

Maternal condition and offspring sex ratio in polygynous ungulates: a case study of bighorn sheep

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The Trivers and Willard model (TWM) predicts that for sexually dimorphic polygynous mammals, mothers able to provide a high level of care should bias offspring sex ratio in favor of sons. Contradictory results of empirical studies, however, suggest that selective pressures for adaptive offspring sex ratio vary with species and environmental conditions. We report the results of a 29-year study of marked bighorn sheep (*Ovis canadensis*) in a population that underwent wide changes in density and where most females were weighed each year. Lamb sex ratio was independent of absolute ewe mass and yearly deviations from individual or population average mass, but there was a nonsignificant trend towards fewer males being born at high population density. Bighorn sheep satisfy all the assumptions of the TWM but not its prediction: lamb sex ratio is independent of maternal ability to provide care. Recent hypotheses to explain the lack of relationship between maternal condition and offspring sex in ungulates are unlikely to apply to bighorn sheep. We suggest that the TWM may only apply when social rank strongly affects the ability to provide maternal care. Those circumstances are likely to occur for only a few species and within a narrow range of environmental conditions. *Key words*: bighorn sheep, habitat quality, sex ratio, social rank, Trivers and Willard model, ungulates. [*Behav Ecol*]

Trivers and Willard (1973) proposed a model of adaptive offspring sex ratio variation when parental fitness returns differ according to offspring sex. Their model makes three assumptions: (1) that offspring phenotypic quality at weaning is correlated with maternal phenotypic quality, (2) that offspring quality at weaning is correlated with quality when adult, and (3) that adult quality affects the reproductive success of one sex more than that of the other. For polygynous and sexually dimorphic mammals, such as most ungulates (Alexander et al., 1979), the model predicts that high quality mothers should produce more sons, while low quality mothers should produce more daughters. Empirical results, however, are inconsistent, both across (Hewison and Gaillard, 1999; Pélabon et al., 1995) and within (Hewison et al., 1999) species, possibly because the model was often tested in species that do not meet its assumptions (Hewison et al., 1999) or because adaptive sex ratio variation is also affected by many environmental factors that were ignored in the formulation of the original hypothesis (Kruuk et al., 1999).

The “advantaged daughter hypothesis,” based on a theoretical basis similar to the Trivers and Willard model (TWM), leads to the opposite prediction for the sex ratio produced by ungulate mothers (Hewison and Gaillard, 1999; Hiraiwa-Hasegawa, 1993; Simpson and Simpson, 1982). According to this hypothesis, mothers able to provide a high level of care should invest more in daughters than in sons if maternal care can affect the fitness of daughters more strongly than the fitness of sons, for example through inheritance of social rank (see also Leimar [1996] for an extension of this hypothesis).

Another hypothesis, based on local resource competition (LRC), was first proposed at the population scale (Clark, 1978). At the individual level (Silk, 1983), it predicts that female mammals in poor condition would benefit from producing males, because males are more likely to disperse than females and therefore adult sons are less likely than adult daughters to compete with their mother for local resources. Some studies of ungulates have provided support for the LRC hypothesis (Caley and Nudds, 1987).

Because a similar theoretical basis predicts sex ratio biases in opposite directions with subtle changes in the assumptions, any significant deviation from parity can be interpreted a posteriori as support for one of these theories. Significant results are easier to publish, and the rarity of replication leads to an important publication bias in many areas of ecology (Csada et al., 1996; Palmer, 2000). A publication bias is particularly likely in sex ratio studies, because both the mechanisms and the potential adaptive significance of this phenomenon are largely unknown (Clutton-Brock, 1985; Festa-Bianchet, 1996; Krackow, 1995). Before concluding that adaptive variation in sex ratio is widespread in mammals, one should consider the reliability of each study, including its sample size (Palmer, 2000), its duration, and most of all to what extent the study species meets the assumptions of the model being tested (Hewison et al., 1999).

