

Sex ratio bias and reproductive strategies: What sex to produce when?

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Abstract. Several theories predict the evolution of bias in progeny sex ratio based on variations in maternal or offspring reproductive value. For mammals, however, tests of sex-bias theories have produced inconsistent results, and no clear patterns have emerged. Each theory is based on assumptions that are difficult to satisfy, and empirical tests require large data sets. Using a long-term study on bighorn sheep (*Ovis canadensis*), we identified several parameters that influence progeny sex ratio according to maternal state. For older females, progeny sex ratio was affected by an interaction between reproductive strategy and environmental conditions. When conditions were good, old females reproduced every year but minimized fitness costs by producing daughters. When conditions were poor, old females produced more sons but did not reproduce every year. Sons of older females were of similar mass to those born to younger females under poor conditions but were smaller and likely disadvantaged under good environmental conditions. For young and prime-aged females, progeny sex ratio was independent of environmental conditions. Environmental conditions and age should be considered when studying sex ratio bias, which appears to be a function of maternal state rather than of maternal condition. We suggest that a conservative reproductive strategy drives progeny sex ratio in older females according to the “cost of reproduction hypothesis.” By manipulating offspring sex ratio, older females reduced the cost of reproduction and increased their expected fitness returns.

Key words: *Alberta, Canada; bighorn sheep ewe; cost of reproduction; maternal state; Ovis canadensis; sex ratio bias; Trivers-Willard hypothesis.*

INTRODUCTION

Since Fisher's equal investment principle, the potential for adaptive manipulation of progeny sex ratio has become one of the most studied and, especially for mammals, controversial subjects in evolutionary ecology (Charnov 1982). Numerous theories predict different bias in progeny sex ratio according to different environmental and individual conditions, making multiple assumptions. Many of these theories are not mutually exclusive and could be seen as additive or interactive (Cockburn et al. 2002). The theory that has attracted the most attention in polygynous mammals is the narrow-sense Trivers-Willard hypothesis (TWH; Trivers and Willard 1973), which considers the direct effect of maternal condition and predicts a male-biased progeny for mothers in good condition. Measuring maternal condition is not trivial and most studies of TWH used measures of mother mass (Trivers and Willard 1973, Blanchard et al. 2005) or dominance (Kruuk et al. 1999) as a proxy for condition (see reviews by Sheldon and West 2004, Cameron 2004). Other hypotheses consider direct effects of maternal age (Saltz

2001, but see Hewison et al. 2002), of sex-specific reproductive cost (Myers 1978, Gomendio et al. 1990), or of environmental conditions (Myers 1978) on progeny sex ratio. These hypotheses differ mainly in their underlying mechanism and assumptions (Cockburn et al. 2002) and many make rather similar predictions. For example, in sexually dimorphic and polygynous species, both the TWH and the cost of reproduction hypotheses predict that females in poor condition would produce more daughters. According to the TWH, because variance in reproductive success is greater for males than for females, additional maternal investment will have a larger fitness return from sons than from daughters. Because mothers in better condition can rear reproductively successful sons, they are predicted to produce a male-biased offspring sex ratio. On the other hand, the cost of reproduction hypothesis (Cockburn et al. 2002) considers that females in poor condition are unable to bear the cost of producing sons, the energetically costlier sex. They should instead produce daughters to minimize the risk of reproductive failure, or to reduce the fitness costs of reproduction, such as a decrease in their subsequent survival. In polytocous species, females in poor condition could reduce fitness costs by producing fewer but not necessarily smaller sons. In monotocous species, however, according to both the TWH and the cost of

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reproduction hypotheses, females in poor condition should produce smaller sons than females in good condition.

The Trivers-Willard model and the cost of reproduction hypothesis are based on maternal condition and do not directly consider the effects of environmental variation or maternal age on progeny sex ratio. Those effects have rarely been considered in studies of offspring sex ratio in mammals, and then only through their impact on maternal condition. For bison (*Bison bison*), Rutberg (1986) suggested that females that had not reproduced the previous year should be in better condition than those that had, and according to TWH should produce more males. Similarly, senescence and poor environmental conditions should decrease maternal condition and increase reproductive costs, possibly leading to a female bias in progeny sex ratio.

