproductive effort should increase with age as reproductive value decreases (Stearns 1992), selection may favour adjustment of offspring sex ratio in old females. Female quality may also be affected by reproductive effort in the preceding year. Rutberg (1986) reasoned that females that had not reproduced the previous year should be of higher quality than those that had weaned an offspring and, according to the Trivers and Willard (1973) hypothesis, should produce more sons than daughters. Finally, if sons are costlier than daughters, as is often the case in sexually dimorphic ungulates (Gomendio et al. 1990; Hogg et al. 1992), females that produced a male one year may be less likely to rear another male the following year (Bérubé et al. 1996; Monard et al. 1997).

Female mountain goats (*Oreamnos americanus*) in our study population have high rates of intraspecific aggression and display a highly linear and stable dominance hierarchy (Côté, in press). Because most of the variance in maternal social rank was explained by age, an objective of this study was to assess the relative effects of both maternal age and social rank on the sex ratio of mountain goat kids. We assessed whether maternal age, social rank and reproduction the previous year affected offspring sex ratio.

Methods

Our study area is situated at Caw Ridge (54° N, 119° W) in the front range of the Rocky Mountains of west-central Alberta, Canada. The mountain goat population uses about 28 km² of alpine tundra and open subalpine forest ranging from 1750 to 2170 m in altitude. Hunting has been prohibited since 1969 at Caw Ridge, but 20 animals were removed for translocations during 1986–1988. We initiated our long-term study in 1989 and the population has since ranged from 76 to 114 individuals.

We captured and marked 207 goats in traps baited with salt. We drugged adult goats with xylazine hydrochloride, whose effect was reversed by injection of idazoxan (Haviernick et al. 1998). We used canvas collars, Allflex plastic ear tags and radio collars to mark animals. The proportion of marked goats increased during the study, and all adult females (≥3 years old) were individually recognizable after 1993. For goats first caught as adults, age was determined by the number of horn annuli, a technique reliable up to 7 years of age (Brandborg 1955; Stevens and Houston 1989; Côté et al. 1998b). The exact age was known for 42 females (82.4% of those studied) and estimated for 9 females (17.6%) first caught when ≥7 years old. Chemical immobilization 3–4 months

before the rut decreased the probability of kid production the following year by 3- and 4-year-old females and increased the risk of kid abandonment (Côté et al. 1998a). Very few adult females, therefore, were captured after 1993, greatly limiting sample size for body weight.

We used spotting scopes (×15 to ×45) to identify goats in the field and sample their behaviour at distances ranging from 200 to 700 m. Observations were conducted almost daily from mid-May to mid-September. For each group sighted, we noted the identity of all individuals and determined which marked females were lactating by observing nursing behaviour. We only documented two cases of twinning (0.8% of all births) and excluded them from the data set. Kids were sexed from when a few days old until they were about 3 months old by the observation of the vulvar patch in females and by their urination posture: females squat while males stretch. The sex of most kids was known before they were 2 months old. For a subset of kids ($n=90$), sex was confirmed at capture: in no case did the sex determined in the field differ from that confirmed at capture.

From 1994 to 1997, we used all-occurrences sampling and focal observations (Altmann 1974) to record agonistic encounters between adult females ($n=2,792$ interactions). The outcome of most agonistic encounters was obvious and we defined an interaction as resolved when one of the opponents withdrew during the encounter (Côté, in press). For each dyadic relationships, an individual was considered dominant if she won >50% of interactions with the other member of the dyad (Hand 1986).

Statistical procedures

Dominance hierarchies were significantly linear during all years according to the methodology recently proposed by de Vries (1995, 1998) (Côté, in press). Briefly, we ordered all females in the population using an iterative procedure (1,000 randomizations) that ranked individuals by minimizing the number and strength of inconsistencies in the matrix. An inconsistency occurs when individual j dominates i, and j is below i in the current rank ordering (de Vries 1998). The absolute difference between the ranks of two individuals involved in an inconsistency is called the strength of that inconsistency (de Vries 1998). All calculations were performed with Matman 1.0 for Windows (Noldus Information Technology 1998).

To take into account variation in matrix size (from 38 females in 1994 to 45 in 1997), we transformed social ranks according to the formula $1-(rank/N_i)$ where N_i is the number of adult females during year i. Social ranks therefore vary from 0 (subordinate) to 1 (dominant). Female age has a very strong effect on the probability of winning an encounter and on social rank: more than 94% of dyadic interactions are won by the older female (Côté 2000, in press). Because age and social rank were strongly positively correlated, we used the residuals of social ranks on age in all models. Therefore, the effects of age-specific social ranks are presented and discussed throughout.