Trivers and Willard (1973) chose the caribou (*Rangifer tarandus*) to illustrate their influential paper, and ungulates appear to be ideal candidates to test their model (Hewison and Gaillard, 1999; Sheldon and West, 2004). Only four species of ungulates, however, are known to meet the three assumptions of the TWM (Hewison and Gaillard, 1999): bighorn sheep, red deer (*Cervus elaphus*), reindeer/caribou, and fallow deer (*Dama dama*). Despite weak adult sexual dimorphism, feral horses (*Equus caballus*) may also be a good model to test the TWM (Cameron et al., 1999; Cameron and

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Linklater, 2000), although it is not clear whether or not mare condition has a different effect on foal reproductive success according to offspring sex. Recently, it has been suggested that feral domestic sheep (*Ovis aries*) also satisfy the TWM assumptions, although there is no relationship between maternal mass and offspring sex ratio (Lindström et al., 2002).

In bighorn sheep, sons receive more maternal care (Festa-Bianchet et al., 1996; Hogg et al., 1992) and have higher fitness costs than daughters; compared to ewes that wean daughters, ewes that wean sons have higher macroparasite counts (Festa-Bianchet, 1989), later subsequent oestrus (Hogg et al., 1992), and lower subsequent weaning success (Bérubé et al., 1996). Mass at weaning is more strongly correlated with adult mass for males than for females (Festa-Bianchet et al., 2000). Male reproductive success appears more strongly affected than female reproductive success by phenotypic characteristics such as horn and body size (Coltman et al., 2002). Finally, in most bighorn sheep populations, including the Ram Mountain population in the current study, litter size is fixed at one, which avoids additional complications in interpreting the TWM predictions (Williams, 1979). Although this species seems an ideal candidate, the TWM's prediction of a relationship between maternal condition and lamb sex ratio remains untested.

In red deer, dominant hinds produce a male-biased offspring sex ratio, but only at low population density (Kruuk et al., 1999). Dominant hinds are likely high quality mothers because they have higher reproductive success than subordinates (Clutton-Brock et al., 1986). Dominance as calculated in the red deer study, however, is cohort-specific and fixed for a hind's lifetime; therefore, it cannot reflect yearly changes in an individual's ability to provide maternal care.

The TWM specifically predicts that a mother should bias offspring sex ratio according to her condition at conception, but very few studies have compared yearly changes in individual maternal condition to offspring sex ratio in ungulates (Cameron et al., 1999). In our study, yearly recaptures of ewes (Festa-Bianchet et al., 1996) allowed us to measure annual condition based on year-to-year changes in individual mass, a variable strongly correlated with individual quality and reproductive potential in this species (Bérubé et al., 1999; Festa-Bianchet, 1998; Gaillard et al., 2000). To test whether individual characteristics and environmental factors affect sex ratio variation, one requires data on many individuals monitored under contrasting environmental conditions (Kruuk et al., 1999). Our 29-year study of marked, known-age and known-mass bighorn sheep is in a unique position for such a test. Population density more than tripled during our study, providing clear evidence of resource limitation at high density (Bérubé et al., 1996; Festa-Bianchet et al., 1998; Jorgenson et al., 1993; Portier et al., 1998). Kruuk et al. (1999) reported a strong effect of density on sex ratio patterns at both the population and individual levels, with poor habitat quality leading to fewer male fetuses being carried to term.

We thus tested (1) whether or not changes in population density affected offspring sex ratio at the population level in bighorn sheep and (2) whether the sex of lambs produced by individual ewes changed according to their body condition. Our null hypotheses were that population density and ewe body condition did not affect lamb sex.

METHODS

Study area and population

Data were collected from 1972 to 2000 at Ram Mountain, Alberta, Canada (52° N, 115° W). The bighorn sheep range

extends over approximately 38 km² of alpine and subalpine habitat at 1082 m to 2173 m asl. Each year, sheep are captured from late May to September in a corral trap baited with salt. Each ewe's individual rate of mass gain was used to adjust her mass to 15 September, about two months before conception. Between 1972 and 2000, 235 adult females were weighed, including 151 aged between 6 and 10 years. Ewes included in our analyses were weighed at least twice during the summer, but most were weighed 3–4 times. Festa-Bianchet et al. (1996) report more details on capture frequencies and mass adjustments. Maternal condition about 2 months before conception is a reliable measure of condition at conception because most ewes complete summer mass accumulation by mid-August (Festa-Bianchet et al., 1996), partly because by then the quality of available forage has declined (Festa-Bianchet, 1988b). By mid-September, lambs have almost stopped suckling (Festa-Bianchet, 1988a). A recent meta-analysis claimed that the relationship between maternal condition and offspring sex tends to be stronger when maternal quality is assessed before conception than after it (Sheldon and West, 2004).