Results of different studies of progeny sex ratio in ungulates are inconsistent (Hewison and Gaillard 1999, Sheldon and West 2004). Contradictory findings could be partly due to a publication bias (Festa-Bianchet 1996), differences in timing of when maternal condition is measured (Cameron 2004), or to interactions between maternal and environmental conditions. In red deer (*Cervus elaphus*), dominant hinds produced more sons than daughters at low density, supporting TWH (Clutton-Brock et al. 1986). However, at high density, the relationship disappeared (Kruuk et al. 1999). Inconsistencies in sex ratio bias in different populations of the same species or over time in the same population indicate that long-term data are essential to study progeny sex ratio (Festa-Bianchet 1996, Cockburn et al. 2002). Long-term analyses of sex ratios, however, inevitably uncover complexity (Cockburn et al. 2002). In some cases, reanalyses including more years of data reveal that sex ratio biases that appeared strong over the short term decrease or disappear (Festa-Bianchet 1996, Kruuk et al. 1999, Cockburn et al. 2002). Inconsistency with previously reported patterns could arise from interactive effects of maternal and environmental conditions (Kruuk et al. 1999, Blanchard et al. 2005). Long-term studies of marked individuals with known age and phenotypic characteristics remain the most powerful tool to disentangle how sex ratio at birth varies according to environmental and maternal conditions.

Here we analyzed how maternal mass, maternal age, environment, and previous reproduction affected progeny sex ratio in bighorn sheep (*Ovis canadensis*), based on long-term monitoring of marked ewes in two populations. Although this species satisfies all assumptions of the TWH, previous studies did not support this model (Festa-Bianchet 1988, Blanchard et al. 2005). Ewe mass before conception, previous reproductive success, and their interaction did not explain variation in lamb sex ratio (Blanchard et al. 2005). Bighorn ewes have a conservative reproductive strategy, and reduce their reproductive effort at high population density or if they had weaned a lamb the previous year (Festa-Bianchet

and Jorgenson 1998). Females favor their own summer mass gain over the growth of their lambs, so that individual mothers maintain a relatively stable body condition at conception in different years (Festa-Bianchet and Jorgenson 1998). Consequently, we hypothesized that females may manipulate offspring sex ratio to reduce the fitness costs of reproduction, according to the "cost of reproduction" hypothesis. We expected to confirm that maternal mass before conception had no effect on sex ratio (Blanchard et al. 2005), but hypothesized that environmental variation, ewe age, previous reproduction, and their interactions would affect progeny sex ratio. Because environmental conditions, ewe age, and reproductive cost have relatively small effects on maternal mass, indirect effects on sex ratio variation through changes in maternal mass appear unlikely. We predicted that senescent ewes would produce the cheapest sex and that in poor environmental conditions progeny sex ratio would be biased toward daughters. We also expected that smaller sons would be produced by ewes in a state that normally favors a sex ratio biased toward daughters.

METHODS

Study areas and populations

Ram Mountain.—Ram Mountain (52° N, 115° W, elevation 1100–2173 m), Alberta Canada, is an isolated mountain 30 km east of the Canadian Rockies (see Plate 1). Since 1971, sheep have been captured several times each summer in a corral trap baited with salt (Jorgenson et al. 1993). Animals are marked and sexed at their first capture (usually as lambs). Since 1975, all ewes have been marked with colored collars and were of known age because they were first captured as lambs or yearlings. At each capture, we used udder examination to classify ewes as lactating or not. During field observations, we recorded mother–lamb associations. Yearly weaning success was measured by lamb survival to late September (Festa-Bianchet 1988), when ewes were classified as failed to wean, weaned a female, or weaned a male. "Failed to wean" included all ewes that did not have a lamb in September, regardless of whether or not they had given birth in that year.

Lambs gained mass linearly with date over the summer. Based on repeated measurements, we adjusted lamb mass to 15 September each year, using a linear mixed model of mass as a function of capture date with individual identity (intercept) and identity \times date interaction (slope) as random factors. A similar procedure was used to adjust maternal mass to 15 September, using a square-root transformation of capture date to linearize the relation of date and mass (Festa-Bianchet et al. 1996). September 15 is about two months before the start of the breeding season, and data from both Ram Mountain and Sheep River suggest that ewe body mass changes little between September and December (M Festa-Bianchet, *unpublished data*). Therefore, ewe mass

