

Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep

Céline H. Bérubé,^a Marco Festa-Bianchet,^a and Jon T. Jorgenson^b

^aGroupe de recherche en écologie, nutrition et énergétique, Département de biologie, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada, and ^bAlberta Fish and Wildlife, Box 1059, Canmore, Alberta T0L 0M0, Canada

Differential maternal investment theory predicts that in sexually dimorphic and polygynous species mothers should invest more in sons than in daughters. We tested the hypothesis that bighorn ewes that raise sons incur greater reproductive costs than ewes that raise daughters. Although ewe mass gain during lactation and subsequent winter body mass loss were independent of lamb sex, lambs born the year following the weaning of a son had lower survival than lambs born after a daughter. The effects of lamb sex on subsequent reproductive success of ewes became more evident at high population density. Lamb sex did not affect maternal survival. Population density, weather, and ewe age did not alter the relationship between lamb sex and subsequent reproductive success of the ewe. The year after weaning a son, ewes were more likely to have a daughter than a son, while ewes that had previously weaned a daughter had similar numbers of sons and daughters. Our results show that for bighorn sheep ewes, sons have a greater life-history cost than daughters, suggesting a differential maternal investment in the sexes. **Key words:** costs of reproduction, differential maternal investment, *Ovis canadensis*, reproductive success, sex ratio. [*Behav Ecol* 7:60–68 (1996)]

Differential maternal investment theory (Clutton-Brock et al., 1982; Maynard Smith, 1980; Reiter et al., 1978; Trivers and Willard, 1973; Willson and Pianka, 1963) predicts that if the fitness consequences of maternal investment vary according to offspring sex, then mothers should be selected to invest more in offspring of the sex benefiting more from maternal investment. In contrast, equal investment theory predicts that natural selection should favor identical maternal investment in offspring of either sex (Charnov, 1979; Fisher, 1958).

In polygynous and sexually dimorphic mammals, the reproductive success of males often depends on body size and fighting ability, because access to estrous females is usually determined by male-male competition (Clutton-Brock et al., 1979; Le Boeuf, 1974; Moss, 1983). Male reproductive success is thought to be more variable (thus potentially very high for some individuals) than female reproductive success (Clutton-Brock, 1988; Trivers, 1972, 1985). Accordingly, in polygynous mating systems, a small percentage of dominant males may father many offspring, while many males may not reproduce at all. In sexually dimorphic species, males often show higher growth rates than females (Lavigne and Barrette, 1992; Reiter et al., 1978) during the period of maternal care. Energetic demands can thus be higher for males than for females during this period. In some species, including bighorn sheep (*Ovis canadensis*), adult male traits influencing reproductive success appear to be affected by growth in the first year of life (Clutton-Brock et al., 1982; Festa-Bianchet et al., 1994). If maternal care could influence the expression and amplitude of such traits in adult males, then a mother could increase her fitness by investing much energy in sons, thereby enhancing their chances of becoming dominant and producing many descendants.

By definition, maternal investment implies fitness costs for the mother (Trivers, 1972), while maternal care does not (Clutton-Brock, 1991; Evans, 1990). Although maternal care

has been used in the past to measure maternal investment, care does not always lead to fitness costs. For example, in some species sons receive more milk than daughters (e.g., Butler, 1983; Odde et al., 1985), and many studies have used lactation as a measure of investment (e.g., Byers and Moodie, 1991; McCann et al., 1989; Trillmich, 1986; Trivers, 1974). Lactation is by far the most energy demanding phase of reproduction for female mammals (Gittleman and Thompson, 1988; Loudon and Racey, 1987; Oftedal, 1985; Sadleir, 1984), but nursing correlates alone cannot differentiate between care and investment, because the energetic costs of nursing do not necessarily entail a decrease in future reproduction. If the energy cost of lactation was met through increased exploitation of available resources, milk production may have no long-term effect on a mother and may not lead to any reproductive costs (Stearns, 1992).

Many studies have shown differential care in sexually dimorphic mammals. In some species, differential prenatal care is reflected by higher birth mass for males (Clutton-Brock et al., 1982; Hogg et al., 1992; Kovacs and Lavigne, 1986; Lavigne and Barrette, 1992; McEwan, 1968; Reiter et al., 1978; Trillmich, 1986), and postnatal differential care is reflected by higher suckling frequency (Clutton-Brock et al., 1982; Lee and Moss, 1986; Trillmich, 1986) or longer suckling bouts (Reiter et al., 1978) for males. Other studies found no differential prenatal (Byers and Moodie, 1991; Campagna et al., 1992; Small and Smith, 1984) or postnatal care (Butler, 1983; Byers and Moodie, 1991; Campagna et al., 1992; Gauthier and Barrette, 1985; Kretzmann et al., 1993; Lavigne and Barrette, 1992; McCann et al., 1989). However, very few studies have effectively investigated differential investment in mammals, because maternal investment must be measured through its effects on the mother's fitness. Subsequent survival and reproduction are important indicators of the effect of reproduction on the mother's future reproductive success (Caswell, 1982; Reznick, 1992; Stearns, 1976; Williams, 1966), as are costs to her body growth (Clutton-Brock, 1991) and to the survival of her offspring (Alados and Escos, 1992). In red deer (*Cervus elaphus*), differential care during gestation and lactation translated into differential investment because, com-