Ewes were marked with visual collars and lambs with ear tags. Lamb sex was determined at first capture, for lambs aged from 1 week to 3 months. All ewes have been marked since 1976. Over 80% of the lambs were caught in most years, and 686 lambs were weighed between 1972 and 2000. We assumed that sex ratio at capture reflected sex ratio at birth; neonatal mortality (deduced for ewes that lactated but were not seen with a lamb) averaged about 19%, and we have no evidence that it was sex-biased (Bérubé et al., 1996). Lamb and yearling survival is not sex-biased (Jorgenson et al., 1997; Portier et al., 1998). We used the number of adult ewes in June to measure population density, because adult rams use different foraging ranges than those used by adult ewes and juveniles (Geist and Petocz, 1977). The number of adult females has been used to measure population density by other studies of sexually dimorphic polygynous ungulates (Côté and Festa-Bianchet, 2001; Kruuk et al., 1999).

Indices of maternal condition

Earlier research revealed that ewe age affected body mass, fertility, and, for very old ewes, lamb sex ratio (Bérubé et al., 1996; Festa-Bianchet et al., 1996; Gallant et al., 2001). Here we focus on mass and body condition of ewes aged 6–10 years, whose mass is mostly unaffected by age (Festa-Bianchet et al., 1996). Including ewes aged 4 to 14 years (therefore excluding the oldest and youngest reproducing ewes) led to similar results to those presented here. Trivers and Willard made no predictions about how maternal age may affect offspring sex ratio (Hewison et al., 2002), and the use of maternal age as a proxy for condition is problematic (Sheldon and West, 2004).

We used three different measures of ewe quality:

- (1) First, we measured proportion by which each ewe each year deviated from her average mid-September mass at 6–10 years. Changes in absolute body mass from year to year for adult ewes are correlated with differences in reproductive potential (Festa-Bianchet, 1998). Therefore, this first measure tested whether ewes produced more sons in years they were in better condition compared to their individual long-term average ($n = 165$ ewes-year and 78 different ewes, with an average of 3.7 [range 2–5] measurements of mid-September mass per ewe). This comparison provides a direct test of the TWM.
- (2) The second measure of ewe quality was the difference between each ewe's mass and the average

Table 1
Model selection for the probability of producing a son by bighorn sheep ewes at Ram Mountain

Model	Deviance	df	Models compared	Difference in deviance	Difference in df	Chi square	<i>p</i> -value
a : (1) General model: $\text{Logit}(\text{sex}) = I + C*S$	226.793	158					
(2) : (1)–C × S	227.630	160	(1) and (2)	0.838	2	0.838	.66
(3) : (2)–C	227.667	161	(3) and (2)	0.037	1	0.037	.85
(4) : (2)–S	227.951	162	(4) and (2)	0.321	2	0.321	.85
Selected model : $\text{Logit}(\text{sex}) = \text{constant}$							
b : (1) General model: $\text{Logit}(\text{sex}) = BW$	112.22	93					
(2) : (1)–BW	112.35	94	(1) and (2)	0.129	1	0.129	.72
Selected model : $\text{Logit}(\text{sex}) = \text{constant}$							
c : (1) General model: $\text{Logit}(\text{sex}) = I + R*S$	233.259	165					
(2) : (1)–R × S	237.051	167	(1) and (2)	3.792	2	3.792	.15
(3) : (2)–R	237.237	168	(3) and (2)	0.186	1	0.186	.67
(4) : (2)–S	237.37	169	(4) and (2)	0.32	2	0.32	.85
Selected model : $\text{Logit}(\text{sex}) = \text{constant}$							

(a) C: mass in mid-September (about 2 months before conception) minus mean mass of that ewe as an adult ($n = 165$ ewe-years, 78 ewes).

(b) BW: mean adult mass ($n = 95$ ewes). (c) R: mass minus the mean mass of adult females that year ($n = 172$ ewe-years, 83 ewes).