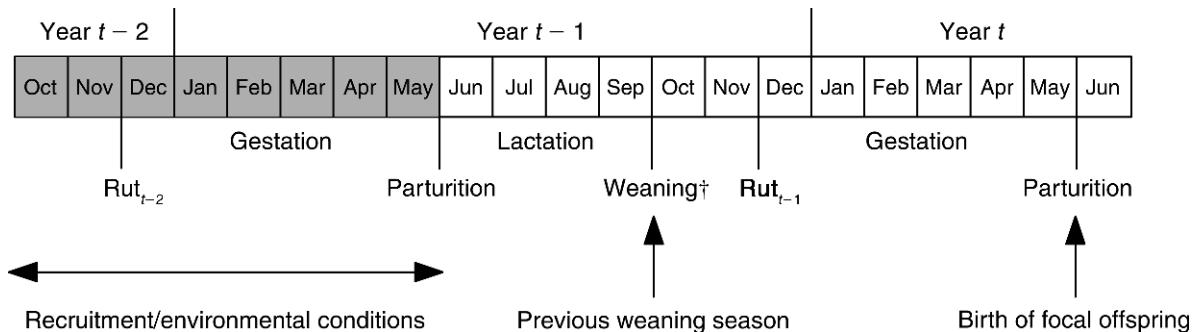


FIG. 1. Reproductive timetable for bighorn sheep (*Ovis canadensis*). In our analyses, sex of the lamb born in year t and conceived during the rut in year $t - 1$ (Rut_{t-1}) was compared to the weaning success of its mother in year $t - 1$ (Weaning) and to recruitment, i.e., mean lamb survival between October in year $t - 2$ and May in year $t - 1$ (gray months). Because recruitment was estimated during the previous winter, it was mathematically independent of weaning success, which was measured for individual females during the summer–autumn just before conception.

on 15 September is a good approximation of mass at conception.

Sheep River population.—Sheep River (50° N, 114° W, elevation 1800–2550 m) is 160 km south of Ram Mountain. Since 1981, about 95% of the sheep have been marked (Festa-Bianchet 1988). Each autumn, lambs aged 4–6 months are immobilized with a dart gun and tagged. Mother–lamb associations were established from field observations. In September, ewes were classified as failed to wean a lamb, weaned a female, or weaned a male. Body mass data were available only for a small subset of adult ewes in the later years and could not be used in the analyses.

For both populations, we used the number of adult females (≥ 2 years old) as an index of density (Festa-Bianchet and Jorgenson 1998) and population recruitment as an index of yearly environmental conditions. We measured recruitment as the proportion of marked lambs alive in October that survived to late May the following year. In ungulates, recruitment is correlated to population trends (Gaillard et al. 2000b, Pelletier et al. 2007) and to environmental conditions (Coulson et al. 2001, Wilson et al. 2006). At Ram Mountain, high recruitment (>0.67) was mostly associated with a phase of increasing population (1975–1989), and low recruitment was related to a long-term population decrease (1990–2008; Pelletier et al. 2007). The increasing phase with high recruitment was also characterized by a higher reproductive effort than the decrease phase (Martin and Festa-Bianchet 2010). Considering that most sex-manipulation mechanisms would occur at conception, we sought to estimate the impact on progeny sex ratio by environmental conditions, measured as recruitment, prior to conception. We thus compared the sex of lambs born in year t (conceived in year $t - 1$) to previous weaning success (in year $t - 1$) of individual mothers and to population recruitment before conception of the focal offspring (winter from $t - 2$ to $t - 1$; Fig. 1). It is important to note that “weaning success” is an individual-level measure, while “recruitment” is a

population average, and these parameters were not measured in the same year. Both density and recruitment varied widely in 1975–2008 at Ram Mountain. At Sheep River, variation was smaller, and accurate estimates of the number of adult ewes and of recruitment were available only for 1985–2003.

Statistical analyses

To avoid bias due to variation of reproductive effort with first reproduction, primiparous females were excluded from analyses. All statistical analyses used R 2.9.0 (R Development Core Team 2009). To avoid pseudo-replication, we used linear mixed models for all analyses, with mother identity and year as random effects. Significance of random effects was assessed using log-likelihood ratio tests (Pinheiro and Bates 2000).

Sex ratio bias.—We analyzed data on 529 lamb–mother pairs from 165 females over 33 years at Ram Mountain and 299 lamb–mother pairs from 90 females over 18 years at Sheep River. We ran mixed logistic regressions of lamb sex using the “glmer” function in the “lme4” package (Bates et al. 2008). By coding “lamb sex” as zero for females and one for males, we modeled the probability to produce a son as a function of a mother’s age at conception, her weaning success the previous year ($t - 1$), population density in the year of conception ($t - 1$), and recruitment the year before conception (winter from $t - 2$ to $t - 1$). For Ram Mountain, we also included these interactions as fixed effects: age \times recruitment, age \times previous weaning success, and previous weaning success \times recruitment. The last two interactions could not be included for Sheep River due to false convergence errors in model parameters.