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pared to mothers that weaned a daughter, mothers that weaned a son had a lower probability of reproducing the following year, and if they did reproduce, estrus was delayed (Clutton-Brock et al., 1981). In a transplanted population of bighorn sheep, mothers that weaned a son experienced a delay in return to estrus compared to mothers that weaned daughters. Late estrus was related to lower survival of both the mother and subsequent offspring (Hogg et al., 1992). African elephant (*Loxodonta africana*) females that weaned sons experienced an increase in interbirth intervals compared to those that had weaned daughters (Lee and Moss, 1986). Neither the Hogg et al. (1992) nor the Lee and Moss (1986) study directly compared offspring production or survival in years following the weaning of sons and of daughters.

Some studies of sexually dimorphic mammals found that offspring sex did not affect mass loss during lactation (McCann et al., 1989), interbirth intervals (Green and Rothstein, 1991), probability of survival or fecundity (Festa-Bianchet, 1989; Green and Rothstein, 1991; Le Boeuf et al., 1989). Festa-Bianchet (1989) reported an increase in parasite counts for bighorn sheep ewes that weaned sons. Therefore, results from different studies disagree regarding the existence of differential investment, despite predictions that this strategy should be optimal for females of sexually dimorphic and polygynous species. The scarcity of studies that have directly tested this theory is in part due to the need for long-term data on individually marked animals to investigate differential costs. Where experimental manipulations and genetic correlations are unfeasible, phenotypic correlations linking offspring sex and survival with fecundity costs have sometimes been useful, as shown above.

Rocky Mountain bighorn sheep are sexually dimorphic and polygynous, and male reproductive success depends on dominance (Geist, 1971; Hogg, 1984, 1988). It is therefore reasonable to expect that differential maternal investment would exist in this species. Here we test the existence of differential mass changes, survival, and subsequent reproductive success of ewes according to lamb sex in a population of Rocky Mountain bighorn sheep. We predicted that mothers that weaned a ram lamb should accumulate less mass over the summer. We also predicted that mothers of ram lambs would incur a reduction in subsequent fecundity or survival. Lamb sex was expected to affect the survivorship of subsequent siblings: those born after a son should have lower survival than those born after a daughter.

The study population more than doubled in density during this project. No study on maternal investment has investigated the potential effect of population density on the expression of differential costs. Increases in population density can enhance the expression of reproductive costs (Clutton-Brock, 1984), and some costs may only appear under conditions of stress or high density (Festa-Bianchet, 1989). A reduction in the availability and quality of food due to high population density can lower juvenile survival and adult fecundity (Klein, 1968; Leader-Williams, 1980). If ewes require more resources to raise ram lambs than to raise ewe lambs, a reduction in food availability should affect mothers of ram lambs more than mothers of ewe lambs. Population density should therefore affect the expression of differential reproductive costs to mothers, and we expected that differential costs would be more evident at high than at low density.

METHODS

Study area and population

Ram Mountain, Alberta (52°N and 115°W), is isolated from other areas of bighorn sheep habitat, being bordered to the

north by the North Saskatchewan River and surrounded by foothills covered with coniferous forests. Some dispersal occurs between the study population and a small group of about 30 bighorns on another mountain 15 km northwest of Ram Mountain. The Ram Mountain sheep range extends over approximately 38 km² of alpine and subalpine habitat, ranging in elevation from 1082 to 2173 m.

The bighorn sheep population on Ram Mountain has been studied intensively since 1972. Between 1972 and 1981, numbers were controlled by annual ewe removals (Jorgenson et al., 1993b). From 1975 to 1982, the density of ewes and yearlings varied between 1.18 and 1.39 sheep/km² (33 ewes in 1975, 36 in 1982). Density increased gradually to 3.05 sheep/km² by 1989 and reached 3.42 sheep/km² in 1992 (72 ewes in 1989, 104 in 1992). We only considered ewes and yearlings for density calculations because adult rams use separate foraging ranges (Geist and Petocz, 1977). It should be noted that bighorn sheep are very traditional in their area-use patterns: population fluctuations do not affect the size of the geographic range. Density can therefore be calculated directly as the ratio of population size to range size. Since the beginning of the study, over 95% of the sheep have been individually marked.

We captured sheep in a corral trap baited with salt and recorded body mass and reproductive status for ewes from the end of May to the beginning of October. Mass was measured with a Detecto spring balance to the nearest quarter of a kilogram. The accuracy of the balance was checked every few weeks with weightlifting weights. Between late May and early October, the study area was searched on foot to monitor ewe and lamb survival. Summer (May to August) precipitation data were obtained from the Environment Canada weather station at Nordegg, Alberta, about 20 km from Ram Mountain.