S: previous reproductive status; A*B refers to the additive effects of the factors A and B as well as the interaction $A \times B$. I: the individual ewe, defined as a random term.

mid-September mass of adult females that year, which provided a measure of a ewe's quality relative to other females each year ($n = 172$ ewes-year and 83 different ewes). Because measures (1) and (2) were correlated ($F = 25.88$, $df = 165$, $r^2 = .14$, $p < .001$), they could not be included in the same analysis.

- (3) Finally, we compared the average mid-September mass of each ewe at 6–10 years of age with her offspring sex ratio during those years ($n = 95$ ewes). We performed a separate analysis for this global measure, in which each ewe was considered only once.

To test whether lamb sex ratio varied according to reproductive effort the previous year, we used three levels of increasing energetic cost for the mother (Bérubé et al., 1996): no lamb weaned, weaned a female, and weaned a male. The category 'no lamb weaned' included 15 ewe-years of no apparent gestation, 55 of neonatal lamb mortality, and 19 lambs that died during summer, mostly before one month of age. Thus, our sample was insufficient to divide this category into further sub-classes of reproductive effort.

Statistical analyses

Individual ewes were included one to five times in the analysis of the effects of yearly body mass variation and of relative quality on the probability of producing a son. We therefore fitted individual ewe identity as a random effect in a generalized linear model (Schall, 1991). We compared the deviance of the general model (including a measure of condition, previous reproduction, individual, and the interaction between the measure of condition and previous reproduction) with the deviance of the additive model: the difference between models is distributed as a χ^2 with degrees of freedom equal to the difference in degrees of freedom between the two models compared. Because the interaction was not significant, we then tested the main factors by successively withdrawing each of the two terms.

The effect of average maternal mass between 6 and 10 years old on lamb sex ratio was analyzed with a logistic regression of the proportion of sons produced by each ewe at 6–10 years of age. A similar analysis was performed to study the relationship between cohort sex ratio and population density. All statistical analyses used R software (R Development Core Team, 2003).

We paid special attention to nonsignificant results by considering the effect size in addition to *p*-values. We did not run a posteriori power analyses because such retrospective analyses are meaningless (Hoenig and Heisey, 2001). Instead, we used the information provided by confidence intervals as recommended by several authors (Di Stefano, 2004; Johnson, 1999; Steidl et al., 1997).

RESULTS

Individual ewes were not significantly more likely to conceive sons in years when they were heavy (mean proportion of males 0.48, 95% CI: 0.37–0.59) than in years when they were lighter than their average adult mass (0.45, 95% CI: 0.34–0.56; Table 1, Model a). Both confidence intervals included 0.50. The effect size (0.03) was positive as predicted by the TWM but was very small and confidence intervals overlapped by 76%. We therefore concluded that sex ratio was independent of ewe body condition. Reproductive status the previous year did not significantly influence lamb sex (means of 0.49, 95% CI: 0.37–0.61; 0.44, 95% CI: 0.31–0.57; and 0.46, 95% CI: 0.32–0.60; for females that weaned no lamb, daughters, and sons, respectively; Table 1, Model a). All confidence intervals included 0.50 and overlapped by 67% or more. The effect was opposite of that predicted by the TWM because sex ratio for females having weaned a son was higher than for females having weaned a daughter. We thus concluded that there was no relationship between previous reproductive status and sex ratio.

There was a slight trend for ewes to produce more sons between 6 and 10 years of age if their average mass was heavier than the population average (71.5 kg; 0.50, 95% CI: 0.41–0.60, compared to 0.42, 95% CI: 0.31–0.54 for females lighter than the population average; Table 1, Model b, and Figure 1). The confidence intervals, however, overlapped by 45% and both included 0.50. Moreover, when we divided the females into three groups according to body mass (first group: less than 69.83 kg; second group: between 69.83 and 73.90 kg; third group: more than 73.90 kg), the heaviest females tended to produce fewer sons than females of intermediate mass (0.425, 95% CI: 0.31–0.54 vs. 0.576, 95% CI: 0.46–0.69), contrary to the TWM prediction. We thus concluded that female body mass did not influence offspring sex ratio in bighorn sheep.