We used generalized linear mixed models (GLMMs) to assess the effects of maternal age, social rank and reproduction in the previous year (fixed effects) on kid sex ratio. GLMMs are a more sophisticated class of generalized linear models (McCullagh and Nelder 1989) that allow random effects to be fitted within the framework of regular logistic regression (Schall 1991; Milner et al. 1999). To account for stochastic between-year variation in kid sex and repeated observations of females contributing >1 kid to the data set, we included the random effects of year and female identity in the models. Kid sex was analysed with a binomial error structure and a probability curve was fitted to the data using the logit link function with fixed and random effects (Milner et al. 1999). The significance of the fitted terms and their interactions was assessed using the Wald statistic at the final iteration of the algorithm. For linear mixed models, referring the Wald statistic (W) with d_n degrees of freedom to a χ^2 distribution is known to give overoptimistic estimates of significance. Reference of a scaled Wald statistic (W/d_n) to an F dn, dd distribution with numerator

Table 1 The effects of maternal age, social rank and weaning success the previous year on the probability of producing a daughter for mountain goat females at Caw Ridge, Alberta. All GLMM models include random effects of mother identity. Maternal rank was only available for 1994–1997

	GLMM estimates±SE	Wald statistic[a]	d_n,d_d	P
Model for 1989–1997 (n=134)				
Maternal age	−0.328±0.092	12.6	1,42	0.001
Kid weaned previous year	0.384±0.397	0.9	1,42	0.3
Constant	−0.155±0.272			
Model for 1994–1997 (n=87)				
Maternal age	−0.382±0.125	9.3	1,33	0.004
Age-specific maternal rank	2.661±2.586	1.1	1,33	0.3
Kid weaned previous year	0.933±0.540	3.0	1,33	0.1
Constant	−0.314±0.368			
Model for mothers that weaned a kid the previous year in 1989–1997 (n=63)				
Maternal age	−0.369±0.135	7.4	1,25	0.01
Sibling sex	0.143±0.566	0.1	1,25	0.8
Constant	0.173±0.474			

[a] The significance of the terms was assessed by the Wald statistic referred to an *F dn, dd* distribution, see text for details

degrees of freedom d_n and denominator degrees of freedom d_d had been shown to yield better results, where d_d has to be estimated from the data (Elston 1998). The performance of the method, however, has not been assessed for GLMMs. Hence we have taken the conservative approach of using as d_d, the minimum available degrees of freedom assuming either all covariates are estimated entirely between individual mothers or assuming all covariates are estimated entirely within mothers. Age of the mother centred on 8 years old was used as a continuous variable to run the final GLMM models. Analyses involving maternal social rank were repeated for a subset of the data because social ranks were only available for 1994–1997. All analyses were performed in GENSTAT 5, release 4.1.

Results

Although the study period covered 9 years (1989–1997), the estimated variance component of year was always very low (<0.007) and excluded from all analyses. We found a small random effect of mother identity and, therefore, we included it in all GLMM analyses. Considering the variance component of mother identity, however, only slightly modified the estimates of the final models because the random effect was small. Thus, simple logistic regression models (GLM) led to very similar results.

The overall sex ratio in 1989–1997 did not differ from unity (75 males, 85 females; *G*-goodness-of-fit test=0.3, P=0.6), but the proportion of female kids produced decreased with female age (Table 1). The observed data fitted the predicted probability curve generated by GLMM relatively well (Fig. 1). Note that only two 3-year-old mothers were monitored. The proportion of daughters decreased from approximately 70% for ≤6-year-old mothers to about 25% for females 10 years of age and older (Fig. 1). Individual females monitored for a minimum of 5 years, including at least 2 years when aged 8 years and older, produced 64% daughters when aged less than 8 years and 43% daughters when aged 8 years or more (n=25). Refitting the model during the 4 years when maternal social rank was available (1994–1997) generated similar results (Table 1). The proportion of females produced decreased with maternal age, but we did
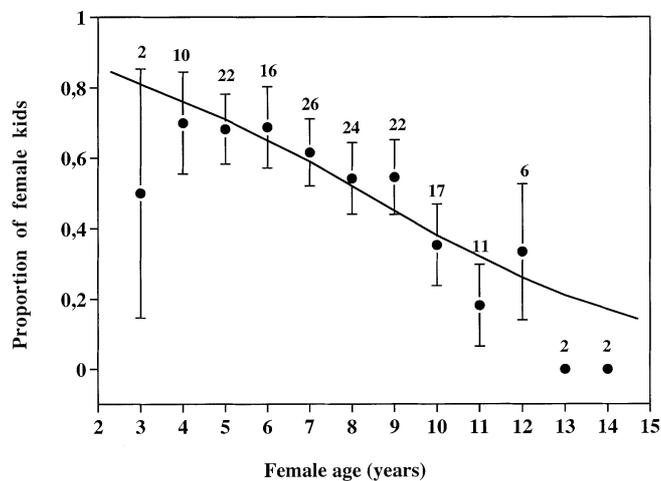