Definition of ewe yearly reproductive status categories

Barren: no evidence of reproduction; udders atrophied and without pigmentation. Barren ewes were never seen with a lamb. *Pregnant*: udders swollen and secreting colostrum, or udders dry but found to secrete milk at a subsequent capture. *Lamb lost neonatally*: udders flaccid and pigmented in late May or early June, usually secreting watery milk. Ewes in this category were never seen with a lamb. *Lactating*: udders swollen and secreting milk. Lamb-ewe matches were established when a lamb was repeatedly seen suckling from and associating with the same ewe.

Definition of lamb survival categories

Summer death: lambs that disappeared before the autumn weaning period (late September). In most cases, the mother was without milk at her next capture. *Winter death*: lambs that survived to late September (the time of weaning), but were not seen the following year. *Survival to 1 year*: lambs that survived their first winter and were seen the following June.

Statistical procedures

We considered the years 1978 to 1988 as low density years (average of 44 ewes in June, and lamb survival to 1 year averaging 70%), and 1989 to 1992 as high density years (average of 90 ewes, lamb survival averaging 37%). We analyzed all Ram Mountain data according to lamb sex, and when possible, compared them between years of high and low population densities. All probability values are two-tailed and follow methods in Sokal and Rohlf (1981). Means are accompanied by their standard deviation.

For analyses of body mass, we used ANOVAs including the effects of population density, summer precipitation (total pre-

Table 1

Mass accumulation between 5 June and 15 September, mass adjusted to 15 September, overwinter mass loss, and mass adjusted to 5 June of the following year, according to lamb sex and population density, for bighorn sheep mothers aged 3 years and older from Ram Mountain, Alberta

Years	Lamb sex	Mean mass gain			Mean mass 15 September			Mean overwinter mass loss			Mean mass following 5 June		
		Mean mass gain	<i>t</i>	<i>p</i>	Mean mass 15 September	<i>t</i>	<i>p</i>	Mean overwinter mass loss	<i>t</i>	<i>p</i>	Mean mass following 5 June	<i>t</i>	<i>p</i>
All years combined	M	14.5 ± 6.2 (142)	0.015	.99	69.1 ± 6.5 (159)	0.30	.77	12.7 ± 5.7 (91)	2.23	.027	56.8 ± 6.6 (105)	2.29	.023
	F	14.5 ± 6.2 (148)			68.9 ± 6.7 (172)			14.5 ± 5.3 (112)			54.7 ± 7.1 (118)		
1978–1988 (low density)	M	13.3 ± 6.1 (92)	0.83	.41	68.8 ± 6.7 (103)	0.59	.56	11.2 ± 6.0 (52)	2.55	.012	58.3 ± 7.2 (64)	3.44	.0008
	F	14.1 ± 7.4 (82)			68.2 ± 6.7 (90)			14.2 ± 5.8 (53)			53.8 ± 7.1 (58)		
1989–1992 (high density)	M	16.7 ± 5.7 (50)	1.91	.059	69.8 ± 6.1 (56)	0.087	.93	13.8 ± 4.0 (24)	0.21	.83	56.2 ± 3.3 (25)	0.35	.73
	F	14.9 ± 4.5 (66)			69.7 ± 6.7 (82)			14.1 ± 5.0 (40)			56.8 ± 6.7 (41)		

Masses are shown as follows: mass (kg) ± 1 SD (*n*).

precipitation from May to August, entered as a covariate) and ewe age (young ewes: 3 to 7 years; old ewes: 8 years and older), to determine whether any of these variables could interact with any effects of lamb sex. Logistic regressions (Trexel and Travis, 1993) were used to analyze the effect of lamb sex on subsequent offspring survival, ewe survival, and sex ratios of subsequent offspring. In addition, to test whether changes in population density altered the relationship between lamb sex one year and lamb survival the following year, we used a goodness-of-fit chi-square test to compare the survival to one year of lambs born after sons and daughters at high density with the survival at low density, after adjusting for the significant negative effect of population density on lamb survival.

Because we used data collected from the same individuals in different years, there was a potential problem of pseudoreplication (Machlis et al., 1985; but see Leger and Didrichson, 1994). Our data were collected from 99 different bighorn sheep mothers. The sample most subject to potential pseudoreplication is that for body mass adjusted to 15 September for ewes with daughters (Table 1), because it is the largest (*n* = 172 ewe-years), therefore we looked at that sample in

more detail to see how often individual ewes contributed to it. The data were obtained from 94 ewes, that contributed 1.8 ± 1.4 observations each (range 1–7). In this subsample, 17 ewes appear once in two consecutive years, seven ewes appear twice in two consecutive years, and two ewes were sampled three and four times respectively in two consecutive years. Only four ewes appear in three consecutive years, and only one was sampled in four consecutive years. In addition, individual characteristics such as age, sex of lamb weaned the previous year, and body mass typically varied for the same ewes in different years. Therefore, it is unlikely that our statistical analyses were affected by pseudoreplication.