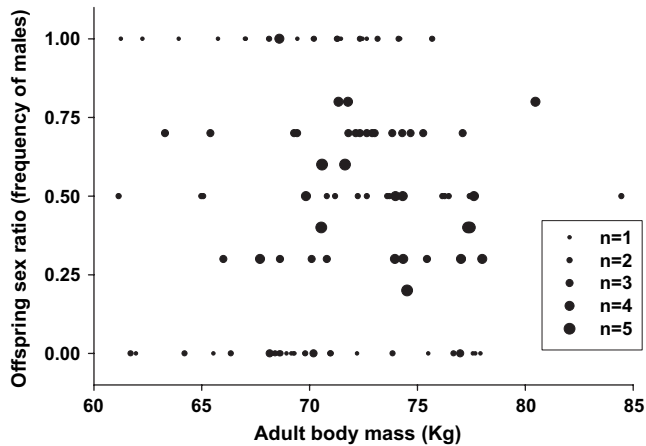


Figure 1
The average adult mass (BW in Table 1, Model b) of bighorn ewes compared to the sex ratio of the lambs they produced at 6–10 years of age. Point size refers to the number of lambs of known sex produced by each ewe.

Females heavier than the population average in the year of conception did not produce significantly more male offspring (0.47, 95% CI: 0.39–0.55) than females lighter than other females (0.43, 95% CI: 0.24–0.62; Table 1, Model c). Both confidence intervals included 0.50 and overlapped by 100%. We thus concluded that a female's quality relative to the population average did not influence offspring sex ratio in bighorn sheep.

Population density may have influenced cohort sex ratio, as our results were somewhat inconclusive. Lamb sex ratio tended to decrease with increasing density (slope of -0.0056 , 95% CI: -0.0119 – 0.0008 , $\chi^2 = 2.99$, $df = 1$, $p = .08$); at high density (>72 ewes), the offspring sex ratio was 0.45 (95% CI: 0.38–0.52) whereas at low density (<72 ewes) it was 0.54 (95% CI: 0.49–0.59), leading to an effect size of 0.09. Although the difference was not significant, the confidence intervals overlapped by only 16%. The overall mean proportion of sons was 0.47 ± 0.039 (SE).

DISCUSSION

Our results suggest that maternal condition has no detectable influence on offspring sex in bighorn sheep, despite the fact that this species is an ideal candidate to test the predictions of the TWM because it satisfies its assumptions, and despite the quality of our long-term data. We monitored the sex ratio of lambs of individual ewes of known age, body mass, and condition in a population that underwent substantial changes in density. Offspring sex ratio is independent of individual maternal condition in this population, because ewes were not more likely to conceive sons in years when they were heavier than their average multi-year adult mass. However, lamb sex ratio may have varied with population density, possibly because at high population density fewer male fetuses were carried to term, as has been suggested for red deer (Kruuk et al., 1999), or because more male lambs died neonatally.

The TWM's prediction is not consistently met in ungulate species that satisfy its assumptions (Hewison and Gaillard, 1999). In fallow deer, maternal body mass or maternal body mass changes are not related to offspring sex (Birgesson, 1998). In red deer and reindeer, the relationship between offspring sex ratio and maternal quality is affected by population characteristics (Kojola and Eloranta, 1989; Kruuk et al., 1999; Reimers and Lenvik, 1997). Maternal condition

has been reported to affect sex ratio and sex-biased maternal investment in horses, where results also vary among study populations (Cameron et al., 1999; Cameron and Linklater, 2000; Monard et al., 1997). Several factors may explain these inconsistent results both across and within species that meet the TWM assumptions.

Within species, some authors reported an effect of environmental conditions on sex ratio patterns, in ungulates and in other groups (Kruuk et al., 1999; Van Shaik and Hrdy, 1991). In primates it has been suggested that when local environmental conditions lead to intense female-female competition for resources, the selective pressures for adaptive sex ratio variation may be different from those existing when resources are more readily available (Dittus, 1998; Johnson, 1988; Packer et al., 2000; Van Shaik and Hrdy, 1991). In red deer, Kruuk et al. (1999) showed that the association between a female's social rank and her probability to produce a son disappeared at high density, probably because the higher growth rates of sons resulted in differential fetal loss. They pointed out that all support for the TWM prediction among ungulates had been found in populations below carrying capacity. The Ram Mountain bighorn sheep population more than tripled during our study, showing clear density-dependence in age at primiparity (Jorgenson et al., 1993), mortality of yearling ewes (Jorgenson et al., 1997), horn growth of males (Jorgenson et al., 1998) and lamb winter survival (Portier et al., 1998). Summer food quality was negatively affected by population density (Blanchard et al., 2003). Together, these results suggest that this population was well below carrying capacity during the low-density years of the study.