Fig. 1 Proportion (±SE) of female kids produced according to maternal age by mountain goats on Caw Ridge, Alberta, 1989–1997. Sample sizes are shown for each age class. The *regression line* is from a generalized linear mixed model including maternal age as a fixed effect and female identity as a random effect {(age-8)}+ e_j~N [0, 0.05 (±0.26)]}

not detect any effect of maternal social rank on kid sex when accounting for maternal age (Table 1). The residuals of social rank for females that produced a daughter (0.028, SE=0.014, n=46) and those that produced a son (−0.013, SE=0.018, n=45) were similar. There was no significant interaction between maternal age and the residuals of social rank.

Reproductive status one year did not affect kid sex ratio the following year (Table 1); females that had weaned a kid the previous year produced 47.7% daughters (n=65), while barren females produced 52.2% daughters (n=69). Considering only females that weaned a kid the previous year, kid sex one year did not affect the probability of producing a male or a female the following year (Table 1). Females that weaned a son produced 38% daughters (n=26) the following year, while females that weaned a daughter gave birth to 54% females (n=37). Within this subsample, the probability of producing a fe-

male also decreased with age (Table 1). There were no significant interactions between maternal age or residuals of social rank with either reproductive status or kid sex the previous year.

Discussion

The existence and adaptive nature of offspring sex ratio adjustments in mammals is controversial (Clutton-Brock and Iason 1986; Hiraiwa-Hasegawa 1993; Festa-Bianchet 1996). Hewison and Gaillard (1999) recently reviewed sex ratio studies of ungulates and concluded that the evidence for facultative adjustment of offspring sex ratio is equivocal at best. A problem with the interpretation of sex ratio data is that competing theories provide adaptive explanations for results of opposite directions. A sex ratio biased towards sons among dominant females can be interpreted as supporting the Trivers and Willard (1973) hypothesis, but a sex ratio biased towards daughters can be seen as support for the LRC hypothesis. This problem could be avoided if the assumptions of the competing theories were considered, but the majority of studies that have addressed variation in offspring sex ratio in mammals did not first test the assumptions of either model (Clutton-Brock and Iason 1986; Hewison and Gaillard 1999).

In mountain goats, the assumptions of the LRC hypothesis are not met. Both sexes may disperse; of seven goats known to emigrate from Caw Ridge since 1990, four were males and three were females. In addition, goats did not form family groups, thus a dispersing individual would not reduce local competition for its mother more than for other goats in the population. Therefore, there seems to be no justification to test the LRC hypothesis in mountain goats.

The first assumption of the Trivers and Willard (1973) model, a positive correlation between phenotypic quality of the mother and phenotypic quality of the offspring at the end of maternal care, was met in our study, as is generally the case in ungulates (Hewison and Gaillard 1999). In mountain goats, maternal mass was positively correlated with kid mass during the month before weaning (Côté and Festa-Bianchet, in press). Unfortunately, we do not have the data required to verify the second assumption of the model, that differences in offspring quality at the end of the maternal care period endure to adulthood. A positive relationship between adult quality and juvenile quality, however, has been documented in other polygynous and sexually dimorphic ungulates (Green and Rothstein 1991; Birgersson and Ekvall 1997; Festa-Bianchet et al., in press). Evidence for the third assumption of the model, that adult phenotypic quality has a greater influence on reproductive success of males than of females, is not available. This assumption has only been tested in red deer (Clutton-Brock et al. 1986) and requires paternity data and many years of individual monitoring. Hewison and Gaillard (1999), however, suggested that this assumption is probably val-

id in most polygynous ungulates where male mating success increases with body size and rank. Mountain goats fit this definition because they are highly sexually dimorphic, polygynous, and male reproductive success is probably related to body size and social rank (Geist 1964; Houston et al. 1989; Côté et al. 1998b).