Ewe body mass

Capture dates were coded starting at 0 for 24 May (earliest beginning of trapping season) and ending at 139 for 10 October (latest end of trapping season). Mass gain over the summer for adult ewes was curvilinear (Figure 1). Plotting masses against the square root of the number of days since 24 May resulted in a linear relationship (Figure 1). For ewes that had

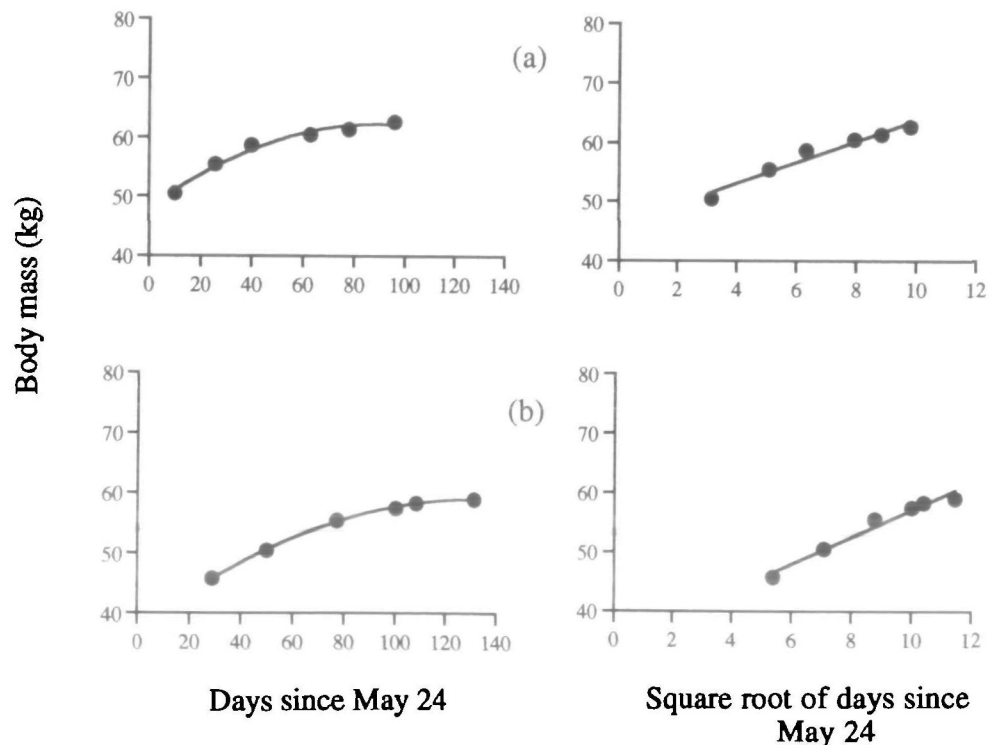


Figure 1 Relationship between mass (kg) of bighorn sheep mothers at Ram Mountain, Alberta, and date of capture. Dates are coded from 0 (24 May) to 139 (10 October). When plotted against the square root of the coded date, the relationship becomes linear: (a) ewe 16F, 1979, weaned a ram lamb; (b) ewe 11I, 1980, weaned a ewe lamb.

been captured at least twice over the summer, we used individual linear rates of mass accumulation to adjust individual mass to 5 June and 15 September. The difference between masses on 15 September and on 5 June was the total summer mass gain. We calculated overwinter mass loss as the difference between mass on 15 September and on 5 June of the following year.

For ewes captured only once during a given summer ($n = 13$, 6% of the total sample), we used average rates of mass accumulation for all mothers in that given year (and with same-sex lambs) to adjust masses to 5 June and 15 September. To minimize errors in adjusted mass, we only considered ewes that had been captured within 50 days of the adjustment dates. Ewes with only one mass measurement were not used to estimate summer mass gain. Ewes still pregnant during their first capture (15 ewes in 1978 to 1988; 4 ewes in 1989 to 1991; 18 ewes in 1992) were omitted from calculations of mass adjustments to 5 June because their mass would have included the fetus.

Reproduction and lamb and ewe survival

For comparisons of lamb survival, sample sizes from low and high density years are less than the total sample size, because reproductive success in 1988, the year intermediate between low and high population density, was not included when analyzing low and high density years separately. This was also the case for analyses of lamb survival to 1 year and analyses of lamb sex ratios (see below). We used two categories of population density, rather than using density each year as a covariate, because changes in ewe reproductive success that appeared to be density dependent became noticeable only after 1988 (Bérubé CH, unpublished Master's thesis).

To compare the probability of survival to 1 year of lambs born following the weaning of a son or a daughter, survival to 1 year was coded as 1 and all other categories (barren, neonatal lamb death, summer lamb death, lamb lost over the winter) were coded as 0. On occasion, lambs lost both ear tags during their first winter, and the identity of yearlings with torn ears could not be established. Lambs born in 1985 were not included in the analyses because 11 lost both ear tags during the winter. Only three lambs lost both tags over winter in the other years of the study. These lambs were classified as having died during winter, even though they were still alive (but unidentifiable).

The survival of a mother the year after weaning a lamb of known sex was coded as 1, a death coded as 0. In calculating the probability of survival of ewes for the years 1975 to 1992, we excluded ewes that had been removed experimentally, those that had not weaned a lamb the year prior to their death, and those still alive in 1992.

Lamb sex ratios

When ewes produced lambs in two consecutive years, we used G -tests and logistic regression to analyze sex ratios in the second year (year 2) according to the sex of the lamb produced in the previous year (year 1). Lamb sex could not be established at birth, and we did not know the sex of most lambs that died before 2 to 3 months of age.