In feral domestic sheep, Lindström et al. (2002) reported no correlation between offspring sex ratio and maternal mass but showed a weak positive correlation with population density. The authors proposed that the time scale of variation in density and weather conditions might be too short in this highly fluctuating environment to allow mechanisms of sex ratio adjustment to evolve. Both the Ram Mountain bighorn sheep and the Hirta Soay sheep populations underwent wide changes in density, but while density for Soay sheep varied substantially from one year to another, population changes at Ram Mountain developed over decades. Therefore, the explanation for the lack of adaptive sex ratio manipulation proposed for Soay sheep is unlikely to apply to bighorn sheep.

As pointed out by Kruuk et al. (1999), variation in habitat quality is probably far from sufficient to explain the inconsistent results in sex ratio patterns across species. Differences in results may also be due to the different measures of maternal quality that were used. Whereas Kruuk and colleagues considered maternal social rank, studies on Soay and bighorn sheep were based on maternal condition. Sheldon and West (2004) pointed out that studies that employed behavioral measures of dominance supported more strongly the TWM than those based on body condition. We suggest that social organization may affect the role of female condition in producing the offspring sex ratio pattern predicted by the TWM.

Within species where the TWM assumptions are met, the selective pressure for a female to manipulate offspring sex ratio should depend not only on her own ability to provide maternal care, but also on the quality of other females in the population. A mother in good condition could increase her fitness by producing a daughter if most other females in the population were in even better condition and thus likely to produce sons of greater competitive ability. Therefore, the evolution of sex ratio manipulation could involve a physiological mechanism dependent directly on social rank, which, under some conditions, will be a reliable clue to a female's

relative potential as a mother (Dittus, 1998; Sheldon and West, 2004). Maternal hormone levels may be involved in determining offspring sex ratio, because they vary according to female rank (Goodwin et al., 1999; James, 1985) and are correlated with litter sex ratio (Flint et al., 1997; James, 1996). Dominant females may have higher fitness than subordinates only if high rank provides better access to some resources (Richards, 1974). The TWM prediction may apply only to species where female social rank directly affects access to resources. Moreover, variance in female condition should be maximized in such species (Clutton-Brock et al., 1997). Across species known to meet the TWM assumptions, those that confirm its prediction (red deer, reindeer, and horses) contrast with species that do not (bighorn and Soay sheep) in their social organization.

In female reindeer and red deer, social rank determines the outcome of interference competition for food (Barrette and Vandal, 1986; Kojola, 1997; Thouless, 1990) and is positively correlated with maternal and offspring mass (Clutton-Brock et al., 1986; Kojola, 1997). Dominant female reindeer lose less mass overwinter than subordinates (Kojola, 1997), and in red deer growth rate declines with increasing population density only for subordinate hinds (Blanc and Theriez, 1998; see also Clutton-Brock et al., 1984). In horses, female rank is also correlated with diet quality and reproductive success (Duncan, 1992). In contrast, dominance does not affect access to food in bighorn ewes (Eccles and Shackleton, 1986; Festa-Bianchet, 1991), a species of low aggressiveness compared to other ungulates (Fournier and Festa-Bianchet, 1995), and female rank is not correlated with mass, activity costs, diet quality (Eccles and Shackleton, 1986), conception date, lamb birth mass or birth date (Hass, 1991), or reproductive success (Festa-Bianchet, 1991). Although we did not measure dominance in ewes at Ram Mountain, we have no reason to believe that it played a stronger role than elsewhere. Soay sheep have a similar social organization to bighorn sheep (Clutton-Brock et al., 1997) and there is no evidence that social rank determines access to resources in that species.

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