The most cited study of sex ratio bias in ungulates, that of red deer on Rhum, revealed that maternal rank influenced differentially the reproductive success of sons and daughters (Clutton-Brock et al. 1984, 1986). Dominant females produced more sons than daughters and had a greater effect on the success of their sons (Clutton-Brock et al. 1984, 1986). A new analysis of the Rhum data set, however, revealed that the effect of maternal social rank on offspring sex ratio disappeared at high population density (Kruuk et al. 1999a). Kruuk et al. (1999a) found that maternal age had no effect on offspring sex ratio. Trivers and Willard (1973) suggested that the amount of maternal care should affect the reproductive success of males more than that of females, because body size and social rank are more important determinants of reproductive success in males than in females (Clutton-Brock et al. 1982; Clutton-Brock 1988). In red deer, male reproductive success increases with body size and growth rate during the period of maternal care (Clutton-Brock et al. 1982; Kruuk et al. 1999b). Therefore, high-quality females that presumably have a greater capacity for investment should produce more sons than daughters because they have a good chance of producing a dominant male that will enjoy high reproductive success (Clutton-Brock et al. 1986; Feh 1990; Arnbom et al. 1994). The results of longitudinal studies of horses (*Equus caballus*) (Feh 1990), rhesus monkeys (*Macaca mulatta*) (Meikle and Vessey 1988) and long-tailed macaques (*M. fascicularis*) (van Noordwijk and van Schaik 1999) suggest that the reproductive success of sons of high-ranking females is greater than that of sons of low-ranking females. In mountain goats, however, we did not detect any effect of maternal social rank on kid sex ratio when taking maternal age into account, despite the fact that female reproductive success increases with social rank (Côté 1999).

Similarly, reproductive effort and kid sex the previous year had no effect on kid sex ratio. Birgersson (1998) found no effect of previous reproductive effort on offspring sex ratio in fallow deer (*Dama dama*). In bison (*Bison bison*), Rutberg (1986) claimed that cows that were barren one year produced more sons than daughters the following year, but Shaw and Carter (1989) found that previous reproductive effort had no effect on offspring sex ratio.

The proportion of female kids, however, decreased substantially with female age in mountain goats (Fig. 1). In roe deer (Wauters et al. 1995) and Cuvier's gazelle (*Gazella cuvieri*) (Alados and Escós 1994), the proportion of female embryos in a litter also decreased with maternal age. Thomas et al. (1989) obtained similar results in barren-ground caribou (*Rangifer tarandus*), where females aged up to 4 years produced 38% males

while females >10 years old produced 67% males. Kojola and Eloranta (1989), however, did not find any relationship between age and birth sex ratio in the same species. In sexually dimorphic ungulates, males are generally costlier to wean than females (Clutton-Brock et al. 1981; Gomendio et al. 1990; Hogg et al. 1992; Bérubé et al. 1996; Monard et al. 1997; Birgersson et al. 1998). Because the proportion of sons produced increased dramatically with age in mountain goats, and because sons appear costlier than daughters in sexually dimorphic ungulates, our data suggest that the ability to provide maternal care may increase with age. Compared to young mothers, old mothers may either increase reproductive investment or may be able to provide greater maternal care without necessarily investing more (Cameron et al. 2000). The increased experience and social rank of older mothers may allow them to reduce some reproductive costs compared to younger females (Green 1990; Cameron et al. 2000). If we accept that older mothers are better mothers because of higher social rank and experience, then our data support the predictions of the Trivers and Willard (1973) model. In our study, however, kid survival did not vary with maternal age (Côté 1999) and there was no significant sexual dimorphism in kid mass (Côté and Festa-Bianchet, in press). The development of sexual dimorphism in mountain goats is slower than in many other ungulates and most of it occurs postweaning (Houston et al. 1989; Festa-Bianchet et al. 1996; Côté 1999). Our results, therefore, do not firmly establish that the link between maternal characteristics and offspring sex ratio is related to differential investment, and caution against assuming that any sex ratio bias is evidence of differential maternal investment in the sexes. Clear evidence of a physiological mechanism explaining sex ratio adjustment is still lacking despite decades of research, suggesting that females may not be able to adaptively vary the sex ratio of their offspring (Williams 1979; Clutton-Brock and Iason 1986; Krackow 1995).

Reproductive success of female mountain goats increased with social rank (Côté 1999). Offspring sex ratio, however, did not vary with social rank when accounting for maternal age. The proportion of sons produced increased with maternal age, possibly because only old females could sustain the repeated production of sons. Continued long-term monitoring of this population, particularly the fate, adult size and reproductive success of males according to maternal age, will be necessary to shed light on the potentially adaptive nature of sex ratio adjustment.

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