Sheep River population

Festa-Bianchet (1989) published data from 1981 to 1988 on reproductive success of ewes following the weaning of ram and ewe lambs for the Sheep River, Alberta, population of bighorn sheep. We reanalyzed the Sheep River data after adding results for 1989 to 1992. Lamb survival to weaning in years

following the weaning of a daughter and of a son was compared using G -tests.

RESULTS

Ewe body mass

On 15 September (about 2 months before the rut), ewes that conceived daughters were about 3% heavier ($n = 62$, $\bar{x} = 71.3 \pm 6.3$ kg) than ewes that conceived sons ($n = 62$, $\bar{x} = 68.9 \pm 6.7$ kg; $t_{122} = 2.06$, $p = .04$). There was also a significant effect of ewe age on lamb sex: mothers of daughters were slightly older ($n = 509$, $\bar{x} = 6.5$ years) than mothers of sons ($n = 529$, $\bar{x} = 5.7$ years, Z -transformation of Mann-Whitney U test = 4.2, $p < .0001$).

Because we expected ewes to provide more maternal care to sons than to daughters, we predicted that mothers nursing sons would accumulate less mass over the summer, and that they would have a lower body mass by 15 September compared to ewes nursing daughters. Lamb sex, however, did not affect summer mass gain, and it affected overwinter mass loss in the direction opposite to our predictions: ewes tended to lose more mass after weaning daughters than after weaning sons (Table 1, Figure 2), although this effect was not significant during high density years and became nonsignificant when other variables were considered (see below). Ewe mass at the end of the summer was independent of lamb sex. Ewe mass the following 5 June was lower for ewes that had weaned daughters during low density years or over the entire study (Table 1, Figure 2), but again this effect became nonsignificant when the effects of other variables were accounted for (see below).

Analyses of variance including the effects of population density, summer precipitation, and ewe age mostly confirmed the results of univariate analyses, indicating that lamb sex had no effect on maternal mass or mass changes: neither lamb sex nor any of the other variables included in the analyses had significant effects on overwinter mass loss, summer mass gain, average mass on 5 June or average mass on 15 September. The analyses also failed to reveal any significant two-way interactions. The smallest probability value from all these analyses was for the effect of ewe age class on summer mass gain ($F_{1,250} = 2.18$, $p = .14$).

Although mass gain over the entire May to October period was curvilinear, mass gain of ewes was linear from late May to early August (Figure 1), when most of the gain took place. It was therefore possible that mothers of sons gained little mass early in lactation (during the linear gain phase), but were able to compensate later in the season. To test whether the pattern of mass gain (rather than the total summer mass gain) differed according to lamb sex, we compared the linear mass gain rate (using untransformed capture dates) of mothers of sons and daughters that were captured at least twice between 25 May and 12 August. Daily mass gain was independent of lamb sex over that period (mothers of sons: $n = 139$, $\bar{x} = 0.177 \pm 0.08$ kg/day; mothers of daughters: $n = 139$, $\bar{x} = 0.178 \pm 0.101$ kg/day; $t_{278} = 0.095$, $p > .5$).

Proportional mass gain (the ratio of total summer mass accumulation to mass on 5 June) for mothers was independent of lamb sex: 0.308 ± 0.114 kg/kg for ewes nursing sons and 0.318 ± 0.128 kg/kg for ewes nursing daughters ($t_{185} = 0.59$, $p = .56$).

Two-year-old mothers

Two-year-old ewes have not completed body growth, and reproduced almost exclusively at low population density (Jorgenson et al., 1993a). Because lactating 2-year-olds must sus-