Lamb mass at weaning.—We analyzed how mass at weaning varied according to lamb sex, environmental condition (density and recruitment), previous weaning success, maternal age, and their interactions. To avoid third-order interactions, we ran separate analyses according to maternal age. We considered females aged

TABLE 1. Effect estimates for the probability that bighorn sheep (*Ovis canadensis*) ewes will produce a male, for two populations in Alberta, Canada.

Variable	Ram Mountain				Sheep River			
	Estimate	SE	<i>z</i>	<i>P</i>	Estimate	SE	<i>z</i>	<i>P</i>
Intercept	-1.82	1.06	-1.72	0.09	1.37	1.44	0.95	0.34
Rut density	-0.005	0.004	-1.20	0.23	-0.05	0.03	-1.62	0.11
Body mass before the rut	0.010	0.018	0.553	0.579
Age at conception	0.27	0.11	2.48	0.01	0.10	0.11	0.91	0.36
Recruitment	2.60	1.51	1.72	0.08	2.10	1.66	1.26	0.21
Age × recruitment	-0.36	0.18	-2.03	0.04	-0.23	0.19	-1.21	0.22
Previous weaning success (PWS)†				0.37				0.04
Weaned a female	1.30	1.05	1.23		0.05	0.47	0.10	
Weaned a male	3.41	1.29	2.63		-0.49	0.25	-1.96	
Age × PWS†				0.04				
Age × weaned a female	-0.13	0.08	-1.57	
Age × weaned a male	-0.19	0.10	-2.01	
Recruitment × PWS†				0.02				
Recruitment × weaned a female	-0.37	1.06	-0.35	
Recruitment × weaned a male	-3.17	1.25	-2.53	

Notes: The logistic analysis was based on 529 lambs over 33 years at Ram Mountain and 299 lambs over 18 years at Sheep River. Significant effects are in boldface. Ellipses represent estimates of effects not fitted in the model. Blank cells are used for categorical effects. The probability is estimated for overall differences between categories, but effect size and CI are estimated for each category. Note that “recruitment” is a population-level parameter measured during the winter preceding conception and used as an index of environmental conditions, while “weaning success” measures individual performance by the mother in the summer before conception.

† “Females that failed to wean a lamb” were considered as references in the analyses.

6 to 10 years as “prime-age” and females aged 11 years or older as “old,” based on the age at which females start losing seasonally adjusted mass (Bérubé et al. 1999). Because age at first reproduction varied substantially over the study period, females younger than six were excluded from these analyses. We then fitted a linear mixed model of lamb mass at weaning for each ewe age category, with lamb sex, density, recruitment, previous weaning success, and their second-order interactions as fixed effects.

RESULTS

Sex ratio analysis

At Ram Mountain, population density and maternal mass before conception did not affect the lamb sex ratio (Table 1), which varied according to interactions between ewe age, recruitment, and the mother’s previous weaning success (Table 1, Fig. 2). When previous weaning success was ignored (Fig. 2a), offspring sex ratio was unbiased for females younger than eight years regardless of population recruitment. For females older than eight years, sex ratio was male biased when recruitment was low (indicating poor environmental conditions in the year before conception) and female biased when recruitment was high (good conditions). Considering only females that failed to wean a lamb the previous year, sex ratio was unbiased for all age-recruitment combinations, except that following years of low recruitment, the offspring sex ratio of older ewes was strongly male biased (Fig. 2b). For females that had weaned a daughter, offspring sex ratio was unbiased, except that following years of high recruitment, the

older ewes had more daughters (Fig. 2c). For females that weaned a son, sex ratio varied from a strong male bias for young mothers following years of low recruitment to a strong female bias for older mothers following years of high recruitment (Fig. 2d). When recruitment was low (poor environmental conditions during gestation of the previous lamb), most lambs were produced by ewes who had failed to wean a lamb the previous year (year $t - 1$; Table 2, Fig. 2), whereas following years of high recruitment, lambs were mostly produced by ewes that had weaned a lamb the previous year (Table 2, Fig. 2). Because recruitment was measured one year before weaning success (Fig. 1), this result suggests that years of poor post-weaning survival were often followed by years with low weaning success. The difference according to previous weaning success was particularly striking for older ewes (upper sections of Fig. 2b–d), where previously unsuccessful females accounted for most reproduction when recruitment was low. When recruitment was high, nearly all old females weaned lambs (Table 2, Fig. 2). In addition, older females conceived more sons in years when they failed to wean a lamb (Fig. 2b), but if they weaned a lamb they conceived more daughters, especially if they had weaned a son (Fig. 2c, d).

Although most trends were not significant, analysis of data from Sheep River provided qualitatively and quantitatively similar results to those from Ram Mountain (Table 1). The one exception was that at Sheep River the female-biased sex ratio the year after weaning a male appeared independent of ewe age and recruitment (Table 1). For both populations, neither

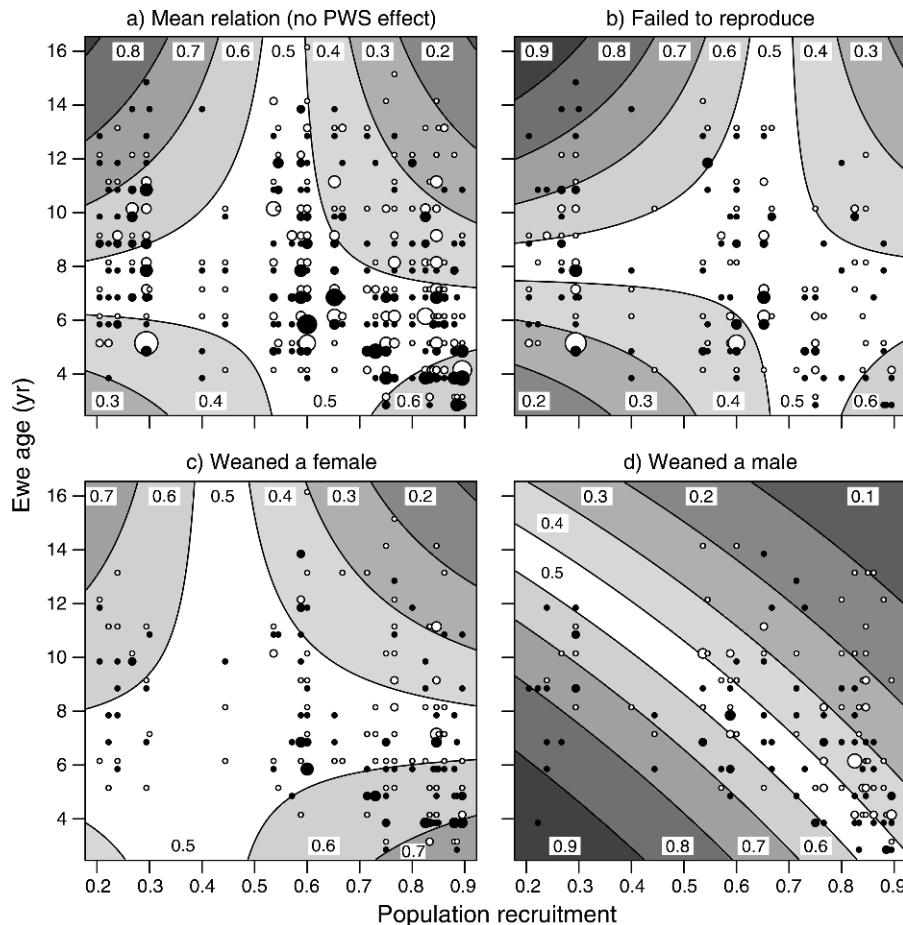


FIG. 2. Contour plots for the predicted probability of producing a male according to recruitment, age, and previous weaning success (PWS) for bighorn ewes at Ram Mountain, Alberta. Each panel illustrates a different weaning success in the previous year: (a) all ewes regardless of previous weaning success ($N = 529$ ewe-years), (b) ewes that did not wean a lamb ($N = 198$), (c) ewes that weaned a daughter ($N = 181$), and (d) ewes that weaned a son ($N = 150$). Average predicted probabilities between contour lines are the values associated with the different shaded areas. Shaded areas with probabilities below and above 0.5 indicate a bias in sex ratio toward daughters and sons, respectively. Open circles represent the number of females produced, and solid circles represent the number of males. The smallest circle represents one lamb, and the largest circle represents 10 lambs.

year nor maternal identity were significant as random effects (Ram Mountain, year variance = 0.01, $\chi^2_1 = 0.02$, $P = 0.88$; identity variance < 0.01, $\chi^2_1 < 0.01$, $P = 0.95$; Sheep River, year variance = 0.11, $\chi^2_1 = 1.38$, $P = 0.24$; identity variance < 0.01, $\chi^2_1 < 0.01$, $P = 0.96$).