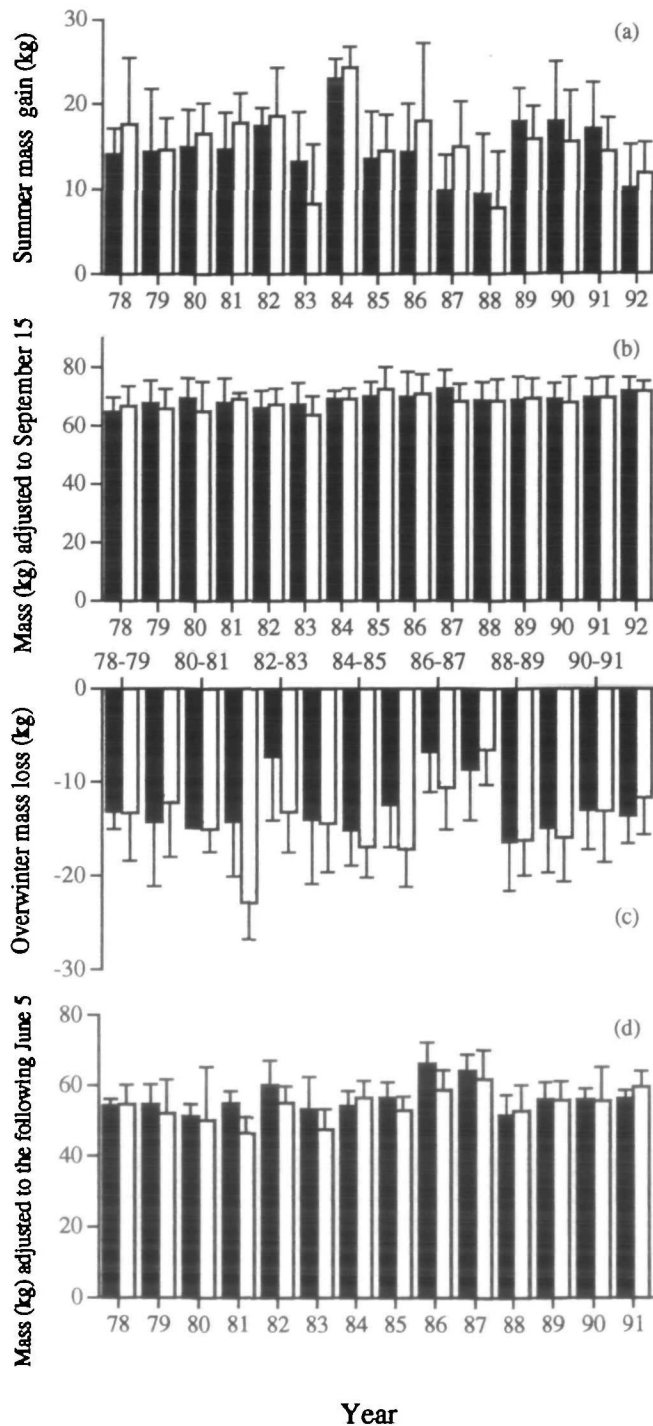


Figure 2
 (a) Summer mass (kg) accumulation (between 5 June and 15 September), (b) mass on 15 September, (c) mass loss between 15 September and 5 June of the following year, and (d) mass on 5 June of the following year, for bighorn sheep mothers aged 3 years and older from Ram Mountain, Alberta, for the years 1978 to 1992. The mean is shown with 1 SD. Black bars represent mothers with ram lambs and white bars indicate mothers with ewe lambs.

tain at the same time the costs of nursing their lamb and their own body growth, and because they experience reproductive costs at high population density (Festa-Bianchet et al., 1995), any potential effects of lamb sex on mass changes should be most evident within this age class. Over all years, however,

Table 2

Mass accumulation over the summer, mass on 15 September (day 114), overwinter mass loss, and mass on June 5 the following year, according to lamb sex, for 2-year-old bighorn sheep mothers from Ram Mountain, Alberta, 1975 to 1983

	Male	Female	<i>t</i>	<i>p</i>
Mean mass gain	13.5 ± 4.7 (10)	15.5 ± 4.0 (7)	0.94	.36
Mean mass 15 September	58.2 ± 4.1 (10)	58.7 ± 4.2 (8)	0.25	.81
Mean overwinter mass loss	8.0 ± 4.9 (8)	9.6 ± 4.9 (8)	0.68	.51
Mean mass following 5 June	49.5 ± 5.5 (8)	48.9 ± 2.4 (10)	0.29	.78

Masses are shown as follows: mass (kg) ± 1 SD (*n*).

lamb sex did not significantly affect summer mass accumulation, mass on 15 September and overwinter mass loss for 2-year-olds, or mass the following 5 June for these same ewes as 3-year-olds (Table 2).

Lamb survival to weaning

Ram Mountain population

At Ram Mountain, ewes that weaned a son were less likely to wean a lamb the following year compared to ewes that weaned a daughter (Table 3). Logistic regression revealed that, in addition to lamb sex, ewe age, summer precipitation, and population density had significant effects on lamb survival (final model $\chi^2 = 41.55$, *df* = 4, *p* < .0001). Of all these variables, however, only population density had a strong effect, with a partial correlation with lamb survival to weaning of -0.283 (*p* < .001). The partial correlation between lamb sex the previ-

Table 3

Reproductive status of bighorn sheep mothers at Ram Mountain, Alberta, in the year following the weaning of a ewe or ram lamb

Population density	Year 1		Year 2			
	Lamb sex	<i>n</i>	RS ^a	<i>n</i>	% ^b	% ^c
Low (1975–1988)	M	98	B	4	4.1	
			LD	23	23.5	24.5
			LW	71	72.4	75.5
	F	91	B	3	3.3	
			LD	12	13.2	13.6
			LW	76	83.5	86.4
High (1989–1992)	M	53	B	6	11.3	
			LD	26	49.1	55.3
			LW	21	39.6	44.7
	F	69	B	8	11.6	
			LD	26	37.7	42.6
			LW	35	50.7	57.4
All years	M	186	B	12	6.7	
			LD	56	30.1	32.2
			LW	118	63.4	67.8
	F	193	B	12	6.2	
			LD	43	22.3	23.8
			LW	138	71.5	76.2

^a RS = reproductive status; B = barren; LD = lamb died, either neonatally or during the first summer of life; LW = lamb weaned.

^b All mothers from year 1.

^c Excluding ewes barren in year 2.