Lamb mass at weaning

Lamb mass at weaning was affected by sex, previous weaning success, and recruitment for prime-aged females. For lambs of old females, there was also a sex \times recruitment interaction (Table 3, Fig. 3). Lambs weaned by prime-aged ewes were heavier when recruitment was high, sons were heavier than daughters (Table 3, Fig. 3a), and lambs whose mothers had weaned a lamb the previous year were lighter (Table 3). Previous-year weaning success had a similar effect for lambs weaned by old ewes (Table 3). However, for old ewes, sons were heavier than daughters when recruitment was low, but

were lighter than daughters when recruitment was high (Fig. 3b). When recruitment was high (>0.5), sons weaned by old females were lighter than sons weaned by prime-aged females ($\Delta\text{mass} = -3.14$ kg, $t_{49,4} = 3.11$, $P = 0.003$; Fig. 3), but when recruitment was low (<0.5), sons weaned by prime-aged and old ewes did not differ in mass ($\Delta\text{mass} = 0.16$ kg, $t_{31,9} = 0.14$, $P = 0.89$; Fig. 3). Finally, for both prime-aged and old ewes, lambs weaned in years following the weaning of a sibling were lighter than those whose mother had failed to wean a lamb the previous year. The decrease in mass for lambs of mothers that weaned lambs in consecutive years was greater after weaning a son than following the weaning of a daughter (Table 3).

DISCUSSION

Our analyses show that progeny sex ratio is independent of maternal mass before conception but varies as a

TABLE 2. The number of male and female lambs produced by bighorn ewes according to their age and population recruitment in the previous winter from 1975 to 2008 at Ram Mountain, Alberta.

Ewe age (yr) and lamb sex	Recruitment rate												Total lambs
	≤ 0.43				> 0.43 and < 0.67				≥ 0.67				
	Previous weaning success				Previous weaning success				Previous weaning success				
	Failed	WF	WM	Total	Failed	WF	WM	Total	Failed	WF	WM	Total	
Ewes ≤ 5													
Female	13	4	0	17	21	7	2	30	15	22	31	68	115
Male	8	1	2	11	14	6	6	26	14	38	20	72	109
Total	21	5	2	28	35	13	8	56	29	60	51	140	224
Ewes 6–10													
Female	19	6	6	31	17	9	18	44	9	26	17	52	127
Male	20	11	9	40	18	16	13	47	9	14	12	35	122
Total	39	17	15	71	35	25	31	91	18	40	29	87	249
Ewes ≥ 11													
Female	2	2	0	4	5	5	3	13	1	6	5	12	29
Male	6	1	2	9	6	5	2	13	1	2	2	5	27
Total	8	3	2	13	11	10	5	26	2	8	7	17	56
All ewes	68	25	19	112	81	48	44	173	49	108	87	244	529

Note: Previous weaning success definitions are: Failed, failed to wean a lamb; WF, weaned a female; and WM, weaned a male.

function of maternal age, previous reproduction, environmental conditions, and their interactions. These relationships are complex: For example, the effect of maternal age was reversed following winters of high and low recruitment, indicating a strong environmental influence on sex ratio bias. Furthermore, the effects of the ewe's previous reproduction and the sex of the lamb weaned the previous year strongly suggest that the costs of reproduction affect offspring sex ratio. Finally, under conditions when old ewes generally produced a sex ratio biased toward daughters, the few sons they produced were smaller than those produced in years with no age-specific female bias.

Changes in sex ratio bias according to mean lamb survival in the winter before conception can be associated with differences in age-specific reproductive strategies and reproductive costs. When conditions were good (leading to high recruitment), most old females reproduced in consecutive years (70.5% of those that weaned lambs had weaned another lamb the previous year) and produced more females. Bighorn ewes show both actuarial and reproductive senescence (Bérubé et al. 1999, Loison et al. 1999) and have a conservative reproductive strategy, favoring their own growth and survival over the development of their lamb (Festa-Bianchet and Jorgenson 1998). Ewes also reduce

TABLE 3. Effects of lamb sex, recruitment, and previous weaning success on lamb weaning mass (15 September) for prime-aged and old bighorn ewes at Ram Mountain, Alberta.

A) Variable	Prime-aged (6–10 years)				Old (>10 years)				
	Factor	Estimate	95% CI	<i>P</i>	Estimate	95% CI	<i>P</i>		
Intercept		20.88	18.07	23.31	<0.001	19.98	14.64	22.79	<0.001
Lamb sex†		2.34	0.04	5.04	0.01	7.46	2.60	12.92	0.005
Recruitment		9.66	5.82	13.95	<0.001	12.14	6.31	18.59	<0.001
Previous weaning success					<0.001				<0.001
Weaned a female		−0.96	−1.96	0.38		−1.23	−2.24	2.00	
Weaned a male		−2.02	−3.15	−0.81		−2.31	−3.74	1.18	
Lamb sex† × recruitment		−0.03	−4.51	4.11	0.982	−13.82	−22.54	−5.03	0.002
B) Random effects									
Factor	Variance	Ratio	χ^2 (df)	<i>P</i>	Variance	Ratio	χ^2 (df)	<i>P</i>	
Mother ID	4.92	28.11	24.41 (1)	<0.001	8.29	44.43	14.46 (1)	<0.001	
Year	3.49	19.92	30.60 (1)	<0.001	5.61	29.74	6.05 (1)	0.013	
Residual	9.10				4.87				

Notes: Results are based on 299 and 90 lambs for prime-aged and old ewes, respectively. *P* values for significant effects are in boldface.

† “Males” were considered as references in the analyses.

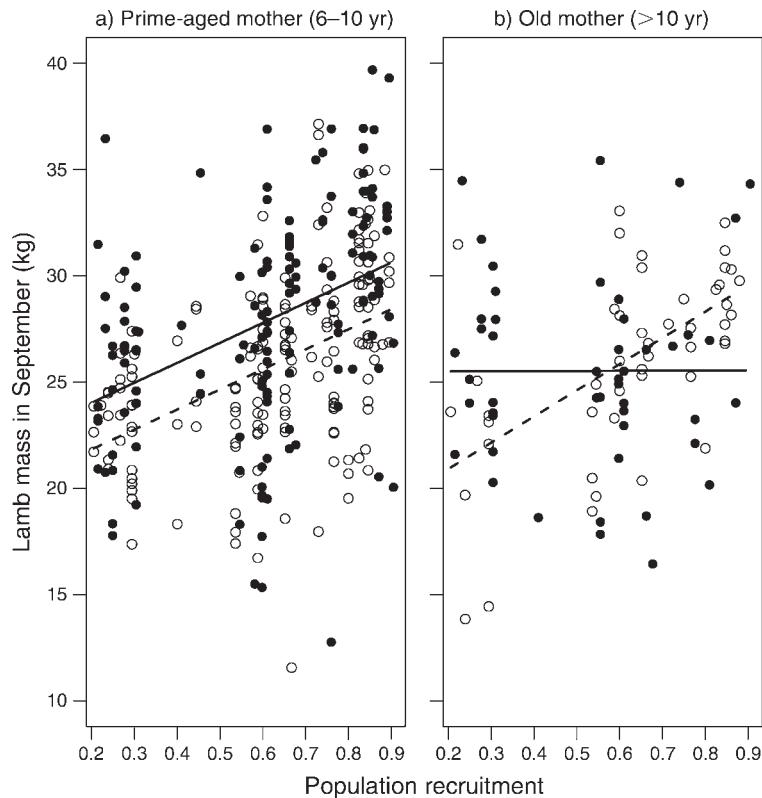


FIG. 3. Lamb mass at weaning as a function of recruitment, maternal age [(a) prime-aged females, 6–10 years; (b) old females, >10 years], and lamb sex. Open circles and dashed lines represent daughters, whereas solid circles and solid lines represent sons.

reproductive effort after weaning a male or when density is high (Festa-Bianchet and Jorgenson 1998). Senescent ewes could maximize their survival by either skipping reproduction or producing the cheaper sex, depending on environmental conditions. Furthermore, when conditions were good, the few sons produced by old ewes were smaller than those produced by prime-aged ewes. Old ewes appeared to wean sons of about the same mass regardless of conditions, while when conditions were good the sons of prime-aged ewes were heavier. Old ewes may have been constrained in their ability to provide sufficient maternal care to wean large sons. That constraint would create an adaptive advantage of producing a daughter when conditions were good. Small sons develop into small adult rams (Festa-Bianchet et al. 2000) that would be outcompeted by larger rams during the rut and have a low reproductive success (Coltman et al. 2002).