Table 4
Reproductive status of bighorn sheep mothers from Sheep River, Alberta, the year following the weaning of a ewe or ram lamb, 1981 to 1992

Year 1		Year 2			
Lamb sex	n	RS ^a	n	% ^b	% ^c
M	131	B	6	4.6	
		LD	43	32.8	34.4
		LW	82	62.6	65.6
F	134	B	3	2.2	
		LD	29	21.6	22.1
		LW	102	76.1	77.9

^a RS = reproductive status; B = barren; LD = lamb died, either neonatally or during the first summer of life; LW = lamb weaned.

^b All mothers from year 1.

^c Excluding ewes barren in year 2.

ous year and lamb survival to weaning was 0.096 ($p = .028$), indicating a higher weaning success following a daughter than following a son, while ewe age and summer precipitation had partial correlations of 0.095 ($p = .029$) and 0.092 ($p = .032$) respectively.

Sheep River population

During the year following the weaning of a son ewes had a significantly lower chance of raising another lamb to weaning, compared to ewes that had weaned a daughter the preceding year (Table 4) ($G = 4.78$, $df = 1$, $p < .05$).

Lamb survival to 1 year

At Ram Mountain, lambs were less likely to survive to 1 year if they were born following the weaning of a son than if they were born the year after their mother had weaned a daughter (Table 5). According to a logistic regression analysis, only population density (partial correlation -0.317 , $p < .001$) and sex of the lamb weaned the previous year (partial correlation of 0.114, $p = .018$, indicating higher survival to 1 year following a daughter than following a son) had significant effects on lamb survival to 1 year (final model $\chi^2 = 46.81$, $df = 4$, $p < .0001$). Ewe age and summer precipitation had no effect.

The sex of the sibling weaned the previous year seemed to

Table 5
For bighorn sheep mothers that reproduced successfully for two consecutive years: effect of lamb sex born in the first year on the probability of survival to 1 year of the lamb born in the second year

Population density	Year 1		Year 2		
	Lamb sex	n	Survival to 1 year		% ^a survival
	Yes	No	Yes	No	
Low (1975–1988)	M	71	42	29	59.2
	F	68	49	19	72.1
High (1989–1992)	M	42	6	36	14.3
	F	54	18	36	33.3
All years	M	139	62	77	44.6
	F	156	94	62	60.3

^a Excluding ewes barren in year 2.

Table 6
Effect of lamb sex in the first year on lamb sex in the second year (U = unknown) for bighorn sheep mothers that reproduced successfully for two consecutive years

Population density	Year 1		Year 2			% ^a	
	Lamb sex	n	Lamb sex			M	F
	M	F	M	F	U	M	F
Low (1975–1988)	M	73	23	31	19	42.6	57.4
	F	77	41	24	12	63.1	36.9
High (1989–1992)	M	21	7	14	0	33.3	66.7
	F	35	14	20	1	41.2	58.8
All years	M	128	39	66	23	37.1	62.9
	F	142	67	62	13	51.9	48.1

^a Excluding lambs of unknown sex.

have a greater effect on lamb survival to 1 year at high than at low population density (Table 5). At low density, the survival to 1 year of lambs born following a son was 82% of the survival of lambs born following a daughter. At high population density, the survival of lambs born following a son was only 43% of the survival of lambs born following a daughter. This effect of population density on the differential cost of sons and daughters was significant (goodness-of-fit $\chi^2 = 5.18$, $p < .025$).

Lamb sex ratio

We looked at the effects of lamb sex on the sex of a mother's subsequent lamb because Festa-Bianchet (1989) had reported such an effect. When mothers produced lambs in two consecutive years, the sex ratio of lambs in year 2 differed according to lamb sex in year 1. Ewes appeared unlikely to have sons in consecutive years (Table 6): in a logistic regression model including population density and ewe age class (model $\chi^2 = 14.86$, $df = 3$, $p = .002$), sex of the previous year's sibling had a partial correlation of -0.089 with lamb sex the following year ($p = .044$), indicating a greater probability of producing a daughter the year after a son, and ewe age had a partial correlation of 0.143 ($p = .007$), suggesting that older ewes produced female-biased sex ratios. Population density had no effect on lamb sex.

Ewe survival

The sex of the lamb weaned in a given year did not affect the mother's probability of surviving to June of the following year (Table 7) ($G = 0.86$, $df = 1$, $p > .1$). In logistic regression, lamb sex, ewe age, population density, and summer precipitation had no significant effects.

Table 7
Overwinter survival (to year 2) of bighorn sheep mothers according to sex of lamb weaned in the fall (year 1), 1975 to 1992

Year 1 Lamb sex	n ^a	Year 2		% survival
		Survival		
		Yes	No	
M	59	49	10	83.1
F	77	59	18	76.6

^a Sample sizes for year 1 are ewe-years; the overall sample is 28 ewes that died overwinter after weaning a lamb of known sex.