When conditions were poor, old females rarely weaned lambs in consecutive years (only 38.4% of their lambs were weaned in years following the weaning of a sibling), probably because of high reproductive costs, and they produced more sons. Despite a gradual decline after 13 years of age, fertility in bighorn ewes remains high at all ages: 70% of old females that failed to wean a lamb had given birth but their lamb had died. Females whose lamb dies before weaning are in better condition

by the following rut than females that bear the full cost of lactation (Bérubé et al. 1996), particularly given that 75% of the pre-weaning lamb mortality at Ram Mountain was at the neonatal stage (Portier et al. 1998) so that lactation costs were very small or nonexistent. The following year, these ewes should have a high reproductive potential (Rutberg 1986) and could afford to produce the more expensive sex. One might argue that, because of reproductive senescence (Bérubé et al. 1999), it would be surprising that old ewes who failed to wean a lamb were in relatively better condition than prime-aged ewes. However, females that survive to older age tend to be of above-average mass as prime-aged adults (Bérubé et al. 1999, Gaillard et al. 2000a), are more experienced and may produce better offspring (Weladji et al. 2006). Furthermore, when conditions were poor, sons produced by older ewes were as heavy as sons produced by prime-aged ones (Fig. 3).

A ewe's mass or body condition are unlikely to fully explain differences in individual reproductive potential, suggesting that body mass should be a weak predictor of sex ratio bias (Cameron 2004, Sheldon and West 2004). We confirmed that maternal mass at conception did not affect progeny sex ratio in bighorn sheep (Blanchard et al. 2005). Maternal age, past reproductive history, experience, and environmental conditions may also affect offspring sex ratio. Our analyses considered the



PLATE 1. Two bighorn ewes with their lambs at Ram Mountain, Alberta, Canada. Adult females have plastic collars. The lamb with the black eartags is a female, and the other lamb without an eartag is a male. Photo credit: J. G. A. Martin.

effects of maternal state rather than just maternal condition. An organism's state (McNamara and Houston 1996) can be defined by four elements: body condition, current environment (mainly food availability), past history (including disease, previous reproduction, experience), and age. These elements are not mutually exclusive and could interact. Our understanding of adaptive manipulations of progeny sex ratio would be improved by an approach based on individual state rather than one limited to body mass or condition. The "cost of reproduction hypothesis" (Myers 1978, Gomendio et al. 1990, Wiebe and Bortolotti 1992) predicts that females in poor state should avoid conceiving sons because they are likely unable to bear the extra fitness costs. Females should manipulate offspring sex ratio according to their state in order to increase their chances of successful reproduction and decrease reproductive costs.

The Trivers-Willard and the cost of reproduction hypotheses predict similar bias in progeny sex ratio, but they differ on the underlying mechanism. Blanchard et al. (2005) found no support for the Trivers-Willard model in the Ram Mountain population of bighorn sheep, and our results support the "cost of reproduction" hypothesis. Confirming the conservative reproductive strategy of bighorn ewes, when conditions were good, old females seemed to produce daughters to minimize fitness costs and enhance their own survival and future reproduction. When conditions were poor, older ewes often failed to wean their lambs, and the following year they were able to produce males because their reduced reproductive effort for one year improved their reproductive potential the following year. Trends in the results for the Sheep River population confirmed

the general patterns observed at Ram Mountain. Furthermore, the strong bias toward daughters after weaning a son for ewes of all ages at Sheep River suggested that ewes might not be able to bear the costs of producing sons in consecutive years.

Most theories of progeny sex ratio bias in mammals were developed for species in which the costs of reproduction vary with offspring sex (Cockburn et al. 2002). If offspring sex ratio manipulation was an adaptive response to differences in fitness costs between sons and daughters, changes in those sex-specific fitness costs with maternal state should lead to variation in sex ratio bias. Variables affecting the relative fitness costs of sons and daughters (such as environmental condition, maternal age, or reproductive strategy) could obscure sex ratio bias patterns. Consequently, potentially adaptive sex ratio bias may be misinterpreted if assessment of maternal condition is restricted to maternal mass instead of maternal state, which includes age, environment, mass, and previous reproduction. Contradictory results on sex ratio bias, such as inverse relationships obtained in two populations of the same species, might be explained by differences in environmental conditions, population dynamics, or maternal age (Myers 1978, Kruuk et al. 1999).

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