DISCUSSION

Ewes that raised sons incurred higher reproductive costs than ewes that raised daughters, both in the Ram Mountain and Sheep River populations. Results presented in this article therefore join those of Hogg et al. (1992) and Festa-Bianchet (1989) in supporting the existence of differential maternal investment in bighorn sheep, as predicted by theory (Maynard Smith, 1980). In both populations, lambs had significantly lower survivorship if they were born after a son than if they were born after a daughter. This could be due to higher maternal expenditure for male offspring leading to poor maternal condition in the fall (but not affecting mass gain). If mothers provided higher investment to sons than to daughters, for some mothers that raised sons, the next ovulation could be delayed, bringing about later birth during the following lambing season. In bighorn sheep (Festa-Bianchet, 1988a; Hogg et al., 1992), as in other ungulates (Clutton-Brock et al., 1982; Mitchell and Lincoln, 1973; White, 1983), late-born offspring experience low survival. Although differences in birthdate may explain the greater mortality of lambs born after sons, we do not have sufficient data on birthdates from Ram Mountain to test this possibility.

At Ram Mountain, lambs had significantly lower survivorship when born after a son than if they were born after a daughter. Mothers that weaned daughters had an 11% greater chance of weaning an offspring the following year than mothers that weaned sons. The difference in reproductive costs of sons and daughters is small, such that a very large sample size is required to show a significant difference in weaning success (Clutton-Brock, 1984). Festa-Bianchet (1989) reported that in the Sheep River population from 1981 to 1988, there was a nonsignificant trend for ewes that weaned ram lambs to be less successful at reproduction the following year compared to ewes that weaned ewe lambs. After adding 4 years of data (Table 4), mothers in that population had significantly lower weaning success in years following the weaning of a son than in years following the weaning of a daughter.

The higher cost of sons was also associated with a low probability of producing male lambs in consecutive years. These results confirm those obtained by Festa-Bianchet (1989) for the Sheep River population and suggest that a pattern of avoiding raising sons in consecutive years is typical of this species. However, caution must be used when interpreting results on sex ratios. We do not know the sex of all lambs at birth, and the sex ratios presented here are typically those of mid-summer. We knew the sex of some lambs by the first week in June, but for others we did not know the sex until late September. Sex-differential mortality during gestation, at birth, or during early lactation may affect our sex ratio data. Altering the sex of lambs produced could be an adaptive strategy for bighorn ewes to avoid sustaining the high cost of sons in consecutive years.

The greater cost of sons in comparison to daughters was accentuated at high population density, suggesting that environmental factors can affect the differential fitness cost of lambs of different sex. Apparently, at low population density mothers were able to compensate partly for the higher cost of sons, but at high population density ewes that raised sons suffered a much greater reproductive cost than ewes that raised daughters. It is likely that at high population density ewes were unable to recover from their greater investment in reproduction following the weaning of a male lamb. At high population density resources appeared to be scarce: lamb survival declined (Table 5) and age of first reproduction of females increased (Jorgenson et al., 1993a).

Since mass accumulation occurs during lactation, the most energy demanding phase of reproduction, it was surprising

that ewes did not show differences in summer mass gain or in overwinter mass loss according to lamb sex. For mothers of all ages, lamb sex alone had no significant effects on body mass. Young primiparous females who are still meeting the energy requirements of somatic growth often incur higher reproductive costs than adult multiparous females (Clutton-Brock, 1984; Clutton-Brock, 1991; Reiter and Le Boeuf, 1991). At Ram Mountain, the youngest mothers were 2-year-olds. Although these mothers should have been subjected to differential mass gains, such was not the case. Male offspring apparently lowered their mother's subsequent reproductive success but did not alter her body mass changes. Therefore, it appears likely that fitness components other than changes in body mass accumulation affect a ewe's ability to reproduce. It is important to note that in the Ram Mountain population body mass of young ewes had limited effects on their age of first reproduction (Jorgenson et al., 1993a), further suggesting that body mass is not strongly correlated with reproductive performance.

Compensation mechanisms might be employed by ewes to moderate accumulation and mobilization of body fat stores. Because bighorn sheep ewes lactate when the forage peaks in abundance and quality (Festa-Bianchet, 1988b), at least at low population density ewes could compensate for higher energy expenditure in sons by modifying their foraging behavior (Bailey, 1991; Clutton-Brock et al., 1982; Mitchell et al., 1976). Ewes nursing ram lambs could increase foraging time and thus achieve adequate mass accumulation during the summer. One problem of using body mass as an index of reproductive effort is the inability to distinguish between somatic (muscle) and fat tissue changes in relation to total body mass. It is therefore possible that changes in body mass are not good indicators of the reproductive potential of ewes, at least not at the level required in this study.

Results from this and other studies (Festa-Bianchet, 1989; Hogg et al., 1992) suggest that in bighorn sheep, maternal investment is greater for sons than for daughters. One may then predict that maternal investment should have a more marked effect on the reproductive success of sons than on the reproductive success of daughters. Festa-Bianchet et al. (1994) showed that in bighorn sheep, the duration of lactation is more important for sons than for daughters: male lambs orphaned before weaning had smaller adult body size compared to nonorphan males, while no difference was found between orphan and nonorphan females. In red deer, maternal characteristics such as social dominance have a stronger effect on the reproductive success of sons (Clutton-Brock et al., 1984). Future work should therefore test the prediction that lamb body size at the end of the period of maternal investment (weaning) will influence adult body size in sons, and therefore affect their reproductive success.

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